Subterranean Biology 13: 55–64 (2014)
doi: 10.3897/subtbiol.13.7412
www.pensoft.net/journals/subtbiol

IN MEMORIAM

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

The scientific contribution of Guy Magniez (1935–2014)

Florian Malard[1], Jean-Paul Henry[2], Christophe J. Douady[1,3]

1 *Université de Lyon, UMR5023 Ecologie des hydrosystèmes Naturels et Anthropisés, Université Lyon1 ENTPE CNRS, Villeurbanne 69622, France* **2** *8, rue des Cygnes, Fontaine-lès-Dijon 21121, France* **3** *Institut Universitaire de France, Paris 75005, France.*

Corresponding author: *Florian Malard* (malard@univ-lyon1.fr)

Academic editor: *O. Moldovan* | Received 3 Mach 2014 | Accepted 19 March 2014 | Published 10 May 2014

Citation: Malard F, Henry J-P, Douady CJ (2014) The scientific contribution of Guy Magniez (1935–2014). Subterranean Biology 13: 55–64. doi: 10.3897/subtbiol.13.7412

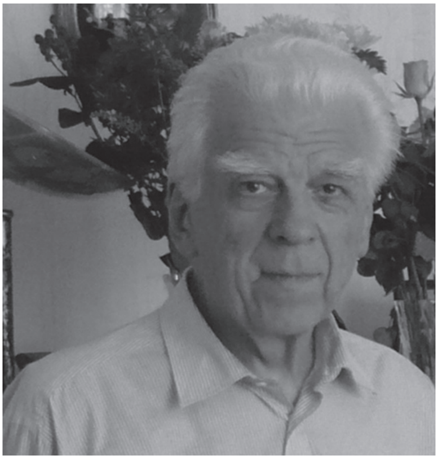

Photo 1. Photography of Guy Magniez.

His career at the laboratory of animal and general biology in Dijon, France

Guy Magniez was born on 23 August 1935 at Marey-sur-Tille, a small village in Côte-d'Or (France). He followed high school studies in Dijon and obtained his high school diploma in 1953. He was an elementary school teacher during one year before joining the University of Dijon where he passed a Bachelor's degree in Natural Sciences in 1958. In 1959, he involved in research at the Laboratory of Geology and obtained a Master degree by submitting a research report on the microfacies of crinoidal Bajocian limestones. Once he successfully passed the Aggregation for secondary education in Natural Sciences in 1960, he integrated the Research Laboratory of Animal and General Biology at the University of Dijon under the direction of Professor Husson. He began with the organization of practical classes for first-year students and a few years later he became responsible for organizing practical classes in general biology and genetics for bachelors. At this time, Guy was in charge of breeding fruit flies for teaching purpose in addition to breeding stenasellids for his research activity (see below). Then, he was offered a teaching assistantship and took the lead of the bachelor program in Natural Sciences. After submitting his state doctoral Thesis in 1976, he delivered lectures to under-graduate and graduate students. He became an associate professor in 1985 and was responsible for preparing graduate students to become teachers. Guy was an exceptional pedagogue: he supervised numerous master students (including the first author of this memorial) and led many students to go into teaching natural sciences. In addition to his heavy teaching duties, Guy also invested much time into social and administrative tasks at the University of Dijon. As a committed educator, Guy was both extremely modest and discrete: he has always been greatly appreciated by his colleagues and students. He was appointed knight of the Order of Academic Palms as soon as 1979, and officer in 1986. His research began in 1960 and he was retired in 1999, but he was still contributing to national and European research projects in the 2010's (Deharveng et al. 2009, Morvan et al. 2013).

