

## Mediterranean Marine Science

Vol 15, No 2 (2014)



**First record of *Echinogammarus pungens* (H. Milne Edwards, 1840) (Crustacea, Amphipoda) from Africa with the checklist of North African freshwater gammarids**

*T. REWICZ, M. RACHALEWSKI, M. GRABOWSKI*

doi: [10.12681/mms.696](https://doi.org/10.12681/mms.696)

### To cite this article:

REWICZ, T., RACHALEWSKI, M., & GRABOWSKI, M. (2014). First record of *Echinogammarus pungens* (H. Milne Edwards, 1840) (Crustacea, Amphipoda) from Africa with the checklist of North African freshwater gammarids. *Mediterranean Marine Science*, 15(2), 443–448. <https://doi.org/10.12681/mms.696>

## First record of *Echinogammarus pungens* (H. Milne Edwards, 1840) (Crustacea, Amphipoda) from Africa with the checklist of North African freshwater gammarids

T. REWICZ, M. RACHALEWSKI and M. GRABOWSKI

Department of Invertebrate Zoology and Hydrobiology, University of Lodz, 12/16 Banacha, 90-237 Lodz, Poland

Correspondence author: [michalg@biol.uni.lodz.pl](mailto:michalg@biol.uni.lodz.pl)

Handling Editor: Argyro Zenetos

Received: 8 November 2013; Accepted: 2 January 2014; Published on line: 17 February 2014

### Abstract

Taking into account the vast area of North Africa, the freshwater gammarid fauna of this area remains rather poorly studied. So far, 20 species of the three following genera: *Echinogammarus* (11 species), *Gammarus* (8 spp.) and *Chaetogammarus* (1 sp.) have been reported from the area in literature. Another species, *Echinogammarus pungens* (H. Milne Edwards, 1840) was found in the river Titria (Oued Titria), north-western Tunisia, in April 2010. Individuals of both sexes including ovigerous females and juveniles were recorded at the site. This is the first report of this species from Tunisia and from North Africa extending the checklist of freshwater gammarid fauna of North Africa to 21 species. Interestingly the species has apparently replaced *Echinogammarus tacapensis* (Chevreux et Gauthier, 1924), reported from the same section of the Titria River in 1981. Such radical exchange of gammarid fauna and sudden appearance of previously unknown species from Africa remains mysterious. Two tentative explanations of that phenomenon are taken into account. First, that *E. pungens* is in fact a circum-Mediterranean species and was simply overlooked in this area before. Second, that the species is a recent migrant to North African inland waters, introduced accidentally either by humans or by waterfowl.

**Keywords:** Freshwater amphipods, checklist, *Echinogammarus*, *Gammarus*, Tunisia, first record, Oued Titria.

### Introduction

Gammaroidea (or gammarids) are the most diverse crustacean group in Palearctic inland surface waters, with 772 species described so far (Balian *et al.*, 2008). The Mediterranean area is one of the most important hotspots of gammarid diversity in this biogeographic region (Väinölä *et al.*, 2008) and an important glacial refugium for European fauna (Hewitt, 2000; 2004; Husemann *et al.*, 2014). Two genera: *Gammarus* Fabricius, 1775 and *Echinogammarus* Stebbing, 1899, are predominant in the Mediterranean in terms of the species number (Pinkster, 1971; Pinkster & Goedmakers, 1975; Karaman & Pinkster, 1977; Karaman, 1993; Pinkster, 1993). However, the gammarid fauna of inland waters of the south Mediterranean coast remains poorly studied – only 19 species belonging to both the aforementioned genera and one species of *Chaetogammarus* Martynov, 1924 (Fadil *et al.*, 2009b) have been reported so far, from a large area of the Maghreb region and adjacent countries. A checklist of all the gammarid species reported from North African countries is provided in Table 1.

