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The legacy of Augusto Vigna Taglianti in amphipod taxonomy and biogeography

Abstract: The contribution to groundwater amphipod taxonomy and biogeography given by Augusto Vigna Taglianti is illustrated. Starting from his master thesis presented in Rome on the genus *Niphargus* under the supervision of prof. Sandro Ruffo, his passion for groundwater amphipods led him to publish several papers, describing 3 genera and 19 species new to Science. His hypothesis on the ancient origin of transadriatic distribution of niphargid amphipods were recently confirmed by sophisticated molecular methods and statistical historical biogeography. The paper is a tribute to Vigna Taglianti's memory and emphasizes his deep knowledge of our fauna, demonstrating the importance of his contribution to the development of current research activities on groundwater amphipod diversity.

Riassunto: *L'eredità di Augusto Vigna Taglianti nella tassonomia e biogeografia degli anfipodi.*

Viene illustrato il contributo fornito da Augusto Vigna Taglianti alla tassonomia e biogeografia degli anfipodi delle acque sotterranee. A partire dalla sua tesi presentata a Roma sul genere *Niphargus*, sotto la supervisione del prof. Sandro Ruffo, la sua passione per gli anfipodi sotterranei lo ha stimolato a scrivere numerosi articoli, descrivendo 3 generi e 19 specie nuove per la Scienza. La sua ipotesi sull'antica origine degli anfipodi Niphargidae a distribuzione transadriatica è stata di recente confermata con l'uso di sofisticate tecniche di biologia molecolare e di statistica applicate alla biogeografia storica. Il lavoro costituisce un omaggio alla memoria di Vigna Taglianti che mette in evidenza la sua profonda conoscenza della nostra fauna e dimostra l'importanza del suo contributo per lo sviluppo degli attuali filoni di ricerca sulla diversità degli anfipodi delle acque sotterranee.

Key words: Amphipoda, morphotaxonomy, biogeography, groundwater, transadriatic.

INTRODUCTION

The study of groundwater fauna has attracted the attention of zoologists during the past two centuries. Long considered devoid of life, groundwaters are now increasingly recognized for their unique and surprisingly biodiverse fauna. "Why did some taxa colonize the subterranean waters?" has been the main question since the mid-nineteenth century (Agassiz, 1851; see also Danielopol & Rouch, 1991). Groundwaters have long been considered a special, unfavourable environment, where few, highly specialized species took refuge, prisoners of their habitat (Danielopol, 1992). The answers to Agassiz's (1851) question gave rise to many debates (Stoch, 1995) and are still an object of active research using modern molecular techniques (Perez Moreno *et al.*, 2016).

The obligate groundwater dwelling organisms are named 'stygo-bionts' (from the mythical Styx, a river that forms the boundary between Earth and the Underworld), and their unusual adaptations and appearance has attracted the attention of zoologists and simple naturalists or observers. As pointed out by

Vigna Taglianti (1972a), the first citation of a groundwater, cave-dwelling animal is reported in an old book named "Descrittione di Tutta Italia", literally "Description of whole Italy" (Alberti, 1588) where the author, the friar Leandro Alberti, reported a letter, dated 5 March 1584 and written by Gian Giacomo Trissino from Vicenza, where some... "gambaretti picciolini simili a li gambarelli marini, chi si vendeno in Venetia" (i.e. "tiny shrimps similar to the marine shrimps sold in Venice") were reported for the groundwaters of the "Covale di Costozza" (i.e. the well known limestone quarry - 'covolo' - near Costozza, Berici Hills, Vicenza). Now the species (4 cm long) is known to be an amphipod crustacean, *Niphargus costozzae* (Schellenberg, 1935) (Fig. 1). It is not surprising this was the first subterranean organism that was observed.

Nowadays, it is well known that the groundwater-dwelling fauna is quite rich - see Botosaneanu's (1986) Stygofauna Mundi - and crustaceans represent by far the most diversified stygobitic taxon. Among them Amphipoda contribute about 21% of the overall groundwater species richness

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in European freshwaters with nearly 500 species (Zagmajster *et al.*, 2014); over 425 described species belong to the genus *Niphargus* (Horton *et al.*, 2019), distributed in the Western Palearctic. In Italy, Ruffo & Stoch (2007) reported 11 families, 17 genera and 94 morphospecies, and the genus *Niphargus* makes up for over 90% of all Italian groundwater amphipods.