The biology of *Stenasellus virei*

Most of the information on the life cycle of *Stenasellus virei* Dolfus, 1897 (Stenasellidae) are from dedicated studies conducted by Guy during the sixties and seventies. From 1960 to 1976, he collected several populations of *Stenasellus* in the Pyrenees and Cantabria and reared them in the Moulis Cave (Pyrenees), Antheuil Cave (Côte-d'Or) and in thermostatic rooms at the University of Dijon. Rearing was a necessary step to document the life cycle of *Stenasellus* because the body size distribution of cave populations was truncated, with almost no juveniles due to a strong cannibalism (Magniez 1973). Collecting *S. virei* alive and rearing them for more than 15 years was obviously a challenging task. Collecting in cave yielded a few individuals with no juveniles and sampling in the hyporheic zone did not provide many more individuals as many of them were killed during pumping. Reproduction events were rare even in controlled conditions and larvae born in aquaria were preyed by adults when they were not rapidly isolated. Moreover, rearing care had to be interrupted for 17 months when Guy had to perform his military service (1961–1963). Despite these difficulties, Guy reported in 1975 his detailed findings on the biology of *S. virei* in a 250-page long article published in International Journal of Speleology (Magniez 1975). The intramarsupial development of *S. virei* lasts 9–10 months but the female keeps an empty marsupium for several months after releasing its larvae because the reproductive intermolt lasts 15–16 months. A reproductive intermolt is always followed by at least one genital-rest intermolt (lasting 9–11 months), so that the shortest interval between successive egg-laying periods of a single female is at least 2 years. Post marsupial larval development is about 11-month long and an additional 5–6 years are needed before the female reaches its age at first reproduction (i.e. 6–7 years or more). Life span in males and females is about 12 and 15 years, respectively. As reproduction events occurs at best every 2 years and the number of eggs per reproduction event is on average 32 (range: 15–60 eggs), a single female would at most produce 150 eggs during its life. Detailed information on the life cycle and reproduction biology of groundwater organisms are scarce. However, biological features such as generation time and number of offsprings per individual are essential for understanding evolution in the subterranean environment. Younger generations of scientists are increasingly becoming aware of the value of detailed biological information on subterranean species provided by tedious studies conducted during the second half of the 20th century.

Systematics of Asellidae and Stenasellidae

Perhaps, the greatest contribution of Guy consisted in clarifying the systematics of Stenasellidae and Asellidae. He described or co-described a total of 109 taxa among which 6 genera (*Bragasellus*, *Gallasellus*, *Metastenasellus*, *Neostenetroides*, *Parastenasellus*, and *Sibirasellus*), 3 species of *Asellus*, 13 species of *Bragasellus*, 48 species of *Proasellus*, 5 species of *Synasellus* and 31 species and subspecies of Stenasellidae (Table 1). As his taxonomic knowledge of the Aselloidea and meticulous morphological descriptions were rapidly recognized by the scientific community, Guy received biological material from all over the world and described species in Africa, America, Asia and Europe (Figure 1). Although Guy never published a single cladogram, his approach of the systematics of Aselloidea was all about finding the relationships among species through time. Relationship between taxa was essentially inferred from the shape of male copulatory organs (second pleopods), the detailed structure of which was revealed by means of scanning electron microscopy as early as the seventies (Henry and Magniez 1969).

Following the seminal work of Racovitza (1919), Henry and Magniez (1968, 1970) initiated the modern systematics of Asellidae by distributing into 8 genera the heterogeneous set of taxa that had long been attributed to the genus *Asellus* E.L. Geoffroy, 1762. Their motivation stood from the necessity to distinguish between distinct “natural groups”, the members of which shared more evolutionary history with each other, than they did with members of other groups. Fifty years later, the foundations of the asellid systematics as described by Henry and Magniez (1968) are still valid, even though the family contains many more genera and species. Many of the evolutionary inferences made by the authors on the basis of morphological characters were corroborated by recent phylogenetic studies using molecular markers (Morvan et al. 2013). The systematics of Asellidae has been continuously refined by Guy and Jean-Paul Henry for the last 20 years (Henry and Magniez 1993, 1995, Magniez 1996, Magniez and Henry 2001). The family is now represented by three distinct lineages. The *Asellus* pattern lineage with its diversification center in the north-Pacific area contains species belonging to the two *Asellus* subgenera *Asellus* (*Asellus*) and *Asellus* (*Arctasellus*) Geoffroy (Boreal Eurasia and Alaska) and the genera *Mesoasellus* Birstein (Baïkal), *Phreatoasellus* Matsumoto (Japan, Korea), *Nipponasellus* Matsumoto (Japan), *Columbasellus* Lewis, Martin & Wetzer (Washington, see Lewis et al. 2003), *Uenasellus* Matsumoto (Japan), *Sibirasellus* Henry & Magniez (Primorye) and *Calasellus* Bowman (West of North-

Table 1. List of genera, species and subspecies described or co-described by Guy Magniez. Numbers refer to the location of species and subspecies as indicated in Figure 1.