### Material and Methods

Amphipods were collected from two localities on the River Titria in April 2010 (Figs 1 and 2). The samples

were gathered with a benthic hand-net, from all available habitats, and preserved in 96% ethanol directly in the field. In the laboratory, the material was identified to the species level under a Nikon SMZ-800 stereomicroscope, based on available literature (Stock, 1968; Pinkster, 1971; Pinkster & Goedmakers, 1975; Karaman & Pinkster, 1977; Pinkster, 1993). Drawings based on the permanent Euparal fixed microscope slides of male gammarid appendages were made according to the procedure described by Coleman (2003).

### Results

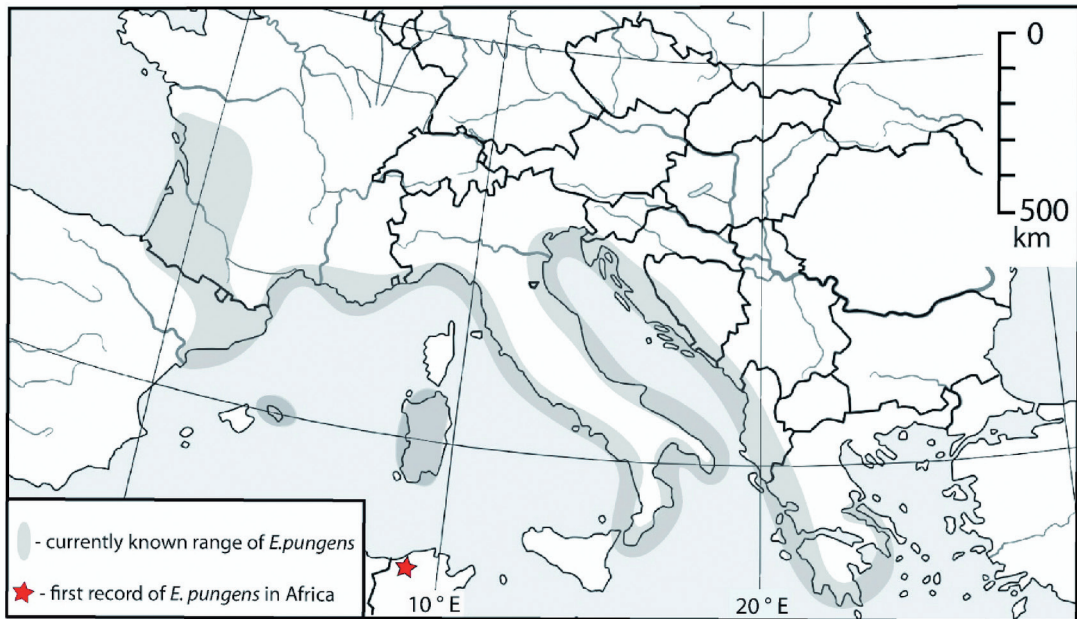
*Echinogammarus pungens* (H. Milne Edwards, 1840)  
*Gammarus pungens* H. Milne Edwards, 1840: 47, figs. 32-34

*Echinogammarus pungens*; G. Karaman, 1993: 71-76, figs. 26-29; Pinkster, 1988: 245-255, fig. 2; Stock, 1968: 22-30 figs. 1-4; Pinkster, 1993: 80-85, figs. 32-34.

**Material:** Tunisia, River Titria, 1 km E from the Ain Sebaa (Ain Sebah) village, N 36.95702, E 8.93602 (Fig. 1); Tunisia, River Titria, vicinity of the Ouchtata village, N 36.95984, E 8.98671. Both samples gathered from stones, clay and tree roots. The material collected included 74 individuals: 45 males, 22 (incl. 10 ovigerous) females, 7 juveniles.

Table 1. Checklist of gammarids recorded in North African inland waters based on the literature and on this study.