Most of the taxonomic knowledge of groundwater amphipods of Italy is due to the work of Sandro Ruffo (1915-2010), who pointed out the extraordinary complexity in defining species and their relationships, especially in the rich genus *Niphargus*. For this reason, it is not surprising that Augusto Vigna Taglianti (1943-2019), one of his students (as he liked to call himself for a lifetime) was attracted by the morphology, taxonomy and biogeography of this taxon. Vigna Taglianti, generally remembered for his entomological papers (see Carpaneto *et al.*, 2019 for a complete bibliography), graduated in Natural Sciences in 1966 at the University of Rome 'La Sapienza' discussing a thesis on "Systematics, zoogeography and ecology of the genus *Niphargus* (Crustacea,

Amphipoda)". The passion for groundwater amphipods accompanied Vigna Taglianti for the rest of his career. Since he was young, he was interested in speleology and later in biospeleology, participating to the activities of the speleological societies in Italy, and exploring later the karstic areas of Slovenia, Dalmatia, and Herzegovina (in 1968, defined "a wonderful journey of about a month, through immense caves rich in fauna": Vigna Taglianti, 2011). From the Dinaric Karst he came back with a rich and extraordinary collection of niphargids. The biospeleological research, intensive in the Apennines and in Sardinia, was extended later especially to other Mediterranean countries and the Near East. After his thesis, he published 19 papers dealing with the taxonomy and biogeography of amphipods, in addition to the numerous faunal data present in his biospeleological publications, especially the monumental work of the cave fauna of the Ligurian Alps (Bologna & Vigna Taglianti, 1985).

Given the important contribution to the knowledge of groundwater amphipods of Vigna Taglianti, it is not surprising that his ideas have shaped



Fig. 1. The cover of the volume by Alberti (1588) where the first citation of a groundwater animal is reported, and the habitus of *Niphargus costozzæ* from Berici Hills, Vicenza (photo F. Stoch).

our taxonomic, faunal and biogeographical vision of this interesting taxon, especially in Italy and the Mediterranean areas. Some of the hypothesis conceived by Vigna Taglianti with traditional morpho-taxonomical methods deserve attention, considering they were recently tested using modern molecular techniques (Delić *et al.*, 2019; Stoch *et al.*, 2020). In this paper, which aims to be a tribute to his stimulating ideas, two main topics will be discussed: (i) the taxonomic relationships between morphospecies in the context of Italian fauna and its origin, and (ii) the problem of the existence of transadriatic clades and their biogeographical explanation.

MORPHOTAXONOMY

The thesis of Augusto Vigna Taglianti on niphargid amphipods (1966) began as a simple proposal to study the groundwater fauna of Latium. As Vigna Taglianti (2011) himself wrote, when he went to the Natural History Museum in Verona, he was then an internal student at the Institute of Zoology of the University of Rome, and he was holding a letter of introduction for “the Professor” [Sandro Ruffo] prepared by Emilia Stella, a well-known hydrobiologist specialized in copepods, supervisor of his degree thesis. The subject of the thesis was the groundwater fauna of Latium, but after the meeting with Ruffo the target was transformed into the study of a difficult genus of groundwater amphipods, the genus *Niphargus*, in an attempt to solve some taxonomic and biogeographical problems he soon encountered. Sandro Ruffo helped him to write his first papers, which Ruffo immediately wanted to be published with Augusto as the single author: the collaborative papers came later, when he had achieved a certain autonomy of research on groundwater amphipods (Vigna Taglianti, 2011).

