

In Memoriam: Ignacio Ribera Galán (1963-2020)

Andrés Millán¹, Pedro Abellán², Paula Arribas³, Susana Pallarés⁴, Félix Picazo⁵, Adrián Villastrigo⁶, Josefa Velasco¹ and David Sánchez-Fernández¹

- ¹ Departamento de Ecología e Hidrología, Facultad de Biología, Universidad de Murcia, Spain.
- ² Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Spain.
- ³ Grupo de Ecología y Evolución en Islas, Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), San Cristóbal de la Laguna, Tenerife. Spain.
- ⁴ Marine Biology and Ecology, Research Centre, School of Biological and Marine Sciences, University of Plymouth, Devon. United Kingdom.
- ⁵ Departamento de Biodiversidad y Restauración. Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza. Spain.
- ⁶ Instituto de Biología Evolutiva (Universitat Pompeu Fabra-CSIC), Barcelona. Spain.



On April 15th 2020, our colleague and dear friend, Ignacio Ribera, passed away. His work on faunistic, systematic, taxonomy, evolution, biogeography and conservation of water beetles has contributed enormously to the growth of the "Iberian Limnology".

Ignacio was born in Martorell on 9th March 1963 and since childhood he was fascinated by insects in general and beetles in particular. He completed a degree in Biology at the University of Barcelona, being awarded as one of the best students. Shortly later, he began his PhD in the Development and

ii Millán et al.

Research Centre (CSIC) in Barcelona, granted by a fellowship from the Spanish Government, and concluded it in 1992 with outstanding marks. In 1995, he moved to the Scottish Agricultural Center in Auchincruive under the supervision of Garth Foster, one of the main specialists in water beetles worldwide. Then, he worked at the University of Murcia (Spain) as "Associate Professor" (1997), consolidating the collaboration with Andrés Millán. After that, he moved to London to work as a postdoctoral researcher in the Imperial College and Natural History Museum supported by both Marie Curie and Leverhulme Special Research fellowships. During this fruitful period, Ignacio worked closely with Alfried Vogler, one of the most recognised researchers on molecular systematics and evolution of insects. He returned to Spain in 2004 awarded with a "Ramón y Cajal" contract to work in Madrid at the National Museum of Natural Sciences (CSIC), where he reached a permanent position in 2005. Finally, in 2008 he moved to the Institute of Evolutionary Biology (UPF-CSIC) in Barcelona.

He published close to 300 scientific documents, including articles, books, book chapters and other outreach works. More than 160 of such papers were published in SCI-indexed journals (citations: 4487, h index: 37). He described 97 new species for science, 16 genera and even a new family of water beetles (Ribera *et al.*, 2002). Besides, he published the first comprehensive checklist of aquatic and semiaquatic Coleoptera for the Iberian Peninsula (Ribera *et al.*, 1999) and was the senior author of the book "Atlas of aquatic Coleoptera from mainland Spain" (Millán *et al.*, 2014).

Ignacio was primarily an evolutionary biologist, who actively worked on the phylogeny and evolution of water and cave beetles, with a particular emphasis on the Western Palaearctic. Early in his career, Ignacio found in molecular phylogenies a promising and powerful tool for addressing many of the questions that he wished to answer about beetle taxonomy, evolution, biogeography and conservation. An important part of Ignacio's research focused on the phylogenetic systematics of aquatic Coleoptera, a field in which he became an internationally recognised authority. His research in this field contributed to the classification and reconstruction of the evolutionary history of different water beetle lineages, both small clades and entire families, therefore making aquatic coleopterans one of the few hyperdiverse insect groups with well-resolved phylogenies (Bilton et al., 2019). In the early 2000s, and in collaboration with the mentioned Prof. Vogler, he started the study of the evolutionary relationships of diving beetles (Dytiscidae) and other aquatic Adephaga groups (Ribera et al., 2002; 2004; 2008), a research line that continued until his last days (e.g. Beutel et al., 2008; Ribera & Faille 2010; Abellán et al., 2013; García-Vázquez et al., 2016; Fery & Ribera, 2018). An important contribution associated with his stay in London was the study of phylogenetic relationships of the whole Coleoptera (Hunt et al., 2007), an overwhelming order-level phylogeny where the multiple transitions to the aquatic realm were for the first time located and dated. Over the years, he enlarged the scope of his research to other water beetle groups, with a special focus on Hydraenidae (Ribera et al., 2010; 2011; Abellán & Ribera, 2011; Trizzino et al., 2011; Villastrigo et al., 2019). Beyond his work with species-level phylogenies, Ignacio made also a substantial contribution in the field of phylogeography and historical biogeography, leading to elucidate the evolutionary history of populations, subspecies and species of water beetles (e.g. Ribera et al., 2003a; Abellán et al., 2009). Among other achievements, his research provided an outstanding contribution to understanding the role of Pleistocene climatic changes promoting water beetles diversification and speciation in Mediterranean refugia (Ribera & Vogler, 2004; Ribera et al., 2011; García-Vázquez et al., 2017; Abellán & Ribera, 2017). Additionally, he also became an expert in cave and soil beetles beyond those those linked with groundwater (e.g. Faille et al., 2013; Cieslak et al., 2014; Andújar et al., 2017).