Species	Countries of records				
	Morocco	Algeria	Tunisia	Libya	Egypt
<b>Gammarus Fabricius, 1775</b>					
<i>G. acalceolatus</i> Pinkster, 1971	Pinkster, 1971 Karaman & Pinkster, 1977	—	—	—	—
<i>G. gauthieri</i> (S. Karaman, 1935)	S. Karaman, 1935 Pinkster, 1971 Karaman & Pinkster, 1977 Fadil <i>et al.</i> , 2009a	Pinkster, 1971 Karaman & Pinkster, 1977	Pinkster, 1971 Karaman & Pinkster, 1977	—	—
<i>G. marmouchensis</i> Fadil & Dakki, 2006	Fadil & Dakki, 2006	—	—	—	—
<i>G. maroccanus</i> Fadil & Dakki, 2001	Fadil & Dakki, 2001 Fadil <i>et al.</i> , 2009a	—	—	—	—
<i>G. microps</i> Pinkster & Goedmakers, 1975	Pinkster & Goedmakers, 1975 Karaman & Pinkster, 1977	—	—	—	—
<i>G. rifalensis</i> Fadil & Dakki, 2006	Fadil & Dakki, 2006	—	—	—	—
<i>G. rouxi</i> Pinkster & Goedmakers, 1975	Fadil <i>et al.</i> , 2009a	—	—	—	—
<i>G. syriacus</i> Chevreux, 1895	—	—	—	—	Karaman & Pinkster, 1977
<b>Chaetogammarus Martynov, 1924</b>					
<i>C. saisensis</i> Fadil <i>et al.</i> 2009	Fadil <i>et al.</i> , 2009b	—	—	—	—
<b>Echinogammarus Stebbing, 1899</b>					
<i>E. afer</i> Stock, 1974	—	—	Pinkster, 1993	Stock, 1974 Pinkster, 1993	—
<i>E. amandalei</i> (Monod, 1924)	—	Monod, 1924 Pinkster, 1993	—	—	—
<i>E. dachylus</i> G. Karaman, 1987	—	—	G. Karaman, 1987 Pinkster, 1993	—	—
<i>E. foxi</i> (Schellenberg, 1928)	—	—	—	—	Schellenberg, 1928 Pinkster, 1993
<i>E. haraktis</i> Piscart <i>et al.</i> 2013	—	Piscart <i>et al.</i> , 2013	—	—	—
<i>E. klaptoczi</i> Schäferna, 1908	—	—	—	Schäferna, 1908 Pinkster, 1993	—
<i>E. oujdae</i> Fadil & Dakki, 2003	Fadil & Dakki, 2003	—	—	—	—
<i>E. pungens</i> (H. Milne Edwards, 1840)	—	—	present study	—	—
<i>E. reductus</i> Pinkster, 1993	—	Pinkster, 1993	—	—	—
<i>E. simoni</i> (Chevreux, 1894)	—	Chevreux, 1894 Pinkster, 1993	Chevreux, 1894 Pinkster, 1993	—	—
<i>E. tacapensis</i> (Chevreux & Gauthier, 1924)	—	Pinkster, 1993	Chevreux & Gauthier, 1924	—	—
<i>E. valedictus</i> Pinkster & Platvoet, 1990	—	Pinkster & Platvoet, 1990 Pinkster, 1993	—	—	—