Asellidae

1. *Asellus (Asellus) levanidovorum* Henry & Magniez, 1995
2. *Asellus (Asellus) primoryensis* Henry & Magniez, 1993
3. *Asellus (Phreatoasellus) joianus* Henry & Magniez, 1991

Bragasellus Henry & Magniez, 1968

4. *Bragasellus afonsoae* Henry & Magniez, 1988
5. *Bragasellus aireyi* Henry & Magniez, 1980
6. *Bragasellus bragai* Henry & Magniez, 1988
7. *Bragasellus comasi* Henry & Magniez, 1976
8. *Bragasellus comasioides* Magniez & Brehier, 2004
9. *Bragasellus escolai* Henry & Magniez, 1978
10. *Bragasellus lagari* Henry & Magniez, 1973
11. *Bragasellus lagarioides* Henry & Magniez, 1996
12. *Bragasellus meijersae* Henry & Magniez, 1988
13. *Bragasellus molinai* Henry & Magniez, 1988
14. *Bragasellus notenboomi* Henry & Magniez, 1988
15. *Bragasellus rouchi* Henry & Magniez, 1988
16. *Bragasellus stocki* Henry & Magniez, 1988

Gallasellus Henry & Magniez, 1981

17. *Proasellus alavensis* Henry & Magniez, 2003
18. *Proasellus albigensis* (Magniez, 1965)
19. *Proasellus aragonensis* Henry & Magniez, 1992
20. *Proasellus bagradicus* Henry & Magniez, 1972
21. *Proasellus bardaunii* Alouf, Henry & Magniez, 1982
22. *Proasellus bellesi* Henry & Magniez, 1982
23. *Proasellus beroni* Henry & Magniez, 1968
24. *Proasellus beticus* Henry & Magniez, 1992
25. *Proasellus boui* Henry & Magniez, 1969
26. *Proasellus bouianus* (Henry & Magniez, 1974)
27. *Proasellus burgundus* Henry & Magniez, 1969
28. *Proasellus cantabricus* Henry & Magniez, 1968
29. *Proasellus chappuisi* Henry & Magniez, 1968
30. *Proasellus chauvini* Henry & Magniez, 1978
31. *Proasellus claudei* Henry & Magniez, 1996
67. *Synasellus hurki* Henry & Magniez, 1995
68. *Synasellus leysi* Henry & Magniez, 1995
69. *Synasellus meijersae* Henry & Magniez, 1987
70. *Synasellus notenboomi* Henry & Magniez, 1987

Stenasellidae

71. *Magniezia gardei* Magniez, 1978

Metastenasellus Magniez, 1966

72. *Metastenasellus leysi* Magniez, 1986
73. *Metastenasellus powelli* Magniez, 1979
74. *Metastenasellus tarrissei* Magniez, 1979
75. *Mexistenasellus parzefalli* Magniez, 1972
76. *Mexistenasellus wilkensi* Magniez, 1972

Parastenasellus Magniez, 1966

77. *Stenasellus bedosae* Magniez, 1991
78. *Stenasellus boutini* Magniez, 1991
79. *Stenasellus bragai* Magniez, 1976
80. *Stenasellus cambodianus* Boutin & Magniez, 1985
81. *Stenasellus chapmani* Magniez, 1982
82. *Stenasellus covillae* Magniez, 1987
83. *Stenasellus deharvengi* Magniez, 1991
84. *Stenasellus escolai* Magniez, 1977
85. *Stenasellus foresti* Magniez, 2002
86. *Stenasellus grafi* Magniez & Stock, 2000
87. *Stenasellus henryi* Magniez & Stock, 2000
88. *Stenasellus javanicus* Magniez & Rahmadi, 2006
89. *Stenasellus kenyensis* Magniez, 1975
90. *Stenasellus messanai* Magnez & Stock, 2000
91. *Stenasellus mongnatei* Magniez & Panitvong, 2005
92. *Stenasellus monodi* Magniez, 2000
93. *Stenasellus rigali* Magniez, 1991
94. *Stenasellus stocki* Magniez, 2001
95. *Stenasellus strinatii* Magniez, 1991
96. *Stenasellus vermeuleni* Magniez & Stock, 2000
97. *Stenasellus virei angelieri* Magniez, 1968
98. *Stenasellus virei boui* Magniez, 1968
99. *Stenasellus virei hussoni* Magniez, 1968
100. *Stenasellus virei margalefi* Magniez, 1996
101. *Stenasellus virei rouchi* Magniez, 1996