Apart from strict phylogenetic and systematic studies, Ignacio used species-level phylogenies to address a number of transversal questions in ecology and evolutionary research, such as: What determines species geographical range size? What mechanisms shape speciation and adaptive divergence? Which are the evolutionary consequences of specialisation? His researches in these diverse areas are well characterised by the use of information from multiple methodological approaches (including ecological modelling, thermal and osmotic physiology, microscopy or morphometrics) integrated within

a robust phylogenetic frame of hypothesis testing. An important part of his research concentrated on the effect of habitat constraints in the genetic structure, macroecology and macroevolution of freshwater invertebrates. In this field, he studied the evolutionary consequences of one of the main habitat constraints in aquatic ecosystems: the division between standing (lentic) and running (lotic) waters. It has been hypothesised that the contrasting ecological stability of these two habitat types has profound implications on the species inhabiting them, driving disparities between specialists from both habitats ranging from dispersal abilities to macroevolutionary patterns (revised in Ribera 2008). Thus, he was a pioneer in reporting range size differences and distinct latitudinal diversity gradients between lotic and lentic specialists (Ribera & Vogler, 2000; Ribera et al., 2003b). These results were linked to the constraints that the long-term persistence of habitats imposes on species dispersal ability and supposed the starting point for subsequent studies, which supported this hypothesis. Later, Ignacio et al. demonstrated that restricted lotic specialists show higher genetic diversity than their widespread sibling species from lentic habitats (Abellán et al., 2009), that lentic specialists have experienced higher range shifts throughout the Quaternary period (Abellán et al., 2011) and that species range size is related to geographic location and phylogeny (Abellán & Ribera, 2011). Further research also supported previous work in this line by reporting a higher degree of equilibrium with the climate in lentic specialists as a consequence of profuse postglacial recolonisation (Sánchez-Fernández et al., 2012). These disparities between lotic and lentic sister species were later demonstrated to be caused by differences in dispersal capacity and not in establishment abilities (Arribas et al., 2012). The most recent large-scale research done by Ignacio dealt with the contrasting geographical range conservation between lotic and lentic specialists (Abellán & Ribera, 2017), the range expansion from glacial refugia after the last glacial maximum (García-Vázquez et al., 2017) as well as the relationship between body size and latitude (Pallarés et al., 2019).

During the last years, Ignacio raised other questions, such as: What is the origin, and what are the evolutionary consequences of novel traits? What is the influence of these novel traits in species diversification? How these traits appeared and evolved in independent lineages? Thus, he led different studies focused on water salinity, which constitutes another strong evolutionary pressure for freshwater species, by addressing the evolution of salinity tolerance in different lineages of water beetles (Arribas *et al.*, 2014; Pallarés *et al.*, 2017; Villastrigo *et al.*, 2018). More recently, an important part of his research aimed to understand the origin and evolutionary consequences of habitat transitions between running and standing waters in aquatic macroinvertebrates and the development of tolerance to salinity. His recent research also contributed to understand the evolution of several key traits of water beetles. For example, he led studies exploring the evolution of physiological changes in thermal tolerance and its association with diversification, range expansion and speciation (Hidalgo-Galiana *et al.*, 2014; 2016) or aimed at disentangling the evolutionary origin of complex patterns in the morphology and diversity of coleopterans' genital structures (Rudoy & Ribera, 201a; Rudoy *et al.*, 2016).