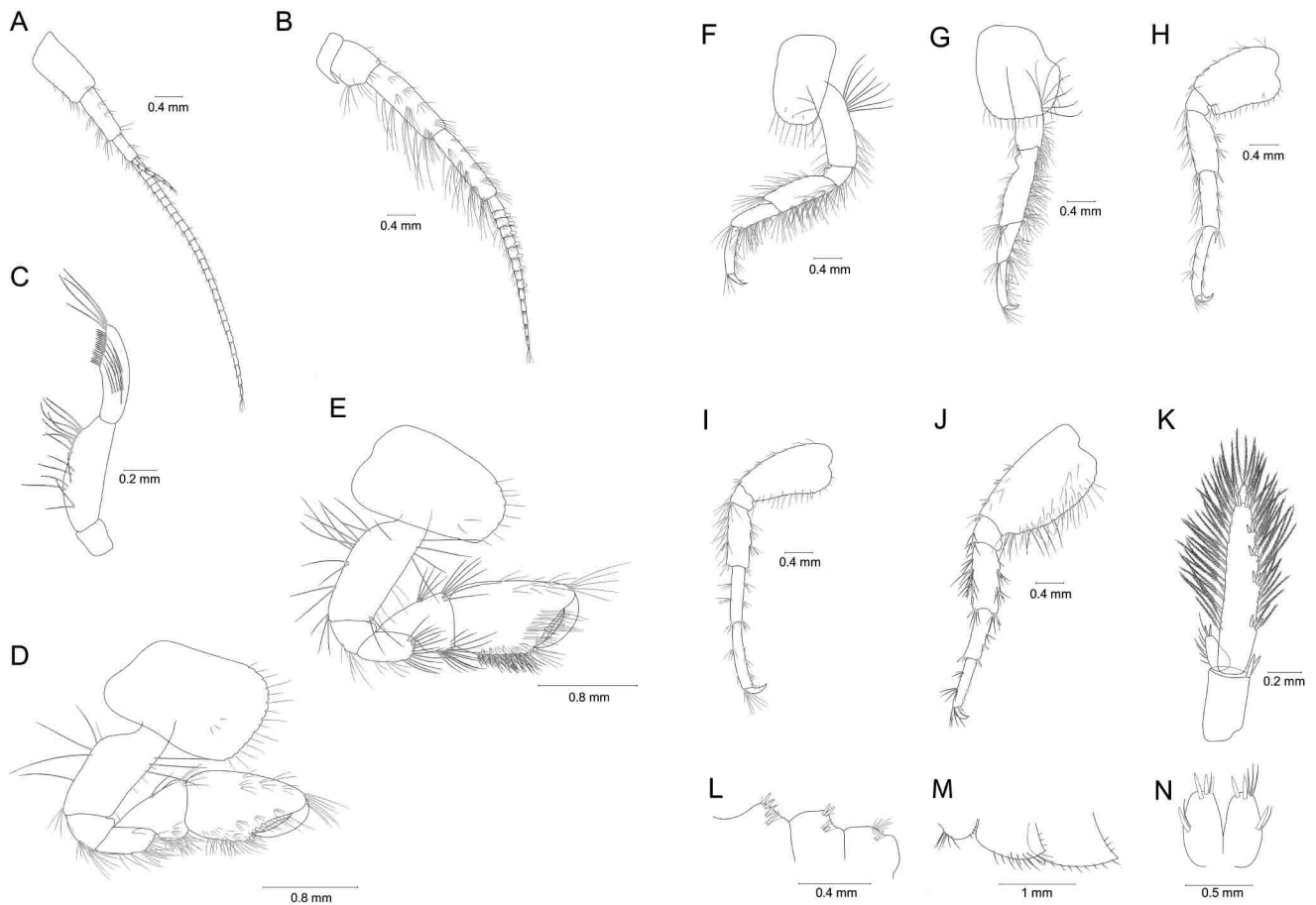
**Fig. 1:** Geographical distribution of *Echinogammarus pungens*.

**Diagnosis of Tunisian male specimens:** All the morphological features described below are illustrated in Fig. 3. Medium large species, the maximum length of males