Some years later, in 1969, he compiled an extensive catalogue (unpublished) of the *Niphargus* collection (‘pompously’, as he said, named Ruffo-Vigna *Niphargus* collection: Vigna Taglianti, 2011) entitled [English translation] “List of the material of the genera of the *Niphargus* group existing in the Ruffo - Vigna Taglianti collection in the Civic Museum of Natural History of Verona” (Appendix 1). This catalogue was the basis for the extensive checklist and the distributional database of the Italian amphipods of the genus *Niphargus* (Ruffo & Stoch, 2007).

Successively, he participated to the “1er

Colloque international sur le genre *Niphargus*”, held in Verona in 1969, presenting a communication (Vigna Taglianti, 1972a) entitled [English translation] “Current knowledge on the genus *Niphargus* in Italy”, which was the first attempt to attribute the species known from Italy to the “species groups” following the awesome work by Straškraba (1972). The paper is still a useful overview of the complexity of the *Niphargus* fauna from Italy; unfortunately, the difficulties in establishing species affinities based on variable morphological characters prevented him to create monophyletic groups, albeit some of these are now recognized as important clades. The problems of exhaustively reviewing the taxonomy of the genus in Italy were partly due to the scarcity of material collected and the incompleteness of the knowledge of actual species richness. Most *Niphargus* species have restricted distribution ranges (Trontelj *et al.*, 2009), sometimes known from single or few localities, and caves and other subterranean habitats are difficult to explore. Moreover, the use of morphological characters in *Niphargus* is unsatisfactory and misleading (Fišer *et al.*, 2008): morphocharacters are highly homoplastic (Fišer *et al.*, 2008, 2010), and pedomorphosis is a widespread phenomenon; moreover, differences between species are quite weak, while intraspecific variation sometimes is high or unknown. These problems, already pointed out in the monograph by D’Ancona (1942), are still a problem in niphargid taxonomy. Some results of the study are still valid, some other questionable, but several affinities remain unknown. For example, Vigna Taglianti (1972a) pointed out some affinities (the group *pedemontanus* Ruffo, 1937 - *speziae* Schellenberg, 1936 - *romuleus* Vigna Taglianti, 1968) which in part still holds, being widely distributed along the Apennines, the Tuscan Archipelago, and Latium, albeit the supposed affinities with *Niphargus tatrensis* Wrzesniowski, 1888 and *N. stygius* (Schjødte, 1849) were discarded using molecular techniques (Stoch *et al.*, 2020).

The difficulties of nomenclature allowed successively the splitting and clumping of species in a chaotic way. Karaman (1993), in his volume of “Fauna d’Italia” on freshwater amphipods, clumped together several species described by Vigna Taglianti in a way that he defined “irrational” (Vigna Taglianti, pers. comm., 1994). For example, Karaman considered under the name of *Niphargus stygius*, described from Slovenian caves, all Italian Pre-Alpine and Apenninic species (including *N.*

romuleus described by Vigna Taglianti, 1968), completely upsetting the biogeographical picture assembled with meticulousness by Vigna Taglianti (1972a). A further questionable point was the division of another well-defined species, *N. pasquinii* Vigna Taglianti, 1966 described from karstic springs (Peschiera, San Vittorino) in Latium, attributing part of the specimens of its populations to the Central European *Niphargus puteanus* (Koch, 1836), which is a biogeographical puzzle. More recent papers based both on morphotaxonomy (Stoch, 1998) and on molecular markers (Stoch *et al.*, 2020) challenged these ideas, allowing these authors to raise back to species rank the taxa of the *Niphargus stygius* complex, including those described by Vigna Taglianti (1966b, 1968).

In his papers published during his long career,

Vigna Taglianti did not only deal with the taxonomy of *Niphargus*; a paper is dedicated to the relictual distribution of a surface gammarid amphipod in Alpine and Apenninic lakes (Iannilli *et al.*, 2005), while several papers are important faunal lists of Italian niphargids in central Italy (Vigna Taglianti, 1966a, 1976; Pesce & Vigna Taglianti, 1975; Ruffo & Vigna Taglianti, 1967). In his taxonomic papers he described (Tab. 1) three new genera (*Ilvanella* from Italy: Vigna Taglianti, 1972b; *Gammaropisa* and *Parhadzia* from Anatolia: Ruffo & Vigna Taglianti, 1988; Vigna Taglianti, 1988) and 19 new species (9 Bogidiellidae, 1 Gammaridae, 2 Hadziidae, 6 Niphargidae, and 1 Ingolfiellidae - now considered a member of the order Ingolfiellida: Lowry & Myers, 2017). Eleven stemmed from the Mediterranean countries (Fig. 2), while eight species of