Gnathostenetroidae

Neostenetroides Carpenter & Magniez, 1982

102. *Neostenetroides stocki* Carpenter & Magniez, 1982

Janiridae

103. *Mackinia birstein*i Henry & Magniez, 1991

America). Magniez (1996) suggested that this lineage could be attributed the rank of a subfamily. The Atlantic lineage is represented in North America by the genera *Caecidotea* Packard, *Lirceus* Rafinesque, *Lirceolus* Bowman & Longley, *Remasellus* Bowman & Sket and *Salmasellus* Bowman and in Europe by the genera *Bragasellus* Henry & Magniez (Portugal and Spain), *Gallasellus* Henry & Magniez (France) and *Synasellus* Braga (Portugal and Spain). Hidding et al. (2003) brought molecular evidence that the genus *Baicalasellus* Stammer (Baïkal Lake) belonged to this Atlantic lineage and the same could hold true for the genus *Stygasellus* Chappuis (Romania). The Mediterranean lineage is represented by the species-rich genus *Proasellus* Dudich (including the genus *Chthonasellus* Argano & Messana [see Morvan et al. 2013]), which extends

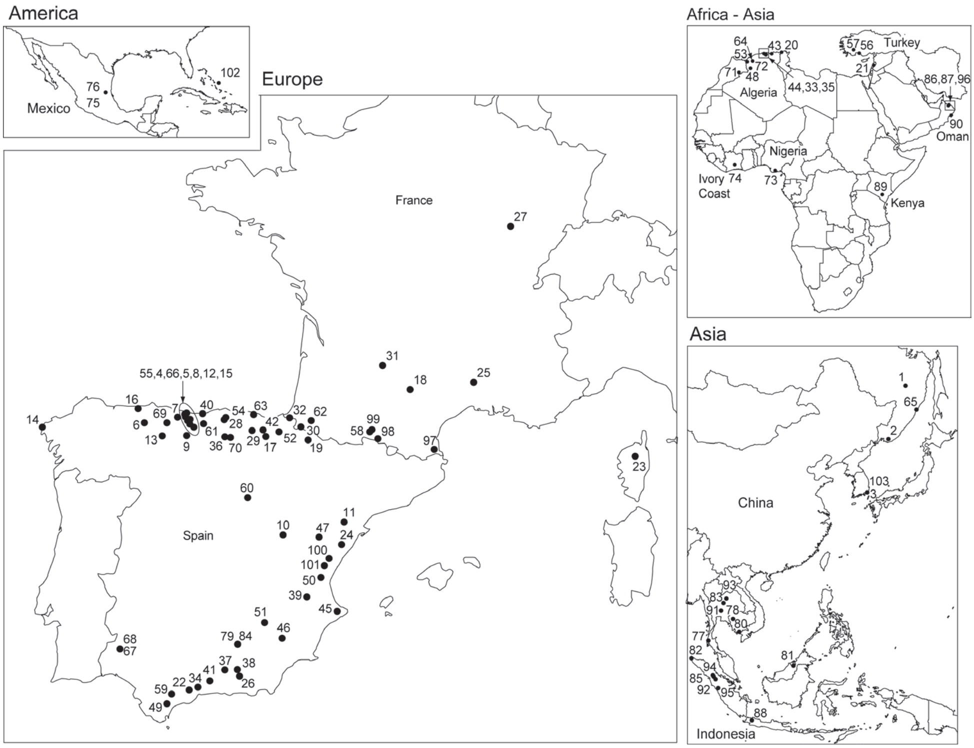

Figure 1. Maps showing the location of the 103 species and subspecies of aquatic isopods described or co-described by Guy Magniez. Numbers indicate taxa, the names of which are provided in Table 1.

longitudinally from Iran to Spain and latitudinally from Algeria to Sweden. This genus was finely dissected into several lineages by Guy and Jean-Paul Henry, many of which were corroborated by recent molecular studies (Morvan et al. 2013).

In his last poster presented at the 19th International Symposium of Subterranean Biology in Fremantle, Australia (21-26 September 2008), Magniez (2008) had a note reminding the thoughts of Armand Viré (1902) when he captured the first stenasellid in Padirac Cave (Lot, France): "he thought *Stenasellus virei* was a relict and he had captured the last specimens!". Today, the Stenasellidae comprises more than 75 taxa belonging to 10 genera. Almost half of these taxa were described by Guy. We provide in Figure 2 the chronology of the discovery of stenasellids as portrayed by Guy in his last poster as well as his own interpretation of the worldwide distribution of the family (see below).

