

Potential influence of Mesozoic and Cenozoic tectonics on the evolution of European Hepialidae (Lepidoptera)

JOHN GREHAN^{1,*}, SVYATOSLAV KNYAZEY²

¹ Associate Researcher, Witt Museum, Munich (Germany), email: Calabar.John@gmail.com

² Russian Entomological Society, Irtyshskaya Naberezhnaya, 14, app. 16, Omsk, 644042 (Russia); Altai State University, Lenina, 61, Barnaul, 656049 (Russia), email: konungomsk@yandex.ru

* corresponding author

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ABSTRACT

The distributions of genera and species of Hepialidae in Europe are documented and mapped, along with species distributions extending to eastern Asia. Patterns of species allopatry in *Korscheltellus*, *Pharmacis*, and *Triodia* are consistent with vicariance resulting from late Cretaceous and early Cenozoic tectonics along the Alpine-Mediterranean Mobile Belt. Widespread northern and sympatric distributions are interpreted as the result of range expansion at the end of the Pleistocene. We suggest that the origin of high elevation endemic species of Hepialidae, particularly in the European Alps, is the result of passive tectonic uplift. Pleistocene cooling and glaciation is seen as responsible for extinction of populations in northern Europe, but without discernible impact on divergence. Absence of the northern Eurasian Hepialidae further south is attributed to an original Laurasian ancestral distribution in the Mesozoic. Fossil-calibrated divergence estimates generate minimum clade ages only, and current estimates for some European Hepialidae probably considerably underestimate their phylogenetic age.

INTRODUCTION

Within Lepidoptera, the Coleolepida comprises most of the family and species diversity. The Hepialidae is the largest family within the sister taxon of Coleolepida (Regier et al. 2015). Hepialidae is an old group, but as with most other Lepidoptera, the fossil record is very poor. The oldest probable fossil hepialid or close hepialid relative is *Prohepialus* Piton,

1940 from the Palaeocene of Europe (Jarzembowski 1980). Molecular divergence estimates suggest differentiation of the family by 100 Ma, but some fossil ditrysian (Coleolepida) wing scales from the Triassic-Jurassic boundary (ca. 200 Ma) (van Eldijk et al. 2018) suggest a considerably older origin. Many Hepialidae in the southwest Pacific Hepialidae have distributional species boundaries and disjunctions correlated with

Mesozoic and Cenozoic tectonics (Grehan & Mielke 2018a). The fossil, molecular, and biogeographic evidence support differentiation of the Hepialidae by the middle Mesozoic and divergence of some modern species by the late Mesozoic (Grehan & Mielke 2018a).

The lack of a resolved inter-generic phylogeny and adequate distribution records remain a major impediment to biogeographic analysis of the Hepialidae. The few biogeographic studies include an analysis of the southwest Pacific taxa and a study of comparisons between generic distributions and Cretaceous seas in North America and Africa (Grehan & Mielke 2018a). Biogeographic explanations have also been proposed for individual genera in Asia (Buchsbaum et al. 2018) and South America (Grehan & Mielke 2018b, Grehan & Rawlins 2018, Mielke & Grehan 2017).

The hepialid fauna of Europe is of potential biogeographic interest, as the region lies on the margins of the Alpine-Mediterranean Mobile Belt. This comprises the western part of the Alpine-Himalayan collision zone, which appeared in the late Cretaceous-early Paleogene after closure of the Tethys Ocean (Sharkov & Svalova 2011). The region is adjacent to the Atlantic Ocean, the opening of which influenced the distribution of plants and animals shared between northern Eurasia and North America (Heads 2012, 2014; Grehan 2018). Although there is no comprehensive systematic treatment of the European Hepialidae, we believe there is sufficient taxonomic resolution and distributional information to provide a preliminary assessment of the biogeography.

The European Hepialidae include *Hepialus humuli* Linnaeus, 1758, among the first species classified by Linnaeus, along with five other genera – *Korscheltellus* Börner, 1920, *Pharmacis* Hübner, 1820, *Phymatopus* Wallengren, 1869, *Triodia* Hübner, [1820], and *Zenophassus* Tindale, 1941. Their phylogenetic relationships remain unresolved, but a close

affinity has been suggested between *Korscheltellus* and *Pharmacis* (Kallies & Farino 2018), and between *Zenophassus* and *Hepialus* (Grehan 2012a). A preliminary molecular phylogeny generated for *Pharmacis* and *Korscheltellus* species by Kallies & Farino (2018) generated morphologically ambiguous results (*P. pyrenaicus* (Donzel, 1838) was placed within *Korscheltellus*), and so the proposed relationships among the other species may also be problematic. In this article we combine the current distributional information from published and unpublished sources to analyse the biogeographic structure of the hepialid fauna of Europe and examine some of the tectonic implications for their divergence.

MATERIALS AND METHODS

This study is concerned with the distributional relationship (both phylogenetic and geographic) between different hepialid taxa, based on the principle that the origin of individual taxa is coeval with the origin of their sister taxa. Where sister or closely related taxa are allopatric, the geographic pattern is considered to represent evidence of their local differentiation (vicariance) over different parts of a widespread ancestral range. Where sister taxa are sympatric (whether complete or partial) the overlap represents evidence of subsequent dispersal through range expansion by one or both of the sister taxa (Fig. 1). Since allopatry involves vicariance of a widespread ancestor, we consider those geological and tectonic features that may have been involved in that process of divergence (cf. Craw et al. 1999, Heads 2012).