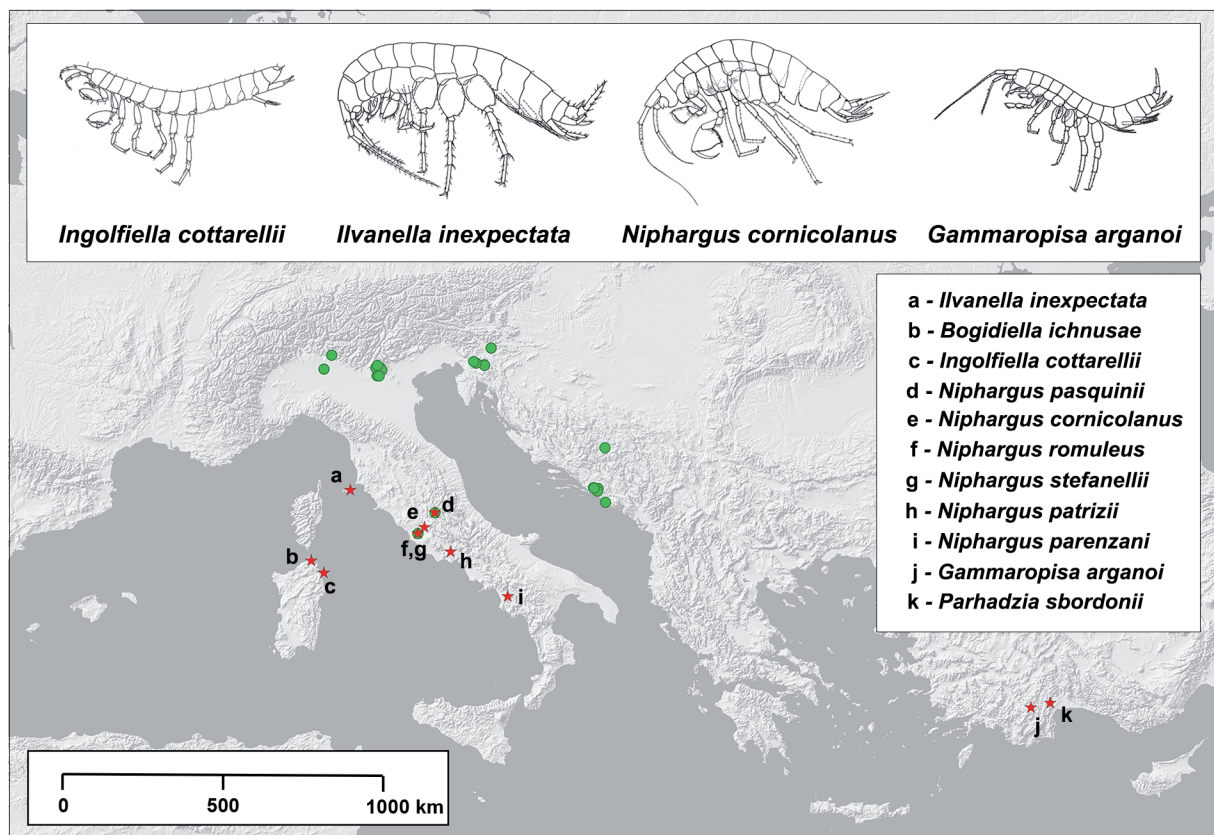


Fig. 2. Map of the sites where Augusto Vigna Taglianti collected amphipods (dots) or described new species (stars). Samples of *Niphargus* were collected in the period 1966-1969 in Italy and in 1968 in Slovenia and Bosnia Hercegovina (only a single further sample was collected in Grotta dei Damati near Verona in 1978). The described species (the habitus of some of them is reported in the upper part of the map) belong to different families (see Tab.1).