**Fig. 2:** Habitat of *E. pungens* in the Titria River, Tunisia.

was 13 mm (females did not exceed 11 mm). Peduncle segments of antenna I progressively shorter, armed with some tufts of setae as long as or slightly shorter than the diameter of peduncle segments. Main flagellum with 22-27 segments, accessory flagellum with 4-6 segments. Gland cone of antenna II short and straight. Peduncle segments 4 and 5 of antenna II armed with 4-6 groups of setae up to twice as long as the diameter of the peduncle segments. Several groups of shorter setae placed on the lateral and dorsal surface of the peduncle segments. Flagellum up to 16 segments with calceoli, armed with short setae. The first segment of mandible palp unarmed. Inferior margin of the second segment armed with up to 15 setae, as long as or slightly shorter than the diameter of the segment. The third segment bears 3 groups of A-setae, 1-2 groups of B-setae, ca. 20 D-setae, and 4-5 E-setae. Coxal plates I to IV with numerous small notches, each set with a long or medium-long setule. Additional few setae may be visible on the lateral surface. Gnathopod I moderately setose with propodus ca. 1.5 times as long as wide. Palm oblique, armed with a medial palmar spine and 2-4 angle palmar spines. Dactylus hardly reaching the palmar angle. Propodus of gnathopod II with more transverse palm, also with medial spine and 2-4 angle spines. Pereiopod III and IV armed with many groups of long setae (on pereiopod III setae are longer than on pereiopod IV), particularly along the posterior margins. Basis of pereiopod V ca. 1.5 times long as wide, almost rectangular with backwards protruding lobe. Posterior margin with small notches, each armed with a short seta. In pereiopod VI and VII, the basal segments are longer and more slender without the backward protruding lobe. The posterior margin armed with longer setae compared to pereiopod V. Inner surface of pereiopods V to VII



**Fig. 3:** Morphology of *E. pungens* (adult male) from the Titria River, Tunisia. A – antenna I, B – antenna II, C – mandibular palp, D – gnathopod I, E – gnathopod II, F – pereiopod III, G – pereiopod IV, H – pereiopod V, I – pereiopod VI, J – pereiopod VII, K – uropod III, L – urosome (lateral view), M – epimeral plates I-III, N – telson

armed with increasing number of setae. Margins of merus and carpus with moderate number to large number of setae, much longer than the accompanying spines. Uropod III elongated, uniramous with squamose endopodite. The second exopodal segment is a little longer than the distal spines. Exopodite bears numerous long and plumose setae along its inner and outer margin. Telson lobes about twice as long as wide, armed with a distal group of a few spines and some longer setae. One more group of spines and setae placed at about half of the telson length. First urosome segment with a distinct dorsal excavation “saddle” in front of a distinctly compressed dorsal elevation. Urosome segments II and III with lower elevations. Armature of urosome segments consists of one dorsal and two dorsolateral groups of spines and setae. Epimeral plate I rounded, epimeral plates II and III moderately to sharply pointed, armed with numerous setae along the inferior margin.

**Type locality:** Since the type material and type locality are not known, Stock (1968) designated the neotype locality: France, dept. Pyrenees Orientales, Fontaine d’Estramar (=Fontaine de Salses), North of Salses.

**Habitat:** The species is known to occur in waters with high ionic content, often brackish, such as river mouths,

deltas, lagoons, mineral springs or lakes with substantial water movement (Stock, 1968; Pinkster, 1993). In Tunisia we found it in a slowly flowing lowland river with clay and stony bottom with banks overgrown by trees, with roots exposed and submerged in water.

**Distribution:** So far the species has been reported from the Northern Mediterranean region (Fig. 1), ranging from the Iberian Peninsula (Ebro River delta) on the west, through the French coastal area, Tyrrhenian and Adriatic coasts, south-east to Peloponnesus Peninsula. *Echinogammarus pungens* was found also on Menorca and Sardinia. Our finding in Tunisia is the first report of this species from the Southern Mediterranean region and from the African continent.

**Remarks:** The species is known for its remarkable morphological variability, not only among populations from different geographic locations but also seasonally (Pinkster, 1988). The differences consist mostly in the length and density of setation on antennae, pereiopods, coxal and epimeral plates as well as the height of urosomal elevations (Pinkster, 1993). After careful examination of the Tunisian material and comparison to the redescription of the neotype material, we can conclude that the specimens from Oued Titria do not depart from the set of mor-

phological features defining *E. pungens* and their variability (Stock, 1968; Karaman, 1993; Pinkster, 1993).