To characterize and analyze the biogeography of European Hepialidae we applied the following procedures:

1. Map and describe the species distributions with reference to current taxonomy.
2. Identify allopatric and sympatric distributions.

3. Identify the tectonic features or geological formations associated with the distributions of genera or species.
4. Refer to spatial correlations between the distributions and the geology to predict the historical origins of the taxa.

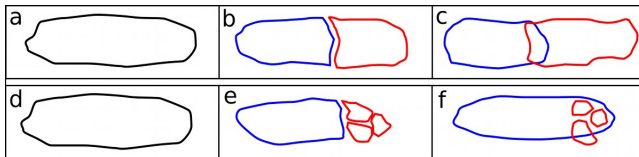


Fig. 1. General conceptual models of allopatry and sympatry: (a-b) widespread ancestor (black outline) diverges by vicariance into two descendants (blue and red outlines); (c) one or both descendants subsequently undergo range expansion resulting in partial sympatry (over time this overlap may increase resulting in complete sympatry); (d-e) widespread ancestor (black outline) diverges by vicariance into four descendants, with one descendant (blue outline) having a much larger range than the other three (red outlines); (f) the widespread descendant undergoes further range expansion and results in partial or complete sympatry with the three localized descendants. Modified from Heads (2012).

Biogeographic-tectonic correlations provide an alternative approach to dating clade divergence, by generating estimates of actual divergence date (precise or broad, depending on the precision of geological dating or the tectonic complexity). This approach has been applied extensively in biogeographic analyses, including some molecular studies. Recognition of a spatial correlation between distributions and tectonics is not a proof of a historical relationship, but it does provide an empirical basis for inferring a historical connection between the two. The fact that many global and local sister taxa distributions show extensive and often very precise tectonic boundaries suggests that former geological and tectonic events have had a profound influence upon the evolution of animal and plant distributions.

These patterns are consistent with a general model of evolution where allopatric distributions are the result of geological and tectonic events that have promoted isolation and divergence over different parts of the ancestral range. Geological and tectonic correlations are inconsistent with the Darwinian model that explains allopatry by chance dispersal from narrow centers of origin where there is no causal relationship when allopatry and geological history (Craw et al. 1999, Heads 2012, 2014, 2017a, 2019).

There are no locality-based distribution maps for any European species over the entirety of their geographic ranges, although there are detailed maps published for some species for particular countries. We use published and unpublished information to characterize the distribution of each species present in Europe. For most species, this information is presented in the form of distribution range maps that are sufficiently accurate for the purposes of our study. In the widespread species, the eastern distribution limits are more generalized than the western ones, but this does not affect our interpretations or conclusions. We refer here to 'Europe' as the region north of the Mediterranean and between the Atlantic and the Urals. Details of some European distributions must be treated with caution due to the lack of verified locality records, particularly for widespread species. The distribution maps are based on published sources that are cited with each distribution map, and unpublished data recorded by the second author.

RESULTS

(a) Taxonomic composition and distributional characteristics

Gazoryctra Hübner, 1820 (Fig. 2)

The monophyly of *Gazoryctra* is supported by the unique morphology of the male genitalia (Grehan 2012b). There is no taxonomic review of the genus other than for species in the Russian Far East (Tshistjakov 1997). DNA

sequence diversity indicates the possible presence of additional species in Asia (Huemer et al. 2018).

Two widespread species of *Gazoryctra* occur in Europe, one or two are endemic to northeastern Asia, and a further nine are endemic to North America. The European *G. uralensis* (Grum-Grshimailo, 1899) (previously known as *G. fuscoargenteus* (Bang-Haas, 1927) (Anikin & Zolotuhin 2017) occurs across northern Scandinavia and Russia, and is widespread over across the tundra zone of northern Eurasia, from Scandinavia to Chukotka and south to the Siberian Mountains and Northern Mongolia (S. Knyazev unpublished data). Its eastern boundary overlaps *G. macilentus* (Eversmann, 1851)

(Tshistjakov 1997, Sinev & Zolotuhin 2008, Lelej 2016), which may be conspecific with *G. ganna* (Hübner, 1808) (there are no genitalic differences) (S. Knyazev unpublished data). The eastern distribution of *G. uralensis* also partially overlaps with *G. chishimana* (Matsumura, 1931) of Japan and Russian Far East. In Europe *G. ganna* occurs at higher elevations in the European Alps and northern Carpathians, and at lower elevations in Scandinavia and northern Russia. It also extends across northern Eurasia but has a wider climatic range than *G. uralensis*; it is distributed in the taiga (forest) zone on the plains (local and rare), in the forest zone in mountains (more common) and sometimes in the alpine zone (S. Knyazev unpublished data).