Tab. 1. Species of Amphipoda (including the recently established order Ingolfiellida) described by Augusto Vigna Taglianti. For each species the current binomial, the name used in the description, the type locality (country, site and habitat of origin), and the reference are reported. (*) The subspecies described up to now deserve species rank; (**) the family allocation of *Gammaropisa* is still uncertain, and no DNA sequences are available, considering it was never recollected.

Species	Synonym	Country	Type locality	Reference
Order AMPHIPODA				
Family Bogidiellidae				
<i>Arganogidiella arganoi</i>	<i>Bogidiella arganoi</i>	Mexico	Veracruz, Cordoba, Paraje Nuevo (well)	Ruffo & Vigna Taglianti, 1973
<i>Bogidiella ichnusae</i> (*)		Italy	Sardinia, Sassari, River Liscia (interstitial)	Ruffo & Vigna Taglianti, 1975
<i>Bogidiella michaelae</i>		Mexico	Oaxaca, Etla (well)	Ruffo & Vigna Taglianti, 1977
<i>Bogidiella niphargoides</i>		Mexico	Oaxaca, Etla (well)	Ruffo & Vigna Taglianti, 1977
<i>Bogidiella vomeroi</i>		Mexico	Chiapas, Sitalà, Cueva de Chanchaniptic	Ruffo & Vigna Taglianti, 1977
<i>Guagidiella holsingeri</i>	<i>Bogidiella holsingeri</i>	Guatemala	Alta Verapaz, Senahu, Cueva Seamay	Ruffo & Vigna Taglianti, 1973
<i>Guagidiella pasquinii</i>	<i>Bogidiella pasquinii</i>	Guatemala	Huehuetenango, S. Eulalia, Cueva de los Resadores	Ruffo & Vigna Taglianti, 1977
<i>Mexigidiella sbordonii</i>	<i>Bogidiella sbordonii</i>	Mexico	Chiapas, Ocozocautla, Cueva de Cerro Brujo	Ruffo & Vigna Taglianti, 1973
<i>Orchestigidiella orchestipes</i>	<i>Bogidiella orchestipes</i>	Mexico	Chiapas, San Cristobal de las Casas (well)	Ruffo & Vigna Taglianti, 1977
Family Gammaridae				
<i>Ilvanella inexpectata</i>		Italy	Tuscany, Elba Island, Bagnaia (interstitial)	Vigna Taglianti, 1972b
Family Hadziidae				
<i>Gammaropisa arganoi</i> (**)		Turkey	Antalya, Kizilcadağ (well)	Ruffo & Vigna Taglianti, 1988
<i>Parhadzia shordonii</i>		Turkey	Antalya, Doşemealti, Mustan Ini cave	Vigna Taglianti, 1988
Family Niphargidae				
<i>Niphargus cornicolanus</i>		Italy	Latium, Sant' Angelo Romano, Pozzo del Merro	Iannilli & Vigna Taglianti, 2005
<i>Niphargus parenzani</i>	<i>Niphargus orcinus parenzani</i>	Italy	Campania, Alburni Mountains, Cave of Castelvica	Ruffo & Vigna Taglianti, 1968
<i>Niphargus pasquinii</i> (*)	<i>Niphargus elegans pasquinii</i>	Italy	Latium, Cittaducale, Spring of San Vittorino	Vigna Taglianti, 1966b
<i>Niphargus patrizii</i>	<i>Niphargus orcinus patrizii</i>	Italy	Latium, Ausoni Mountains, Cave of Pastena	Ruffo & Vigna Taglianti, 1968
<i>Niphargus romuleus</i>		Italy	Latium, Roma, Foro Romano (wells)	Vigna Taglianti, 1968
<i>Niphargus stefanellii</i>		Italy	Latium, Roma, Foro Romano (wells)	Ruffo & Vigna Taglianti, 1968
Order INGOLFIELLIDA				
Family Ingolfiellidae				
<i>Ingolfiella cottarellii</i>		Italy	Sardinia, Tavolara Island, Grotta del Papa	Ruffo & Vigna Taglianti, 1989

Bogidiellidae were described on material collected by his friends from Mexico and Guatemala (Ruffo & Vigna Taglianti, 1973, 1977).