Subterranean biogeography

Guy has voluntary remained unprecise as to when the colonization of groundwater by marine ancestors and diversification of groundwater lineages occur. This is because he

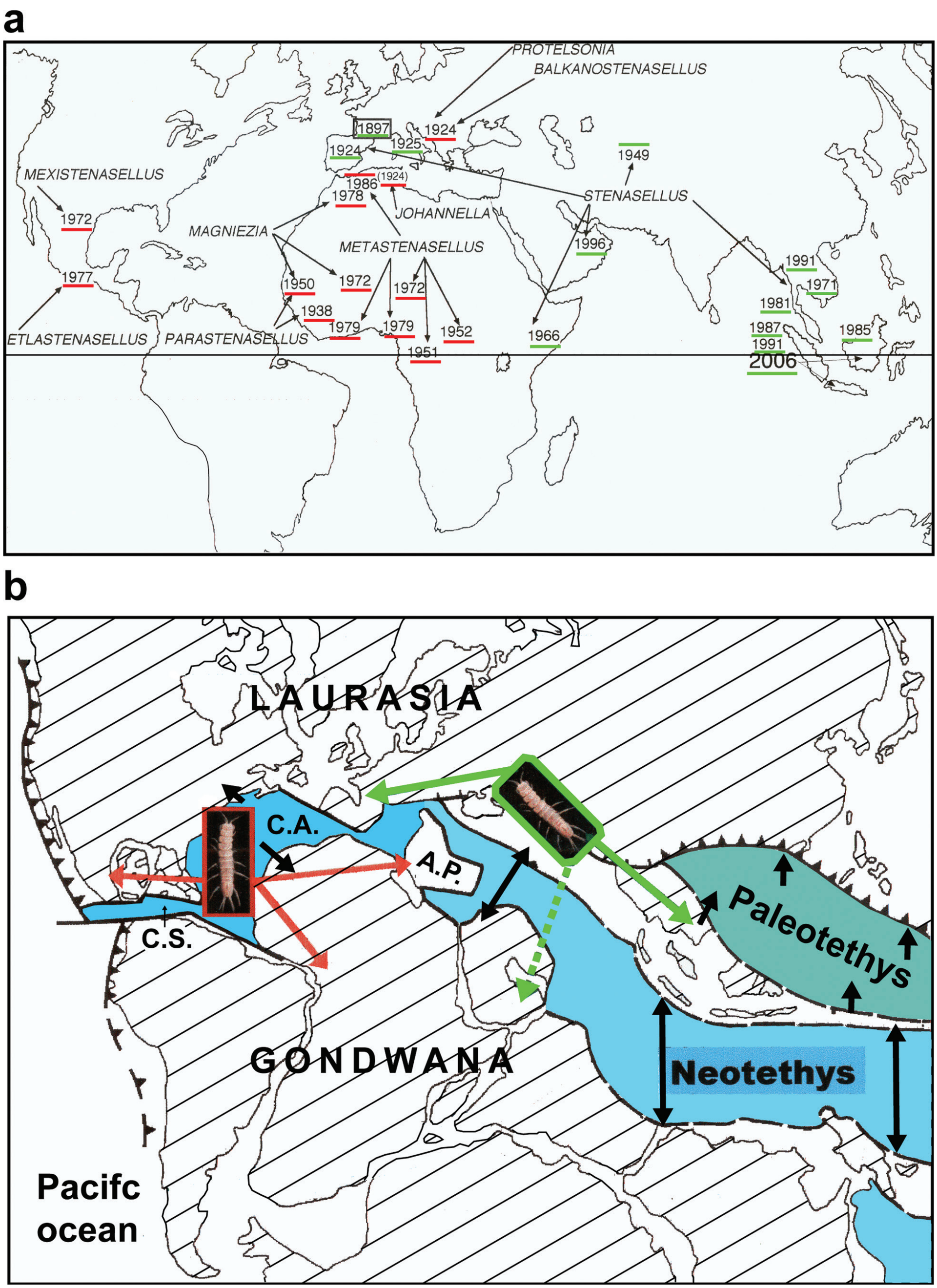

Figure 2. a. Chronology of the discovery of stenasellids. Red and green lines refer to as the "Atlantic" and "Mesogean" stocks as indicated in the lower panel. The genus *Acanthastenasellus* Chelazzi & Messana 1985 (Somalia) was not mapped by Guy **b** Hypothetic colonization of groundwater by ancestor of the stenasellids. C.S. Caribbean sea C.A. Central Atlantic Ocean A.P. Apulian plate. Panels a & b are modified after Magniez (2008). The paleogeographical map in panel b was modified after Monod (2005), Encyclopaedia Universalis.