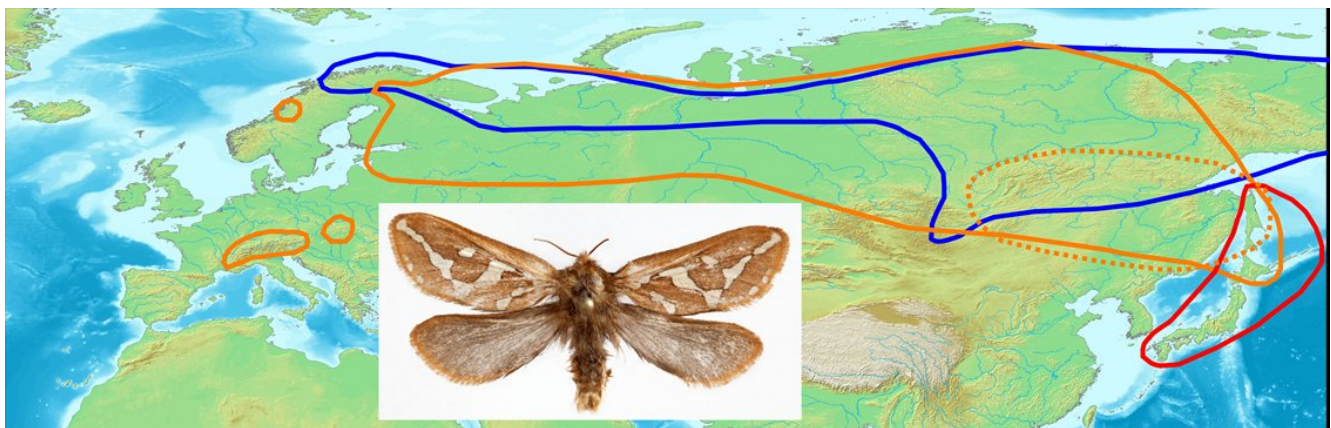


Fig. 2 Distribution of *Gazoryctra* species across Eurasia: *G. ganna* (orange outline), *G. macilentus* (orange dotted line – probably conspecific with *G. ganna*), *G. uralensis* (blue outline), *G. chishimana* (red outline). Distribution information based on de Freina & Witt (1990), Tshistjakov (1997), Sinev & Zolotuhin (2008), and S. Knyazev (unpublished data). Inset: *G. macilentus* (photo by Svyatoslav Knyazev).

Hepialus Fabricius, 1775 (Fig. 3)

The single species, *H. humuli*, is widespread across Europe and eastwards to central Siberia, but is absent from the Iberian Peninsula. A record of *H. humuli* from northwestern China (Heilongjiang Province) (Zhu et al., 2004: p. 160) is incorrect as the illustrated genitalia conform to those of *Thitarodes* Viette, 1961.

Korscheltellus Börner, 1920 (Fig. 4)

The monophyly of the genus is supported by a unique configuration of the male genitalia (Grehan 2012a, b, Kallies & Farino 2018). The widespread species *K. fusconebulosa* (De Geer, 1778) occurs across most of Europe south to northern Spain, northern Italy and the Balkans, and across northern Eurasia, although further taxonomic work on eastern populations is desirable. A record of ‘*Hepialus fusconebulosa*’ from northern China (Sichuan province) by Zhu et al. (2004: p. 150) is probably incorrect as the

genitalia illustrated conform to those of *Thitarodes*. The native distribution of *K. lupulina* (Linnaeus, 1758) extends to

southeastern Spain, western Turkey and east to the Urals, while *K. castillanus* (Oberthür, 1883) is limited to central Spain.

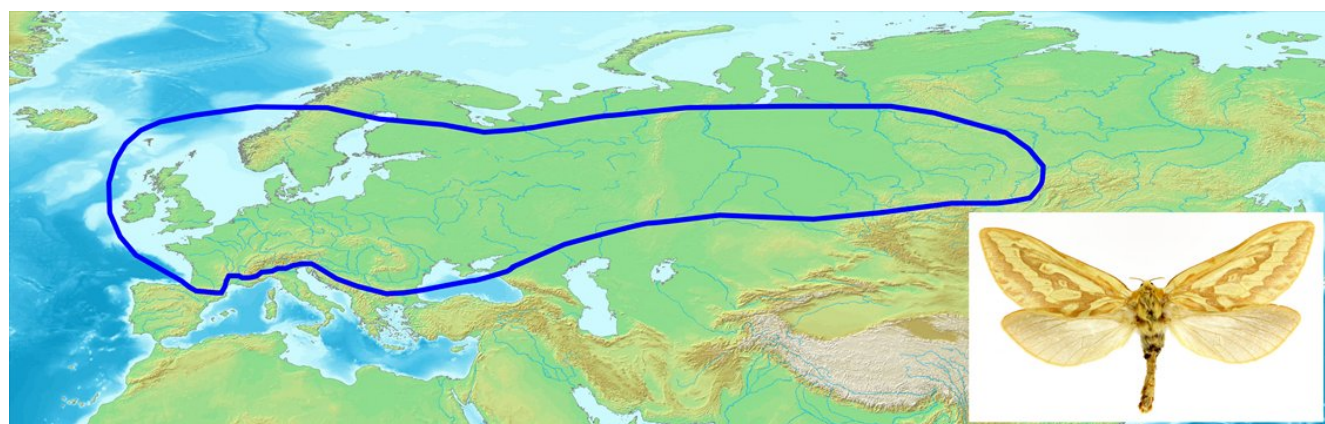


Fig. 3. Distribution of *Hepialus humuli* in Eurasia (blue line). Distribution information based on de Freina & Witt (1990), Garcia et al. (1983), Bertaccini et al. (1997), Sinev & Zolotuhin (2008), Simonsen & Huemer (2014) and S. Knyazev (unpublished data). Inset: *Hepialus humuli* (photo by Svyatoslav Knyazev).