BIOGEOGRAPHY

Although the biogeographical interest of Vigna Taglianti concentrated on the definition of chorotypes (Vigna Taglianti *et al.*, 1993, 1999), from a point of view of amphipod research the most important studies were dedicated to the problem of the so called ‘transadriatic’ species.

Species distributed on both sides of the Adriatic Sea are well known and quite well documented especially in the entomological literature. Gridelli (1950) published the first revisory work, entitled [English translation] “The problem of species with current transadriatic distribution with particular reference to Coleoptera”. The main explanation of this pattern was found in the level fluctuations of the Adriatic Sea during Pleistocene glaciations. However, Gridelli admitted that some disjunct distribution patterns required a more ancient, Miocenic, sea regression, and due to the ancient name of the ‘Aegean plate’, these more ancient species were called ‘paleo-Aegean’.

However, the discovery of the presence of morphologically similar, obligate subterranean amphipods along the Dinaric Karst as well as along peninsular Italy is quite surprising due to their low dispersal ability. This was noticed by Ruffo & Vigna Taglianti (1967, 1968) for the “*Niphargus* (*Orniphargus*) *orcinus*” complex (*Niphargus orcinus* Joseph, 1869 is a stout species inhabiting caves in the Dinaric Karst in Slovenia and northeastern Italy). Ruffo & Vigna Taglianti (1968) described two subspecies of *N. orcinus* from Italy, namely *N. orcinus patrizii* (from a cave on Ausoni Mts., Latium) and *N. orcinus parenzani* (from Alburni karstic massif, Campania) and considered *N. orcinus* as a ‘paleo-Aegean’ transadriatic species sensu Gridelli (1950). Moreover, they described a third representative of the same group from the groundwaters of Rome, *N. stefanellii*, remarking its affinities with other Dinaric species, especially with *N. hebereri* Schellenberg, 1933. More recently, Iannilli & Vigna Taglianti (2005) described a further member of the same group (reported dubitatively as *N. orcinus parenzani* in the previous paper), *N. cornicolanus*, from the deep sinkhole named Pozzo del Merro (Cornicolani Mts.,

near Rome). It is quite surprising that all these taxa with Dinaric affinities are distributed near the Thyrrhenian coast, and not along the Adriatic coast, where only a further species of the same group (i.e., *N. ictus* Karaman, 1985) was described from Frasassi caves (Marche region) (Fig. 3).

Members of the obsolete sugenus *Orniphargus* S. Karaman, 1950 are specialized dwellers inhabiting the phreatic karstic zones, usually with small distribution ranges both in the Dinaric and in the Apenninic karst, which implies their poor dispersal abilities. How these ecologically specialized species live on both sides of the Adriatic Sea and along the Thyrrhenian coast is an intriguing question that can be framed within at least three testable scenarios: (i) convergence (i.e. Dinaric and Italic species are phylogenetically unrelated and attained their morphological similarity convergently); (ii) vicariance (Italo-Dinaric species share widespread ancestors which broad areal was split by the Adriatic Sea), and (iii) dispersal (the clades originated on only one peninsula and dispersed across the Adriatic basin during marine regressions, from Messinian to later Pleistocene glaciations).

In a recent paper dedicated to the memory of Augusto Vigna Taglianti (Delić *et al.*, 2019), we tested the above-mentioned hypotheses. The taxonomic structure of the species group was revised using unilocus species delimitation methods using several molecular markers, and the timeframe of cladogenetic events was inferred using a multi-locus time-calibrated phylogeny. The geographical origin of the studied clade as well as dispersal and vicariance events were assessed through sophisticated statistical models of historical biogeography. The results of this study may be summarized as follows: (i) the transadriatic species of *Niphargus* form a monophyletic unit which does not include *N. orcinus* (i.e. the species *N. orcinus* sensu Ruffo & Vigna Taglianti, 1968, is paraphyletic); (ii) the reconstructions of ancestral ranges suggest that the clade emerged in the Balkan Peninsula, dispersed three times independently to the Apennine Peninsula and once back to the Balkans; (iii) the dispersal–vicariance events correspond to historical regression–transgression cycles during Miocene.