has always been much skeptical about the assumptions of the climatic relict hypothesis. In particular, he never associated inland groundwater colonization to any marine transgression because colonization was necessarily an active process to him. Moreover, he was convinced that some species of asellids and stenasellids had experienced considerable range expansion by dispersing into extensive alluvial systems (Magniez 1999). Again, Magniez'view of diversification and species range dynamics in groundwater aselloids recently received support from molecular studies. Morvan et al. (2013) documented a constant diversification rate during most of the course of Aselloidea evolution, thereby challenging the view that species diversification in temperate groundwater has been primarily driven by continental-scale perturbations in the physical environment. Then, Eme et al. (2013) provided evidence that the large geographic range of *Proasellus cavaticus* (Leydig, 1871) in northern Europe reflected recent, presumably postglacial, dispersal.

To end up this memorial, we provide below two biogeographic scenarios elaborated by Guy that would warrant further testing by today's generation of subterranean phylogeographers. The first scenario is an attempt to explain the distribution of stenasellids at global scale (Figure 2). It was a part of his poster presented at the 19th International Symposium of Subterranean Biology but Guy did not publish this work. Guy hypothesized that the ancestors of stenasellids were anophtalmous thermophilic burrowers living in coastal unconsolidated sediments of the Neo-Tethys Sea, the sediments of which accumulated from Trias to Eocene. He further suggested on the basis of morphological taxonomy that the initial colonization of groundwater gave rise to two distinct groups of stenasellids. The first one, to which he referred as the "Atlantic stock", includes species from the New World, West Africa and the Balkans (red lines in Figure 2). He speculated that the drift of the Apulian block (a fragment of Gondwana) and its fusion with Eurasia might account for the presence of *Protelsonia* Méhely and *Balkanostenasellus* Cvetkov in the Balkans. The second group, to which he referred as the "Mesogean stock" corresponds to the genus *Stenasellus* Dolfus which extends from southern Europe (Iberian Peninsula, southern France, and Italy) to the eastern horn of Africa and Asia. According to Guy' predictions , a phylogenetic tree of Stenasellidae would exhibit a clear basal dichotomy with all genera except *Stenasellus* clustering into a monophyletic group and all *Stenasellus* species clustering into another monophyletic group.

The second scenario attempts to explain the evolutionary history of the Iberian stenasellids (Magniez 1999; Figure 3). Guy suggested that the '*breuili*' and the '*virei*' groups might have evolved independently during Cretaceous on two separate emerged continental blocks to which he referred as the "Iberian Meseta" and the "Catalona-Corbières-Corsica-Sardinia block" (the "Thyrrhenian continent" in Figure 3) (but see Dercourt et al. 1993 for detailed paleogeographical maps). Then, the fragmentation of the Thyrrhenian block and south-eastern migration of the Corsica-Sardinia plate (from 30 to 6 my BP) isolated *Stenasellus racovitzai* Razzauti, 1925 from the '*virei*' group. Finally, each group experienced a more recent geographical expansion as some eurytopic and eurytherm species dispersed along alluvial corridors of the Guadalquivir, Duero, Ebro and Garonne river systems (Figure 3).