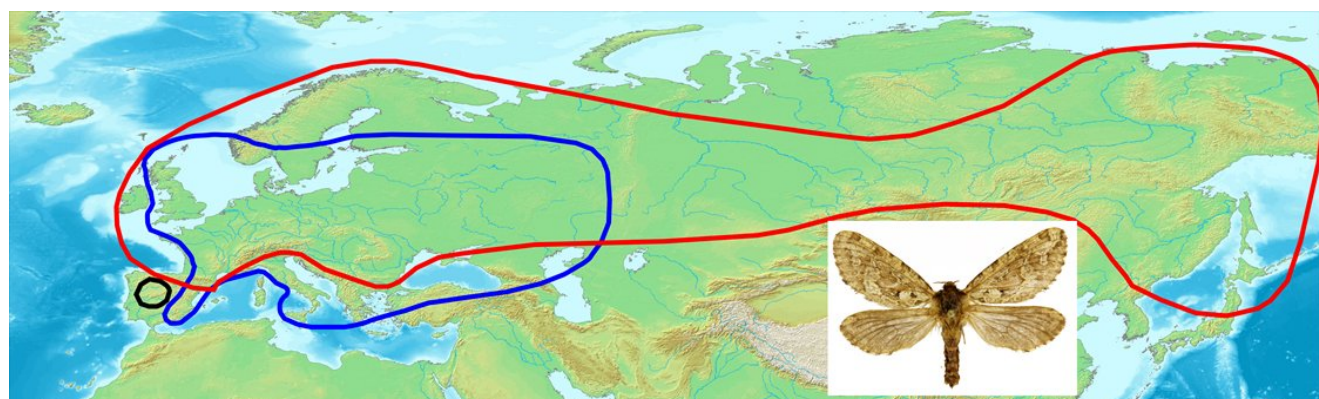


Fig. 4. Distribution of *Korscheltellus* species: *K. castillanus* (black outline), *K. lupulina* (blue outline), *K. fusconebulosa* (red outline). Distribution information based on Agenjo (1942), Garcia et al. (1983), de Freina & Witt (1990), Ylla and Masó (1990), Bertaccini et al. (1997), Sinev & Zolotuhin (2008), Kallies & Farino (2018), and S. Knyazev (unpublished data). Inset: *K. fusconebulosa* (photo by Svyatoslav Knyazev).

Pharmacis Hübner, [1820] (Fig. 5a)

The genus is probably monophyletic, but its status with respect to *Korscheltellus* may need further study (Kallies & Farino 2018). Verified records are known only from Europe. The identity of a Japanese species listed as ‘*Pharmacis fusconebulosa*’ by Hirowatiri et al. (2013) cannot be corroborated until specimens are examined. All species but one are allopatric in the mountains of southern Europe.

Pharmacis carna (Denis & Schiffermüller, 1775) is more widespread in the vicinity of the European Alps and Carpathians, and its distribution overlaps those of *P. anselminae* (Teobaldelli, 1977), *P. bertrandi* (Le Cerf, 1936) and *P. claudiae* Kristal & Hirneisen, 1994 endemic to the eastern European Alps (Fig. 5b). The remaining species are *P. aemilianus* (Constantini, 1911) along the Apennines, *P. pyrenaicus* along the Pyrenees

and *P. cantabricus* Kallies & Farino, 2018 in the Cantabrian Mountains of northern Spain. A record of '*Pharmacis carna*' from northern

China (Sichuan province) by Zhu et al. (2004: p. 161) is probably incorrect as the genitalia illustrated conform to *Thitarodes*.



Fig. 5a. Distribution of *Pharmacis* species: *P. carna* (blue outline), *P. aemelianus* (red outline), *P. cantabricus* (orange outline), *P. pyrenaicus* (dark green outline), *P. bertrandi* (yellow outline), *P. claudiae* (black circle), *P. anselminae* (black square). Distribution information based on Agenjo (1942), Bertaccini et al. (1997), Kallies & Farino (2018) with the eastern range of *P. carna* limited to the European Alps and the Carpathians (S. unpublished data). Inset: *P. claudiae* (Photo by Svyatoslav Knyazev).

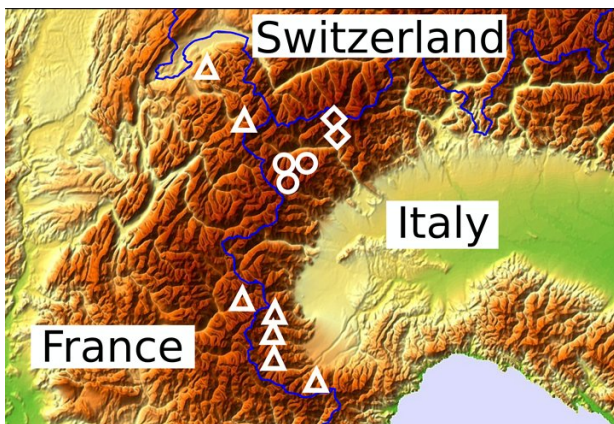


Fig. 5b. Distribution of locally endemic species of *Pharmacis* in the European Alps: *P. claudiae* (diamonds) on south-facing slopes above 2200 m at Valtournenche above Antey-Saint-André, and at 2100 m at Breuil-Cervina (Bertaccini et al. 1997); *P. anselminae* (circles) on north-facing slopes between 1900-2200 m at Val di Vailille, Cal di Vailille, Val di Cogne, Val di Champorcher and 1800 to 2500 m at Conca di Pila (Teobaldelli 1977a, b, Kristal et al. 1994, Bertaccini et al. 1997); *P. bertrandi* (triangles) at d'Abriès, Alta Savòia, Monte Bianco a Chamonix in France (Bertaccini et al. 1997), and Castelmagno, Colle di Fauniera 2400 m, Crissolo, Pain del Re at 2100 m,

Piemonte, Valle Grana, Colle di Fauniera at 2500 m, Valle Varaita (Sampeyre, Becetto, and Mt. Garitta Nuova) at 1900 m (Gianti & Delmastro 2006).