Already Flot & Stoch (2011) suggested that the large species aggregate *N. hebereri*–*N. ictus*–*N. stefanellii* is composed of several cryptic species.

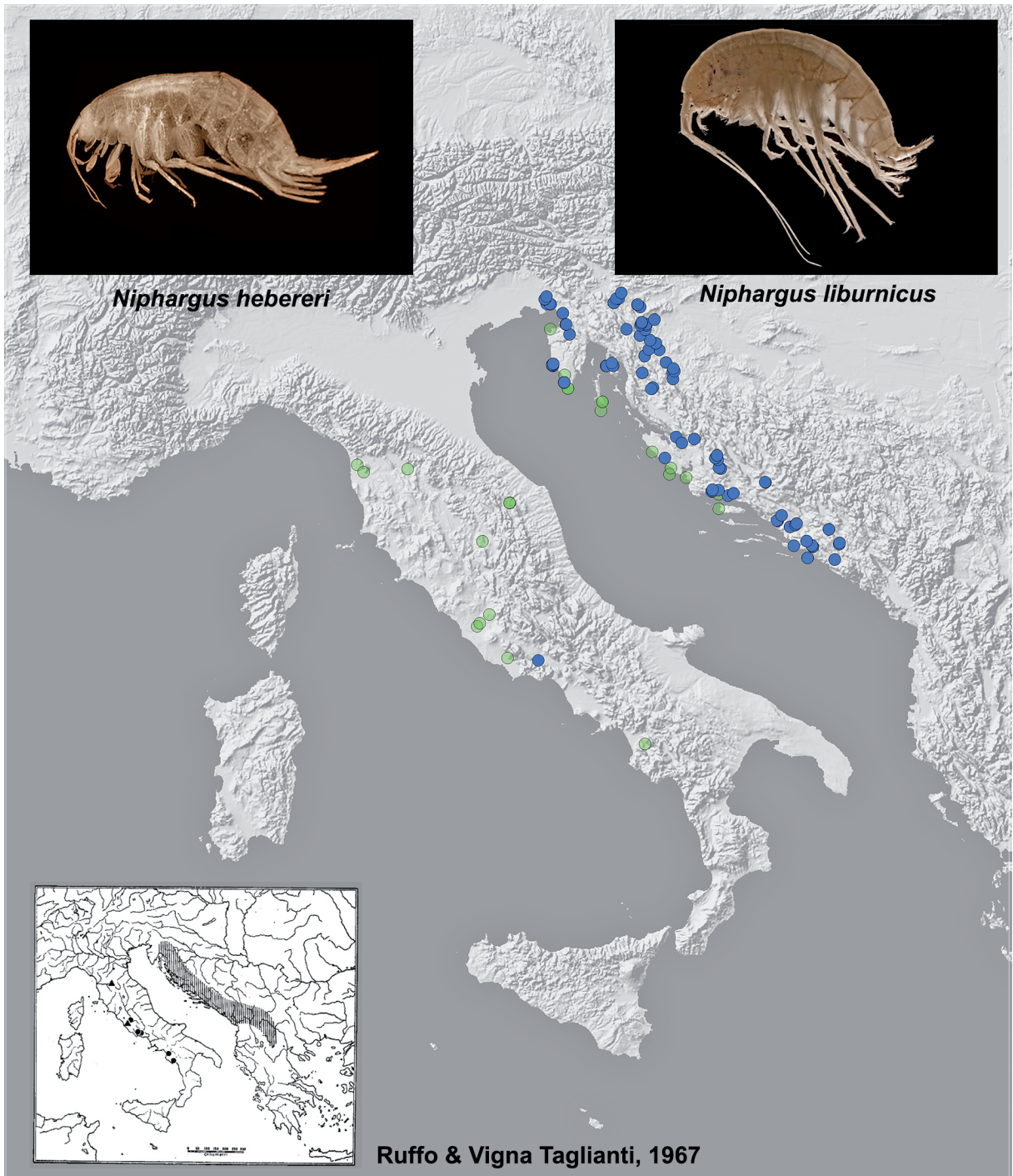


Fig. 3. The transadriatic distribution in two clades of the genus *Niphargus*, the *N. hebereri* clade (green dots) and the *Niphargus steueri* clade (blue dots); the habitus of two representatives of these clades is illustrated (photos F. Stoch). The small map in the lower left corner reports the reconstruction of the species ranges known in 1967, which allowed Ruffo and Vigna Taglianti to develop the theory of the paleo-Aegean Italian endemics.

More recent molecular research revealed that further species in peninsular Italy (*N. cornicolanus* from Latium and *N. parenzani* from Campania) belong to this species aggregate. On the Dinaric side, this clade includes also several species of the *N. steueri* complex: *N. patrizii* is the only Italian species that belongs to the *N. steueri* subclade.

The first two hypotheses, viz. convergence and vicariance, were thus definitively rejected. The age of the common ancestor of the transadriatic clade was dated to the late Oligocene – early Miocene, with a mean estimate of 24 Ma, and the earliest splits took place between 10 and 20 Ma. The ancestor of the *N. hebereri* – *N. ictus* clade split from its Dinaric relatives approximately 14 Ma. Somewhat younger (11 Ma) was the split between the *N. steueri* complex and *N. patrizii*. Later on, during the Messinian Salinity Crisis, the *N. hebereri* clade split from *N. ictus*.

During Pleistocene glaciations, several times the sea level lowered over 100 m, and the Adriatic coast moved southwards favouring faunal exchanges. However, Delić *et al.* (2019) definitively ruled out the recent origin of the Italian transadriatic elements, favouring the hypothesis proposed by Ruffo & Vigna Taglianti (1967). Although Ruffo & Vigna Taglianti (1967) were not able to separate clearly the Italian species from the Balkan ones on a morphological basis, their hypothesis received a strong support: the actual distribution of transadriatic niphargid faunas apparently reflects old biogeographical event, and our endemics correspond to their old-fashioned definition of ‘paleo-Aegean’ species.