An important part of Ignacio's research has been also focused on conservation of freshwater biodiversity. This research has developed different approaches and strategies from the double perspective of setting conservation priorities for species and areas. Indeed, he was a pioneer in identifying Iberian water beetles which could be the target of conservation efforts, firstly revising the status of the species included in the IUCN red list (Ribera, 2000) and, more recently, identifying endemic threatened species (Sánchez-Fernández *et al.*, 2008). He was also actively involved in studies focussed on the assessment of the effectiveness of protected areas in terms of conserving taxonomic (Sánchez-Fernández *et al.*, 2008, 2011) and phylogenetic diversity (Abellán *et al.*, 2013) as well as some specific niche features and their response under future climate scenarios (Sánchez-Fernández *et al.*, 2013).

He supervised 6 PhD (+ 2 on going), and advised a number of postdocs and researchers from anywhere in the world, being one of most demanded mentors in evolution of aquatic insects. He was an exceptional "field worker", spending a lot of time traveling and sampling in all possible water bodies around the world, usually accompanied by PhD students and colleagues. The suggestions of key ques-

iv Millán et al.

tions and how to test them, and his brilliant research advice whenever it was needed were essentials to successfully guide students under his supervision. Ignacio was a true team player, who generously inspired so many researchers around him. Wisdom, humanity and calm were his main personal features. Undoubtedly, aquatic ecologists and evolutionary biologists have lost one of their reference figures. He was the star, which was shining without wishing so, and likely, the most humble genius we ever met. We'll never forget him.

A full list of Ignacio's publications together with the species new for the science described by him and collaborators can be found at: https://www.um.es/ecoaqua/index.php/external-collaborators.

BIBLIOGRAPHY

- ABELLÁN, P., C. J. BENETTI, R. B. ANGUS & I. RIBERA. 2011. A review of Quaternary range shifts in European aquatic Coleoptera. *Global Ecology and Biogeography*, 20: 87-100.
- ABELLÁN, P., A. MILLÁN & I. RIBERA. 2009. Parallel habitat-driven differences in the phylogeographical structure of two independent lineages of Mediterranean saline water beetles. *Molecular Ecology*, 18(18): 3885-3902.
- ABELLÁN, P. & I. RIBERA. 2011. Geographic location and phylogeny are the main determinants of the size of the geographical range in aquatic beetles. *BMC Evolutionary Biology*, 11(1): 344.
- ABELLÁN, P. & I. RIBERA. 2017. Using phylogenies to trace the geographical signal of diversification. *Journal of Biogeography*, 44(10): 2236-2246.
- ABELLÁN, P., D. SÁNCHEZ-FERNÁNDEZ, F. PICAZO, A. MILLÁN, J. M. LOBO & I. RIBERA. 2013. Preserving the evolutionary history of freshwater biota in Iberian National Parks. *Biological Conservation*, 162: 116-126.
- ANDÚJAR, C., S. PÉREZ-GONZÁLEZ, P. ARRIBAS, J. P. ZABALLOS, A. P. VOGLER & I. RIBERA. 2017. Speciation below ground: Tempo and mode of diversification in a radiation of endogean ground beetles. *Molecular Ecology*, 26(21): 6053-6070.
- ARRIBAS, P., C. ANDÚJAR, P. ABELLÁN, J. VELASCO, A. MILLÁN & I. RIBERA. 2014. Tempo and mode of the multiple origins of salinity tolerance in a water beetle lineage. *Molecular Ecology*, 23(2): 360-373.
- ARRIBAS, P., J. VELASCO, P. ABELLÁN, D. SÁNCHEZ-FERNÁNDEZ, C. ANDUJAR, P. CALOSI, A. MILLÁN, I. RIBERA & D.T. BILTON. 2012. Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, 39(5): 984-994.
- BEUTEL, R. G., I. RIBERA & O.R. BININDA-EMONDS. 2008. A genus-level supertree of Adephaga (Coleoptera). *Organisms Diversity & Evolution*, 7(4): 255-269.
- BILTON, D. T., I. RIBERA & A. E. Z. SHORT. 2019. Water beetles as models in ecology and evolution. *Annual Review of Entomology*, 64: 359-377.
- CIESLAK, A., J. FRESNEDA & I. RIBERA. 2014. Life-history specialization was not an evolutionary dead-end in Pyrenean cave beetles. *Proceedings of the Royal Society B: Biological Sciences*, 281(1781): 20132978.
- FAILLE, A., A. CASALE, M. BALKE & I. RIBERA. 2013. A molecular phylogeny of Alpine subterranean Trechini (Coleoptera: Carabidae). *BMC Evolutionary Biology*, 13(1): 248.
- FERY, H. & I. RIBERA. 2018. Phylogeny and taxonomic revision of Deronectina Galewski, 1994 (Coleoptera: Dytiscidae: Hydroporinae: Hydroporini). *Zootaxa*, 4474(1): 1-104.
- GARCÍA-VÁZQUEZ, D., D. T. BILTON, R. ALONSO, C. J. BENETTI, J. GARRIDO, L. F. VALLA-DARES & I. RIBERA. 2016. Reconstructing ancient Mediterranean crossroads in *Deronectes* diving beetles. *Journal of Biogeography*, 3(8): 4 1533-1545.
- GARCÍA-VÁZQUEZ, D., D. T. BILTON, G. N. FOSTER & I. RIBERA. 2017. Pleistocene range shifts, refugia and the origin of widespread species in western Palaearctic water beetles. *Molecular*