## Discussion

Our discovery of *E. pungens* in Tunisia is the first record of this species on the African coast of the Mediterranean Sea. Interestingly, Pinkster (1993) based on the material collected in 1981, reported exclusive presence of another species, *Echinogammarus tacapensis* (Chevreux & Gauthier, 1924), from the very same section of Oued Titria near the Ain Sobaa village. *Echinogammarus pungens* and *E. tacapensis* differ significantly in their morphology. At first sight, the former species is significantly bigger, reaching over 10 mm of total length, while the latter does not usually exceed 5 mm. The most striking difference between the species is visible in the armature of appendages. In *E. tacapensis* the setation of pereopods III-VII, uropod III, telson and also epimeral plates is extremely poor – there are only few setae and their length does not usually exceed the length of spines. Setation of all these appendages and of epimeral plates is much longer and denser in *E. pungens*. Also peduncle of antenna I and mandibular palp have much fewer and shorter setae in *E. tacapensis* if compared to the other. The accessory flagellum in antenna I is only single-segment (rarely 2 segments are visible in biggest individuals) while it has 4-6 segments in *E. pungens*. Besides, *E. pungens* is characterized by the presence of calceoli on the flagellum of antenna II, but these were never observed in *E. tacapensis*. As seen from the above, a potential misidentification of *E. pungens* individuals from the Titria River may be ruled out, as they all fit the features provided as diagnostic for this species well.

Nevertheless, such a radical exchange of gammarid fauna in this small semidesert river and the sudden appearance of previously unrecorded species from Africa remains a rather mysterious phenomenon. Two possible explanations may be taken into account. One is that the *E. pungens* has always been present but overlooked in the area and that, in fact, it is a circum-Mediterranean species. Its sudden appearance in the Titria River could be the result of colonization from one of its permanent tributaries after extirpation of a former inhabitant, e.g. due to a temporary desiccation of the river in the past. Obviously, such explanation remains only speculative. Besides, the rivers and springs of northern Tunisia are among the best studied regions of North Africa with *E. tacapensis* being the only gammarid species recorded in the coastal area (Pinkster, 1993). The only other gammarids known from adjacent parts of the country are two easily identifiable species: *E. simoni*, widespread in Tunisia and Algeria, and *E. dactylus*, known only from the type locality in the Djebel Gorra Mountains (Pinkster, 1993). Another, tempting, explanation would be that *E. pungens* may be

a recent colonizer in North Africa, either introduced by humans (making it an alien species in the area) or via ectozoochory, e.g. by waterfowl. Human-mediated introduction of amphipods is a well-known phenomenon in Europe, and it may occur overland, presumably via boat traffic (Bącela-Spychalska *et al.*, 2013) or even overseas (MacNeil *et al.*, 2010). *Echinogammarus pungens*, often inhabiting estuarine waters, would be a perfect candidate for such overseas transport in ship ballast waters or residual waters that are usually present in smaller boats or within biofouling. However, Titria is a small river of no shipping importance, and far away from any major ports. Thus, the dispersal of *E. pungens* by waterfowl would seem more probable. A possibility that amphipods may hitch-hike among isolated water bodies using water birds as a vector was mentioned already by Segerstråle (1954) and confirmed later by several studies (eg. Daborn, 1976; Rachalewski *et al.*, 2013). Also, the estuarine habitats favored by *E. pungens* are usually inhabited by thousands of water birds that migrate across the Mediterranean Sea (Newton, 2008). On the other hand, Rachalewski *et al.* (2013) demonstrated experimentally that e.g. for *Cranogonyx pseudogracilis*, such dispersal is effective only on short distances, below 10 km. To conclude, the unexpected appearance of *E. pungens* in the inland waters of North Africa remains unexplained. Further studies employing molecular markers to compare the Tunisian population of the species to those from other regions of Mediterranean are planned by the authors and will definitely help to reveal its origin and possible history.