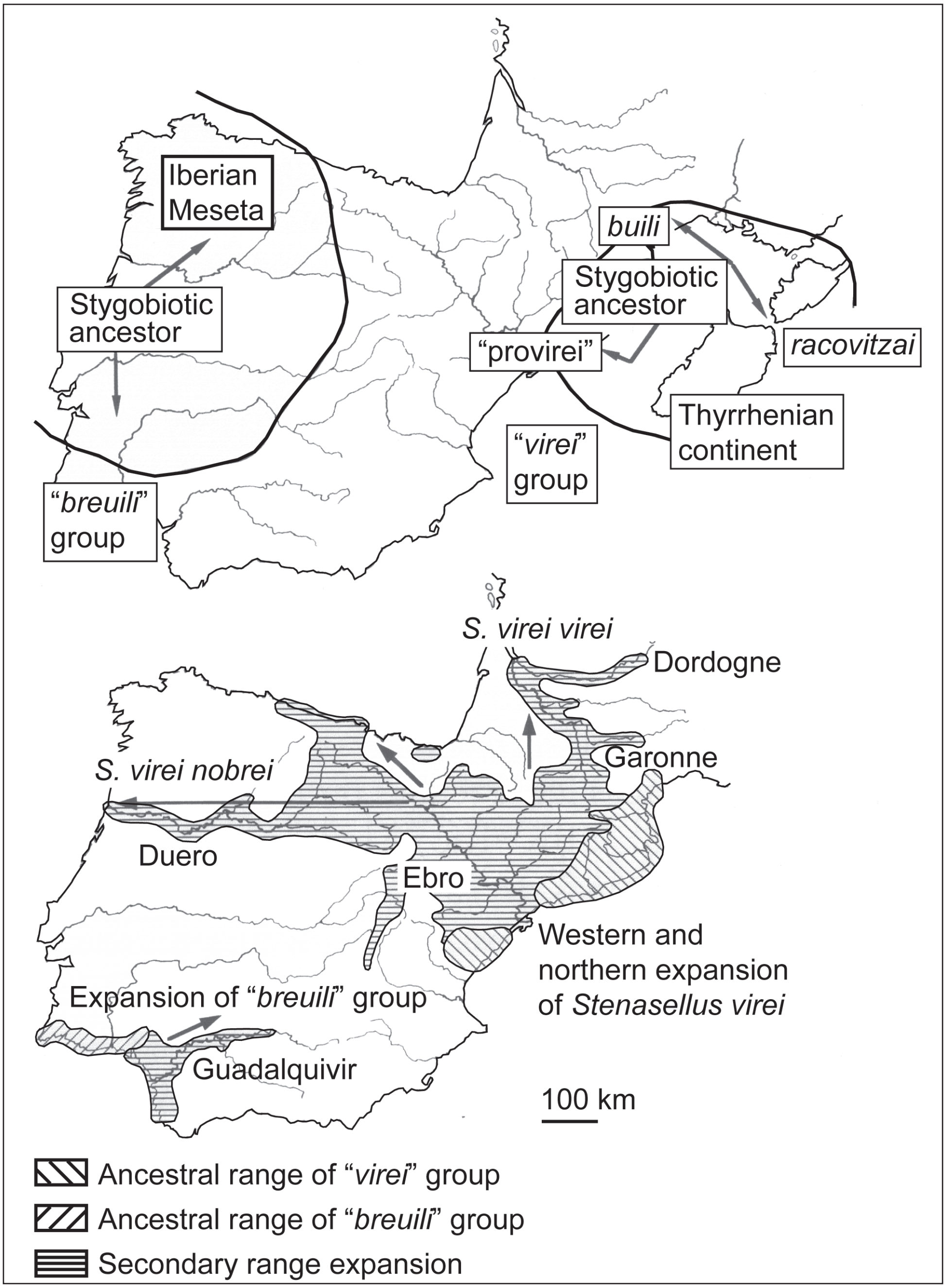

Figure 3. Paleobiogeography of the Ibero-Aquitanian stenasellids. Upper panel. Palaeogeographic continental areas attributed to the stygobiotic ancestors of the "*breuili*" and "*virei*" groups before migration of the Corsica-Sardinia plate. Limits are very approximate. Lower panel. Recent expansion of geographic ranges of the "*breuili*" and "*virei*" groups due to dispersal along large Ibero-Aquitanian river systems. Modified after Magniez (1999).

Guy Magniez devoted much of his life to the taxonomy of the Aselloidea and described, named and classified more than 100 taxa. Yet, his scientific contribution goes well beyond the taxonomy of the Aselloidea. All along his career, he attempted to merge information from biology, ecology, and evolutionary biology to explain the geographic distribution of groundwater species through geological time. His name would be forever associated to the modern systematics of the Aselloidea but he has also left us many predictive biogeographic scenarios that warrant further testing.

References

Deharveng L, Stoch F, Gibert J, Bedos A, Galassi D, Zagmajster M, Brancelj A, Camacho A, Fiers F, Martin P, Giani N, Magniez G, Marmonier P (2009) Groundwater biodiversity in Europe. Freshwater Biology 54: 709–726.