Phymatopus Wallengren, 1869 (Fig. 6)

The monophyly of the genus was supported in a systematic study by Wagner (1985). The single European species, *Phymatopus hecta* (Linnaeus, 1758), is widespread in the continent, although absent from Italy and Spain. The distribution extends across northeastern Asia to the Russian Far East and partially overlaps the range of *E. japonicus* Inoue, 1982 in Japan. [*Phymatopus hectica* (Bang-Haas, 1927) of northeastern Asia shows no genitalic differences from *P. hecta*, and the two could be conspecific (S. Knyazev pers. obs.)]. Three further species are present in northwestern North America, and these comprise the sister group of *P. hecta* (Wagner 1985).



Fig. 6. Distribution of Eurasian *Phymatopus* species: *P. hecta* (blue line) and *P. japonicus* (red line). Distribution data from de Freina & Witt (1990), Tshistjakov (1996), Bertaccini et al. (1997), Sinev & Zolotuhin (2008), Hirowatiri et al. (2013), and S. Knyazev (unpublished data). Inset: *P. hecta* (photo by Svyatoslav Knyazev).

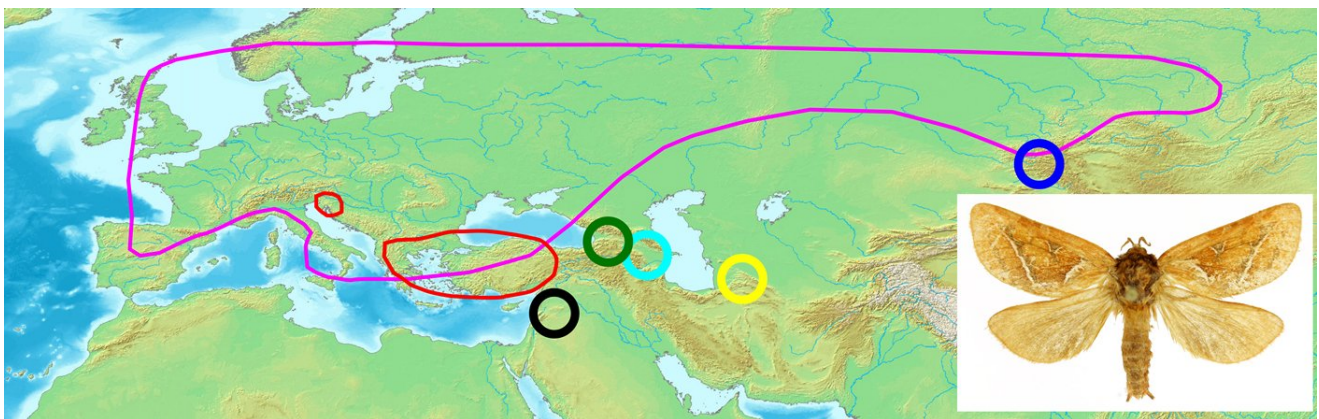


Fig. 7. Distribution of *Triodia* species: *T. sylvina* (crimson outline), *T. adriaticus* (red outline), *T. amasinus* (red outline), *T. mlokossevitschi* (pale blue circle), *T. laetus* (green circle), *T. froitzheimi* (black circle), *T. nubifer* (blue circle), *Triodia* new species (yellow circle). Distribution data from Staudinger (1877), Romanoff (1884), Osthelder et al. (1939), Daniel (1967), de Freina & Witt (1990), Sinev & Zolotuhin (2008), Dubatolov & Knyazev (2011), Dubatolov & Kosterin (2015) and S. Knyazev (unpublished data). Inset: *T. sylvina* (photo by Svyatoslav Knyazev).

Triodia Hübner, [1820] (Fig. 7)

The genus is probably monophyletic, based on the distinct wing pattern and genitalia features of the male. All but one species are confined to western Eurasia. *Triodia sylvina* (Linnaeus, 1761) is widespread across most of Europe and east to Lake Baikal, although it is absent from Ireland and parts of the Iberian Peninsula. In the Balkans, *T. adriaticus* (Osthelder, 1931) is partially sympatric with *T. amasinus* (Herrich-Schäffer, 1851). Two Caucasus species are

from nearby localities in Georgia – *T. laetus* (Staudinger, 1877) in Manglisis (labeled as ‘Armenia’) and *T. mlokossevitschi* (Romanoff, 1884) in Lagodekhi. *Triodia* also extends to the Middle East with *T. froitzheimi* (Daniel, 1967) from Amman, Jordan. Further east, *T. nubifer* (Lederer, 1853) is restricted to the Russian Altai and East Kazakhstan between Ust-Kamenogorsk and Ustbuchtarminsk on the Irtysh River, and there is an undescribed species in Turkmenistan (S. Knyazev unpublished data).