## Acknowledgements

The fieldwork in 2010 was performed during the TBQuest expedition, organized and financed by Dr Radomir Jaskuła, Department of Invertebrate Zoology & Hydrobiology, University of Lodz. Thanks are due to Jacek Hikisz for help in collecting samples during that trip.

## References

- Balian, E.V., Segers, H., Leveque, C., Martens, K., 2008. The Freshwater Animal Diversity Assessment: an overview of the results. *Hydrobiologia*, 595, 627-637.
- Bącela-Spychalska, K., Grabowski, M., Rewicz, T., Konopacka, A., Wattier, R.A., 2013. The “killer shrimp” *Dikerogammarus villosus* (Crustacea Amphipoda) invading Alpine Lakes: overland transport by recreational boats and scuba-diving gears as potential entry vectors? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23, 606-618.
- Chevreux, E., 1894. *Gammarus simoni*, nov. sp., Amphipode des eaux douces d’Algérie et de Tunisie. *Bulletin de la Société zoologique de France*, 19, 171-176.
- Chevreux, E., Gauthier, H., 1924. Description d’un nouveau Gammare de Tunisie. *Bulletin de la Société d’histoire naturelle de l’Afrique du nord*, 15, 53-55.

- Coleman, C.O., 2003. "Digital inking": How to make perfect line drawings on computers. *Organisms Diversity and Evolution, Electronic Supplement*, 14, 1-14.
- Daborn, G.R., 1976. Colonisation of isolated aquatic habitats. *Canadian Field Naturalist*, 90, 56-57.
- Fadil, F., Dakki, M., 2001. Remarques sur la présence du genre *Gammarus* (Crustacés, Amphipodes) au Maroc avec description d'une nouvelle espèce. *Beaufortia*, 51, 153-162.
- Fadil, F., Dakki, M., 2003. A new species of *Echinogammarus* Stebbing, 1899 from Moroccan fresh waters. *Beaufortia*, 53 (2), 53-59.
- Fadil, F., Dakki, M., 2006. Deux espèces nouvelles du genre *Gammarus* (Crustacés, Amphipodes) du Maroc. *Bulletin de l'Institut Scientifique, Rabat, section Sciences de la Vie*, 28, 13-24.
- Fadil, F., Fadil, K., Dakki, M., 2009a. Dynamique et cycle de reproduction de trois populations de *Gammarus* (Amphipodes) du Saiss, Maroc. *Crustaceana*, 82 (10), 1225-1236.
- Fadil, F., Fadil, K., Dakki, M., 2009b. A new species of *Chaetogammarus* Martynov, 1925 (Amphipoda) from Moroccan fresh waters, including notes on the Moroccan epigeic Gammaridae. *Crustaceana*, 82 (8), 969-979.
- Hewitt, G.M., 2000. The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907-913.
- Husemann, M., Schmitt, T., Zachos, F.E., Ulrich, W., Habel, J.C., 2014. Palaearctic biogeography revisited: evidence for the existence of a North African refugium for western Palaearctic biota. *Journal of Biogeography*, 41 (1), 81-94.
- Karaman, S., 1935. *Rivulogammarus gauthieri* n. sp., nouvel amphipode dulçaquicole d'Algérie. *Bulletin de la Société d'histoire naturelle de l'Afrique du nord*, 26, 47-53.
- Karaman, G.S., 1987. Two new species of the family Gammaridae from Tunisia and Madagascar (Contr. to the knowledge of the Amphipoda 164). *Poljoprivreda i Sumarstvo*, 24 (1), 17-38.
- Karaman, G.S., 1993. *Fauna d'Italia. Vol. 31. Crustacea Amphipoda di acqua dolce*. Edizione Calderini Bologna, Italia, 337 pp.
- Karaman, G.S., Pinkster, S., 1977. Freshwater *Gammarus* species from Europe, North Africa and adjacent regions of Asia (Crustacea Amphipoda). Part I. *Gammarus pulex*-group and related species. *Bijdragen tot de Dierkunde*, 47 (1), 1-97.