- Phylogenetics and Evolution, 114:122-136.
- HIDALGO-GALIANA, A., M. MONGE, D. BIRON, G. F. CANALS, I. RIBERA & A. CIESLAK. 2016. Protein expression parallels thermal tolerance and ecologic changes in the diversification of a diving beetle species complex. *Heredity*, 116(1): 114-123.
- HIDALGO-GALIANA, A., D. SÁNCHEZ-FERNÁNDEZ, D. T. BILTON, A. CIESLAK & I. RIBERA. 2014. Thermal niche evolution and geographical range expansion in a species complex of western Mediterranean diving beetles. *BMC Evolutionary Biology*, 14(1): 187.
- HUNT, T., J. BERGSTEN, Z. LEVKANICOVA, A. PAPADOPOULOU, O. S. JOHN, R.WILD, P. M. HAMMOND, D. AHRENS, M. BALKE, M. S. CATERINO, J. GÓMEZ-ZURITA, I. RIBERA, T. G. BARRACLOUGH, M. BOCAKOVA, L. BOCAK & A. P. VOGLER. 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science*, 318(5858): 1913-1916.
- JÄCH, M. A. & M. BALKE. 2008. Global diversity of water beetles (Coleoptera) in freshwater. *Hydrobiologia*, 595(1): 419-442.
- MILLÁN, A., D. SÁNCHEZ-FERNÁNDEZ, P. ABELLÁN, F. PICAZO, J. A. CARBONELL, J. M. LOBO & I. RIBERA. 2014. *Atlas de los coleópteros acuáticos de España peninsular*. Ministerio de Agricultura, Alimentación y Medio Ambiente. Madrid.
- PALLARÉS, S., P. ARRIBAS, D. T. BILTON, A. MILLÁN, J. VELASCO & I. RIBERA. 2017. The chicken or the egg? Adaptation to desiccation and salinity tolerance in a lineage of water beetles. *Molecular Ecology*, 26(20): 5614-5628.
- PALLARÉS S., M. LAI, P. ABELLÁN, I. RIBERA & D. SÁNCHEZ-FERNÁNDEZ. 2019. An interspecific test of Bergmann's rule reveals inconsistent body size patterns across several lineages of water beetles (Coleoptera: Dytiscidae). *Ecological Entomology*, 44: 249–254.
- RIBERA, I. 2000. Biogeography and conservation of Iberian water beetles. *Biological Conservation*, 92(2): 131-150.
- RIBERA, I. 2008. Habitat constraints and the generation of diversity in freshwater macroinvertebrates. In: *Aquatic insects: challenges to populations*, J. Lancaster & R. A. Briers (eds.): 289-311, CAB International, UK.
- RIBERA, I., T. G. BARRACLOUGH & A. P. VOGLER. 2001. The effect of habitat type on speciation rates and range movements in aquatic beetles: inferences from species-level phylogenies. *Molecular Ecology*, 10(3): 721-735.
- RIBERA, I., R. G. BEUTEL, M. BALKE & A. P. VOGLER. 2002. Discovery of Aspidytidae, a new family of aquatic Coleoptera. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1507): 2351-2356.
- RIBERA, I., D. T. BILTON & A. P. VOGLER. 2003a. Mitochondrial DNA phylogeography and population history of *Meladema* diving beetles on the Atlantic Islands and in the Mediterranean basin (Coleoptera, Dytiscidae). *Molecular Ecology*, 12: 153-167.
- RIBERA, I., A. CASTRO & C. HERNANDO. 2010. *Ochthebius (Enicocerus) aguilerai* sp. n. from central Spain, with a molecular phylogeny of the Western Palaearctic species of *Enicocerus* (Coleoptera, Hydraenidae). *Zootaxa*, 2351(1): 1-13.
- RIBERA, I., A. CASTRO, J. A. DÍAZ, J. GARRIDO, A. IZQUIERDO, M. A. JÄCH & L. F. VALLA-DARES. 2011. The geography of speciation in narrow-range endemics of the *'Haenydra'* lineage (Coleoptera, Hydraenidae, *Hydraena*). *Journal of Biogeography*, 38(3): 502-516.
- RIBERA, I. & A. FAILLE. 2010. A new microphthalmic stygobitic *Graptodytes* Seidlitz from Morocco, with a molecular phylogeny of the genus (Coleoptera, Dytiscidae). *Zootaxa*, 2641(1): 1-14.
- RIBERA, I., G.N. FOSTER & A. P. VOGLER. 2003b. Does habitat use explain large scale species richness patterns of aquatic beetles in Europe? *Ecography*, 26: 145–152.
- RIBERA, I., C. HERNANDO & P. AGUILERA. 1998. An annotated checklist of the Iberian water beetles (Coleoptera). *Zapateri*, 8: 43-111.