Fig. 8. Distribution of *Zenophassus schamyl* (blue circles). Data compiled from Abdurakhmanov et al. (2007), Christoph (1888), de Freina (1994), Estonian Museum of Natural History, InsectaPro (<http://insecta.pro/gallery/11765>), Lepiforum (<http://www.lepiforum.de/>), Nekrutenko (1982), Siberian Zoological Museum (<http://szmn.eco.nsc.ru/old/Lepidop/Hepial.htm>), Tigran Oganegov (pers. comm.). Inset: *Z. schamyl* (photo by Svyatoslav Knyazev).

Zenophassus Tindale, 1941 (Fig. 8)

Monophyletic by monotypy. The single species, *Z. schamyl* (Christoph, 1888), occurs on the forested slopes and surrounding lowlands of the Greater Caucasus Mountains between the Black sea and the Caspian Sea, and in the eastern Pontic Mountains. The sister group of *Zenophassus* is unknown, but some morphological similarities are shared with the widespread *H. humuli* (Grehan 2012b).

(b) Biogeography

Based on the haplotype variation, the distribution range of *Hepialus humuli* north of the European Alps has been interpreted by Simonsen & Huemer (2014) as the result of range expansion following Pleistocene glaciation. This post-Pleistocene reoccupation

may also apply to the widespread ranges of European *Gazoryctra* (Fig. 2), *Korscheltellus fusconebulosa* and *K. lupulina* (Fig. 4), and *Phymatopus hecta* (Fig. 6). In contrast, the localized *P. castillanus* of central Spain may represent an originally allopatric distribution; in *K. fusconebulosa* and *K. lupulina* the original allopatry has since been obscured by subsequent range expansion.

The genera *Pharmacis* and *Triodia* both comprise largely or completely allopatric species, but each genus has one widespread species that overlaps some of the allopatric species. The two widespread species may be comparable to the widespread species of other genera where range expansion has occurred following the Pleistocene. Allopatry within *Pharmacis* is associated with mountain systems between Italy and Spain, and the tectonic history of these mountains could have

contributed to their speciation by generating geographic isolation and vicariance over a widespread ancestral range. A similar biogeographic mode may be suggested for *Triodia* with an ancestral range between the Balkans and the Middle East where *Pharmacis* is absent, and also extending further east across central Asia to the Altai. The localized distribution of *Zenophassus schamyl* (Christoph, 1888) is also associated with a region of mountain building in the Caucasus and adjacent Pontic Mountains of Turkey, and its differentiation may be the result of uplift there.

(c) Tectonic correlations

Apart from the widespread species, the Hepialidae of Europe are all located within a region of broken topography that falls within the Alpine-Mediterranean Mobile Belt. This is the western part of the Alpine-Himalayan collision zone that appeared in the late Cretaceous-early Paleogene after closure of the Tethys Ocean (Sharkov & Svalova 2011). While the current distribution ranges lies within particular mountain ranges this does not mean that the species necessarily differentiated as a result of the current topography.

Pyrenees-Cantabrians. Tectonic uplift of these areas led to Cretaceous and Eocene geological inversions of early Cretaceous basins during convergence of the African and Asian plates (Canérot 2017). This uplift may be responsible for the differentiation of *Pharmacis pyrenaicus*, which is endemic to the Pyrenees region, and also for the isolation and differentiation of *K. castillanus* in central Spain. The Cantabrian Mountains extend along the Atlantic coast, and although topographically separated from the Pyrenees by the Basque-Cantabrian basin, they are part of the same Cenozoic alpine deformation. Uplift progressed westwards from the Pyrenees to the Cantabrian Mountains where a north-south plate convergence took place and partially closing

the Bay of Biscay to the north (Gallastegui et al. 2016).

European Alps: The Alps consist of parts of the European Plate, a former Jurassic to Lower Cretaceous ocean floor, and part of the African Plate. During the Middle Cretaceous, plate convergence resulted in an Alpine orogenic episode about 90–80 Ma. A second phase of mountain uplift began in the Upper Eocene and Oligocene. Up to the Miocene, the Alps appeared as an undulating planation surface with isolated mountains. This planation ceased with strong uplift during the Miocene/Pliocene (Fitzsimons & Veit 2001)

Apennines: This range has a complex origin, with parts being the remnants of an eastward-moving island arc that separated from eastern Spain and France ~25 Ma and eventually collided with the Adriatic plate (Gueguen et al. 1998, Rosenbaum et al. 2002, Handy et al. 2015). The endemic *P. aemilianus* may have originated on the island arc, which is consistent with similarities in COI gene sequences and morphology shared between *P. aemilianus* and *P. cantabricus* (Kallies & Farino 2018).

Dinarides-Hellenides: The allopatric boundary between *Pharmacis* and *Triodia* (other than the widespread *T. sylvina*) is in the northern Adriatic, where the eastern limit of *Pharmacis* meets the western limit of *Triodia*. This allopatry suggests a vicariance event influencing their respective origins, whether or not they constitute sister taxa. The boundary region also marks a difference in subduction polarity subdue between a south-dipping Alpine-Carpathian subduction zone and a northeast-dipping Dinaric-Hellenic subduction zone. The northeastern subduction direction was initiated ~35 Ma that previously shared the same subduction polarity as Alpine-Carpathian zone (Handy et al. 2015). The region between these two patterns of subduction is marked by a transform fault between them and this tectonic break may have generated a geological impact

affecting patterns of isolation and divergence in the Hepialidae.