- MacNeil, C., Platvoet, D., Dick, J.T.A., Fielding, N., Constable, A., Hall, N., Aldridge, D., Renals, T., Diamond, M., 2010. The Ponto-Caspian 'killer shrimp', *Dikerogammarus villosus* (Sowinsky, 1894), invades the British Isles. *Aquatic Invasions*, 5 (4), 441-445.
- Milne Edwards, H., 1834-1840. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Vol. 1-3*. Librairie Encyclopédique de Roret. Paris: Roret. (1) 468, (2) 532, (3) 638 pp, Atlas 1-32, Plates I-XLII.
- Monod, T.H., 1924. On a new species of fresh-water Amphipod, *Carinogammarus annandalei*, sp. n., from Algeria. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology, London*, 9 (14), 233-240.
- Newton, I., 2008. *The Migration Ecology of Birds*. Elsevier Ltd, London, 976 pp.
- Pinkster, S., 1971. Members of the *Gammarus pulex*-group (Crustacea Amphipoda) from North Africa and Spain, with description of a new species from Morocco. *Bulletin Zoologisch Museum, Universiteit van Amsterdam*, 2 (7), 45-61.
- Pinkster, S., 1988. Problems in the taxonomy of the freshwater gammarids with special emphasis on the genus *Echinogammarus* in Italy. *Crustaceana*, Supplement 13, 245-255.
- Pinkster, S., 1993. A revision of the genus *Echinogammarus* (Stebbing, 1899) with some notes on related genera. *Memorie del Museo civico di storia naturale di Verona, IIa Serie A, Biologica, Sezione Scienze della vita*, 10, 1-185.
- Pinkster, S., Goedmakers, A.M., 1975. On two new freshwater species of the genus *Gammarus* from North Africa (Crustacea Amphipoda). *Beaufortia*, 23 (301), 93-103.
- Pinkster, S., Platvoet, D., 1990. Some remarks on the genus *Echinogammarus* Stebbing, 1899 with description of a new species *E. valedictus* from Algeria (Crustacea, Amphipoda). *Bijdragen tot de Dierkunde*, 60 (3-4), 263-269.
- Piscart, C., Merzoug, D., Hafid, H., 2013. A new species of *Echinogammarus* from Algerian freshwaters, *Echinogammarus haraktis* n. sp. (Crustacea, Amphipoda). *Crustaceana*, 86 (13-14), 1623-1633.
- Rachalewski, M., Banha, F., Grabowski, M., Anastacio, P., 2013. Ectozoochory as a possible vector enhancing the spread of an alien amphipod *Crangonyx pseudogracilis*. *Hydrobiologia*, 717, 109-117.
- Segerstråle, S.G., 1954. The freshwater amphipods *Gammarus pulex* (L.) and *Gammarus lacustris* (Sars) in Denmark and Fennoscandia – a contribution to the late and post-glacial immigration history of the aquatic fauna of northern Europe. *Societas Scientiarum Fennica Commentationes Biologicae*, 15, 1-91.
- Schäferna, K., 1908. Über Gammariden von Tripolis und Barka (Gesammelt von Dr. B. Klaptocz). *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, 26, 447-452.
- Schellenberg, A., 1928. Report on the Amphipoda. In: Zoological results of the Cambridge Expedition to the Suez Canal, 1924. *Transactions of the Zoological Society of London*, 22, 633-692.
- Stock, J.H., 1968. A revision of the European species of the *Echinogammarus pungens*-group (Crustacea, Amphipoda). *Beaufortia*, 16 (211), 13-78.
- Stock, J.H., 1974. *Echinogammarus afer* sp. nov.; un nouvel Amphipode Gammaride d'Afrique du Nord. *Memorie del Museo civico di storia naturale di Verona*, 1, 1-10.
- Väinölä, R., Witt, J.D.S., Grabowski, M., Bradbury, J.H., Jazdzewski, K., Sket, B., 2008. Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. *Hydrobiologia*, 595, 241-255.