Dercourt J, Ricou LE, Vrielynck E (1993) Atlas Tethys Palaeoenvironmental Maps. Commission de la Carte Géologique du Monde, Paris.

Eme D, Malard F, Konecny-Dupré L, Lefébure T, Douady CJ (2013) Bayesian phylogeographic inferences reveal contrasting colonization dynamics among European groundwater isopods. Molecular Ecology 22: 5685–5699. doi: 10.1111/mec.12520

Henry J-P, Magniez G (1968) Sur la systématique et la biogéographie des Asellides. Comptes Rendus de l'Académie des Sciences 267: 87–89.

Henry J-P, Magniez G (1969) Etude au microscope électronique à balayage des pléopodes copulateurs de deux espèces de *Proasellus* (Crustacea, lsopoda, Asellota). Comptes Rendus de l'Académie des Sciences 269: 718–720.

Henry J-P, Magniez G (1970) Contribution à la systématique des Asellides (Crustacea Isopoda). Annales de Spéléologie 25: 335–367.

Henry J-P, Magniez G (1993) Présence d'asellides stygobies (Crustacea, Isopoda, Aselloidea) dans la region du Primorye, Sibérie sud-orientale. Bijdragen tot de Dierkunde 62 (3): 179–191.

Henry J-P, Magniez G (1995) Nouvelles données sur les Asellidae épigés d'Extrême-Orient (Crustacea, Isopoda, Asellota). Contributions to Zoology 65 (2): 101–122.

Hidding B, Michel E, Natyaganova AV, Yu Sherbakov D (2003) Molecular evidence reveals a polyphyletic origin and chromosomal speciation of Lake Baikal's endemic asellid isopods. Molecular Ecology 12: 1509–1514. doi: 10.1046/j.1365-294X.2003.01821.x

Lewis JJ, Martin JW, Wetzer R (2003) *Columbasellus Acheron*, a new genus and species of subterranean isopod from Washington (Crustacea: Isopoda: Asellidae). Proceedings of the Biological Society of Washington 116 (1): 190–197.

Magniez G (1973) Les populations naturelles de *Stenasellus virei* Dollfus (Crustacé Asellote troglobie). International Journal of Speleology 5: 31–48. doi: 10.5038/1827-806X.5.1.3

Magniez G (1975) Observations sur la biologie de *Stenasellus virei* (Crustacea lsopoda Asellota des eaux souterraines). International Journal of Speleology 7: 79–228. doi: 10.5038/1827-806X.7.1.8

Magniez G (1996) *Asellus aquaticus* et ses proches parents: un étranger parmi la faune asellidienne d'Europe. Mémoires de Biospéléologie XXIII: 181–187.

Magniez G (2008) From 1896 to 2008, a sight of the stygobitic family Stenasellidae (Crustacea, Isopoda, Asellota). In: Symposium abstracts of the 19th International Symposium of Subterranean Biology, Fremantle (Australia), 21-26 September 2008, Snap Printers, Belmont (Australia), 60.

Magniez G, Henry J-P (2001) Présence d'un asellide stygobie dans une île: causes et conséquences. Mémoires de Biospéologie XXVIII: 143–147.

Magniez GJ (1999) Isopodes asselloïdes stygobies d'Espagne, IV – Stenasellidae: taxonomie, histoire évolutive et biogeographie. Beaufortia 49 (11): 115–139.

Monod O (2005) Thétys. In: Encyclopaedia Universalis. Encyclopaedia Universalis, Boulogne Billancourt, France, 1–9.

Morvan C, Malard F, Paradis E, Lefébure T, Konecny-Dupré L, Douady CJ (2013) Timetree of Aselloidea reveals species diversification dynamics in groundwater. Systematic Biology 62 (4): 512–522. doi: 10.1093/sysbio/syt015

Racovitza EG (1919) Notes sur les isopodes. I. *Asellus aquaticus* auct. est une erreur taxonomique. 2. *A. aquaticus* et *A. meridianus* n. sp. Archives de Zoologie Expérimentale et Générale 58: 31–43.

Supplementary material 1

Publications by Guy Magniez

Authors: Florian Malard, Jean-Paul Henry, Christophe J. Douady

Data type: References list.

Explanation note: A list of 153 articles authored or co-authored by Guy Magniez.

Link: doi: 10.3897/subtbiol.13.7412.app1