Caucasus: The Greater Caucasus Range is located in the south of the Eurasian plate and was uplifted along the Main Caucasian Fault. This is part of a mega fault extending from the Kopetdag Mountains to the Trans-European Suture Zone. The modern alpine altitudes of the Caucasus were formed by collision of the Arabian and East European plates (Sharkov et al. 2015). Collision during the Oligocene–Middle Miocene inverted earlier back arc basins into fold-thrust belts forming the Great and Lesser Caucasus mountains and the Transcaucasian intermontane depression (Adamia et al. 2011).

DISCUSSION

The widespread, northern European distributions such as that of *Hepialus humuli* can be explained by range expansion following the recession of the Pleistocene glaciers (Simonsen & Huemer 2014). Regions with locally endemic species such as *Zenophassus schamyl* in the Caucasus (Gegechkori 2011) and *T. nubifer* in the Altai (Dubatolov & Kosterin 2015) have been identified as local survivors in Pleistocene 'refugia'. This concept is widely used to explain the localized distribution of various taxa in Europe (e.g., Tribsch & Schönswetter 2003, Stehlik 2003, Schönswetter et al. 2005, Simonsen & Huemer 2014). In the sense that such areas maintained patterns of distribution that existed before the Pleistocene, the 'refugia' concept refers to survival of taxa (cf. Heads 2017a) that were already present in those regions (Croizat 1958, 1961). The diverse endemism of hepialid species seen in southern Europe may have also previously characterized parts of northern Europe, but any examples were obliterated by climatic cooling.

Kallies & Farino (2018) attributed the evolution of narrowly endemic *Pharmacis* species to frequent glaciation in the Pleistocene,

or earlier, causing *Pharmacis* populations to "withdraw" into isolated mountain refugia in southern Europe. The low pairwise sequence difference of 2–2.7% in COI between closely related species was interpreted as evidence for this model. Based on an average substitution rate of 1.0–2.3% per million years from other molecular studies, Kallies & Farino (2018) proposed diversification of some species coinciding with early Pleistocene glaciations ~2.58 Ma. Kallies & Farino (2018) noted that the use of molecular techniques to date the age of taxa is controversial, because of possible taxon dependent rate differences. However, the method is also compromised by the widespread practice of representing fossil (and sometimes island age) calibrated divergences as actual or maximal clade ages (Heads 2005). Fossils represent minimum ages because there is no way to know how much older a taxon maybe than its oldest fossil record (Heads 2005). Fossil-calibrated divergence dates have often been portrayed as falsifying earlier origins, but this is a flawed approach. While tectonic predictions for origins well before the oldest fossil are often rejected in molecular studies (such as when setting 'priors' in Bayesian analyses), some molecular estimates predate the oldest fossil by tens of millions of years, and new fossil discoveries continue to reset the stratigraphic age of taxa by a similar scale (Heads 2012, 2014, 2017a, b). This means that the divergence dates proposed by Kallies & Farino (2018) cannot falsify the possibility of earlier origins for *Pharmacis* species.

A tectonic mechanism of differentiation is applicable to the patterns of complete or marginal allopatry in *Pharmacis* and *Triodia*. These are consistent with each genus having a widespread ancestor that differentiated locally into different descendants over the ancestral range, followed by marginal range expansion by *P. carna*, extensive range expansion in *T. sylvina*, and marginal range expansion between *T. adriaticus* and *T. laetus*. The allopatric break in the distributions of *Pharmacis* and *Triodia* (apart from the single widespread species in

Triodia) occurs at the northern end of the Adriatic between *T. adriaticus* (Fig. 6) and *P. carna* (Fig. 4a). This boundary is in the vicinity of a reversal in subduction polarity (the direction of subduction) that occurred at about 35 Ma, and this tectonic disruption may have contributed to divergence between these taxa (as part of a larger clade if they are not sister taxa).

The distributions of *Zenopassus*, *P. cantabricus* and *P. pyrenaicus* are restricted to localized to sectors of geological uplift, but this has taken place over extended periods of time and there are no particular tectonic correlations to suggest a more precise divergence date for these species. The proposed sister species

relationship of *P. cantabricus* in the Cantabrians with *P. aemelianus* in the Apennines (rather than the adjacent *P. pyrenaicus* of the Pyrenees) might be the result of tectonic displacement of the Apennine-Cantabrian arc beginning 30-25 Ma that eventually collided with Italy (Fig. 9). This timescale considerably predates the molecular divergence estimate (Kallies & Farino 2018), but since that molecular estimate represents a minimum age there is no real conflict. Further phylogenetic studies of the European genera and species will be necessary to identify sister taxa relationships in more detail to help identify the extent of geological correlations with generic and species patterns of allopatry.