CONCLUSIONS

As Augusto Vigna Taglianti wrote in a recent tribute to Sandro Ruffo (Vigna Taglianti, 2011), he was all the life very proud of those periods in which he worked side by side with his mentor in the Verona museum and on “their” collection, starting with the synthesis of the fauna of Italian *Niphargus*, and then studying other groundwater amphipods, but occasionally

coming back to the beloved *Niphargus*. However, he was left with the impression that Ruffo, while pushing him to continue the study of carabid beetles, basically never forgave him for having “betrayed” the amphipods, neglecting their study in favor of the most diversified insects (Vigna Taglianti, 2011).

Most of Vigna Taglianti’s papers are dedicated to carabid beetles or are contributions to the knowledge of Italian Dermaptera and mammals (see the exhaustive list in Carpaneto *et al.*, 2019), nevertheless his minor production with Ruffo on taxonomy and biogeography of Amphipods represents a groundwork for modern research and depicts a scenario which is now being tested using the advanced molecular techniques currently available.

After his thesis, (i) the huge amount of new amphipod species described, (ii) the first attempt of a coarse subdivision of Italian niphargids in species groups, and (iii) the biogeographical hypotheses postulated in his papers make his contribution to amphipodology of paramount importance for current research. In an era where molecular barcoding and ‘big questions’ are becoming the only important fields of study (the so-called era of ‘speleogenomics’: Perez Moreno *et al.*, 2016), and taxonomy is losing its importance as a ‘Science’ (Hopkins & Freckleton, 2002), I cannot forget that all the research I am currently carrying out was made possible by the studies of this old-fashioned naturalist, by his teachings and the discussions during my visits to his laboratory or the collaboration in systematising the chorotypes of the Italian fauna (Stoch & Vigna Taglianti, 2007). The present paper is a tribute to his knowledge of groundwater amphipods, but, especially, to his deep fondness for our fauna and of what we call today, in a much more resounding way, biodiversity.

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