vi Millán et al.

- RIBERA, I., J. E. HOGAN & A. P. VOGLER. 2002. Phylogeny of hydradephagan water beetles inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution*, 23(1), 43-62.
- RIBERA, I., A. N. NILSSON & A. P. VOGLER. 2004. Phylogeny and historical biogeography of Agabinae diving beetles (Coleoptera) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 30(3): 545-562.
- RIBERA, I. & A. P. VOGLER. 2000. Habitat type as a determinant of species range sizes: the example of lotic–lentic differences in aquatic Coleoptera. *Biological Journal of the Linnean Society*, 71(1): 33-52.
- RIBERA, I. & A. P. VOGLER. 2004. Speciation of Iberian diving beetles in Pleistocene refugia (Coleoptera, Dytiscidae). *Molecular Ecology*, 13(1): 179-193.
- RIBERA, I., A. P. VOGLER & M. BALKE. 2008. Phylogeny and diversification of diving beetles (Coleoptera: Dytiscidae). *Cladistics*, 24(4): 563-590.
- RUDOY, A., R. G. BEUTEL & I. RIBERA. 2016. Evolution of the male genitalia in the genus *Limne-bius* Leach, 1815 (Coleoptera, Hydraenidae). *Zoological Journal of the Linnean Society*, 178(1): 97-127.
- RUDOY, A. & I. RIBERA. 2016. The macroevolution of size and complexity in insect male genitalia. *PeerJ*, 4: e1882.
- SÁNCHEZ-FERNÁNDEZ, D., P. ABELLÁN, F. PICAZO, A. MILLÁN, I. RIBERA, & J. M. LOBO. 2013. Do protected areas represent species' optimal climatic conditions? *Diversity and Distributions*, 19: 1407-1417.
- SÁNCHEZ-FERNÁNDEZ, D., D. T. BILTON, P. ABELLÁN, I. RIBERA, J. VELASCO & A. MILLÁN. 2008. Are the endemic water beetles of the Iberian Peninsula and the Balearic Islands effectively protected? *Biological Conservation*, 141(6): 1612-1627.
- SÁNCHEZ-FERNÁNDEZ, D., J. M. LOBO, A. MILLÁN & I. RIBERA. 2012. Habitat type mediates equilibrium with climatic conditions in the distribution of Iberian diving beetles. *Global Ecology and Biogeography*, 21(10): 988-997.
- TRIZZINO, M., P. A. AUDISIO, G. ANTONINI, E. MANCINI & I. RIBERA. 2011. Molecular phylogeny and diversification of the "*Haenydra*" lineage (Hydraenidae, genus *Hydraena*), a north-Mediterranean endemic-rich group of rheophilic Coleoptera. *Molecular Phylogenetics and Evolution*, 61(3): 772-783.
- VILLASTRIGO, A., H. FERY, M. MANUEL, A. MILLAN & I. RIBERA. 2018. Evolution of salinity tolerance in the diving beetle tribe Hygrotini (Coleoptera, Dytiscidae). *Zoologica Scripta*, 47(1): 63-71.
- VILLASTRIGO, A., M. A. JÄCH, A. CARDOSO, L. F. VALLADARES & I. RIBERA. 2019. A molecular phylogeny of the tribe Ochthebiini (Coleoptera, Hydraenidae, Ochthebiinae). *Systematic Entomology*, 44(2): 273-288.