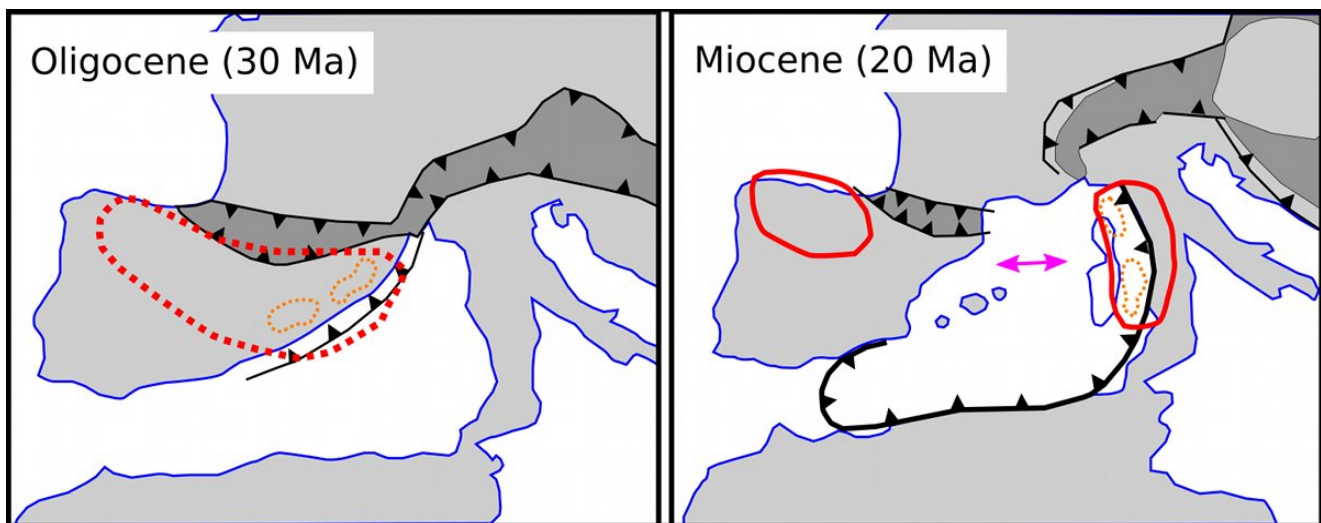


Fig. 9. Conceptual model for displacement and vicariance of common ancestral range (red dotted outline) for *P. cantabricus* (red outline, Spain) and *P. anselminae* (red outline, Italy). Cantabrian arc as orange dotted lines. Tectonic model simplified from Rosenbaum et al. (2002).

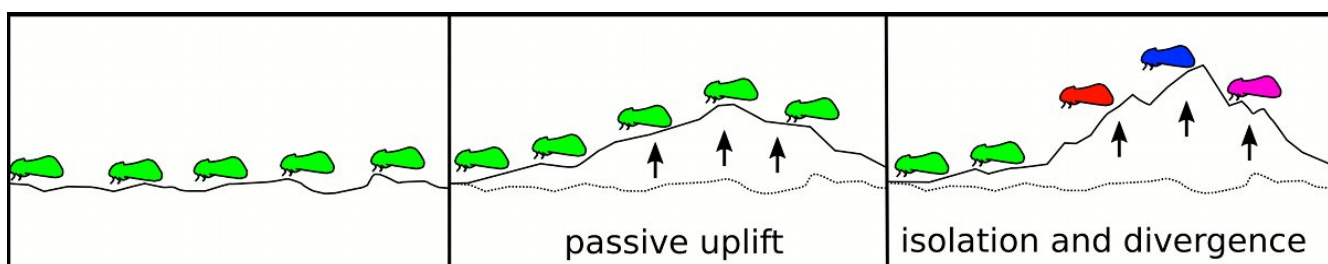


Fig. 10. Conceptual model for origin of high elevation endemic Hepialidae in Europe. Passive uplift of a lowland ancestor (green symbols) disrupts a formerly continuous population and results in vicariance and differentiation (red, blue, crimson symbols).

The high elevation endemics can be interpreted as the result of passive tectonic uplift, a process in which lowland ancestors are raised to higher elevations (Heads 2019). If an uplifted population lacks the biological requirements needed to survive under the new ecological conditions it will be extirpated, and the ancestral range will continue to have a lowland distribution up to the limiting conditions of elevation. This is illustrated by *Aenetus virescens* (Doubleday, 1843), which in some New Zealand localities is absent above 600 m, while some of its host plants range to higher elevations (Grehan 1988). Those ancestral species that have a broad ecological or climatic tolerance may end up being distributed continuously from sea level to the alpine zone, as seen in various species of Hepialidae (Grehan & Mielke 2018a). If population continuity is disrupted, the high elevation populations may become isolated and differentiate into new taxa. This process would explain the origin of the high elevation species in the European Alps, the Pyrenees and possibly in northern Spain (Fig. 10). Passive uplift provides a general mechanism for vicariance in animal and plant life in general, and it is widely documented for many parts of the world, although it is often overlooked in biogeographic and ecological studies (Heads 2019).

The distributions of *Korscheltellus*, *Phymatopus*, *Gazoryctra* species include the Russian Far East and Japan, and perhaps northern China (as suggested by a record of '*Hepialus sylvina*' from Sichuan with male genitalia similar to those of European genera

Zhu et al. 2004, p. 170-171). The southern geographic limit of the 'European' genera is consistent with their differentiation north of the Alpine-Himalayan collision zone and its former western Pacific extension as part of an ancestral 'Laurasian' biota. Much of eastern Asia consists of accreted Gondwanan plates (Heads 2012), and European genera have remained largely to the north of the suture zone and only marginally overlapping genera in eastern and southern Asia (cf. Grehan 2011). This Laurasian ancestry would explain the distributions of *Gazoryctra*, *Korscheltellus* and *Phymatopus* in North America, and their absence in Central and South America. Vicariance at the Atlantic basin is consistent with the European *K. fusconebulosa* being the sister species of the North American *K. gracilis* (Grote, [1865]) (Grehan 2012a), and *Phymatopus hecta* being sister to a North American group through Atlantic vicariance in the Mesozoic or early Cenozoic.

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AUTHOR CONTRIBUTIONS

J.R. Grehan provided biogeographic interpretations. S. Knyazev verified and supplemented distributional information.

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