

## MALE GENITALIA VARIABILITY IN *CRANIOPHORA LIGUSTRI* (LEPIDOPTERA: NOCTUIDAE: ACRONICTINAE)

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*Craniophora ligustri* is the most widely distributed species within the genus *Craniophora*. We used geometric morphometry to assess the shape variation of male valvae in the Western Palaearctic and Russian Far East populations of *C. ligustri* including the subspecies *C. l. carbolucana* and *C. l. hyrcanica*. Outlines were transformed using Hangle Fourier method followed by shape analyses using multivariate statistics (CVA, UPGMA). Based on the results the Far Eastern sample is clearly separated from the Western Palaearctic populations. The West Palaearctic samples were split to two demes, a Northern and a Southern one. The probable refugia of the Southern deme may have extended from South Italy, the Balkan Peninsula across the Euxinic coast of Asia Minor to the Talysh and Northern Iran (Hyrcanian part of Elburs Mts), while the refugia of the Northern deme have been supposedly extra-Mediterranean.

Keywords: geographical differentiation, Noctuidae, multivariate statistics.

### INTRODUCTION

Lepidoptera is one of the largest orders of insects with approximately more than 150 thousand species described (NIEUKERKEN *et al.* 2011). The first lepidopterans have already appeared in the Late Triassic and most of the main lineages have evolved during the Upper Cretaceous, following the radiation of the flowering plants (GRIMALDI & ENGEL 2005, WAHLBERG *et al.* 2013). Noctuidae is commonly regarded as one of the largest lepidopteran family (FIBIGER & LAFONTAINE 2005, MITCHELL *et al.* 2006, ZAHIRI *et al.* 2011) with more than 11.000 described taxa (NIEUKERKEN *et al.* 2011). Such a high number is resulted from the immense radiation of higher Ditrysiid clades as a consequence of the diversification of the vegetation mostly in the Upper Tertiary (GRIMALDI & ENGEL 2005, WAHLBERG *et al.* 2013). Acronictinae, one of the phylogenetically younger subfamilies, belongs to 'trifid noctuids' (FIBIGER & LAFONTAINE 2005).

This subfamily can be divided into two main branches according to the external morphology and genital characters (FIBIGER *et al.* 2009). The first clade includes the genus *Acronicta* Ochsenheimer, 1816 and related taxa (e.g. *Moma*, *Oxycesta*, *Simyra*) with approximately more than 200 described species. In this clade, an additional subclade can be distinguished, the genus *Cranio-nycta* de Lattin, 1949 which shows intermediate traits between *Acronicta* and *Craniophora* (DE LATTIN 1949, INOUE & SUGI 1958, KONONENKO *et al.* 1998). The other clade includes the genus *Craniophora* Snellen, 1867 with less than 30 described species (HAMPSON 1909, KOZHANTSHIKOV 1950, HOLLOWAY 1989, POOLE 1989, HAN & KONONENKO 2010). The identification of a *Craniophora* species is difficult, especially in the main species-groups (*fasciata*-, *harmandi*- and *pontica*-group) due to the high similarity of external characters (KISS & GYULAI 2013). The species of this genus mainly occur in the Eastern Palaearctic, Indo-Malaysian and Australian Regions, with only a few species known from the Afrotropical Region (POOLE 1989, FIBIGER *et al.* 2009).

The type species of the genus, *Craniophora ligustri* ([Denis & Schiffermüller], 1775) is a polytypic, European-East Asiatic species with disjunct range. It occurs across Europe except for Iceland, Malta, northern Fennoscandia and the eastern part of European Russia (eastward from the Saint Petersburg–Kazan–Volograd line, KOZHANTSHIKOV 1950, MATOV pers. comm.). Outside Europe, the species is found in Turkey, Israel, Caucasus and Transcaucasia, North Iran, Turkmenistan, Russian Far East, Central and Eastern China, Korea, and Japan (DRAUDT 1937, 1950, KOZHANTSHIKOV 1950, EBERT & HACKER 2002, KONONENKO 2005, KRAVCHENKO *et al.* 2006, FIBIGER *et al.* 2009). Larvae feed on the leaves of various species of Oleaceae, mainly *Fraxinus*, *Ligustrum*, *Syringa*, but – according to some references – occasionally also on some Aceraceae, Betulaceae, Corylaceae, Elaeagnaceae and Viburnaceae (FIBIGER *et al.* 2009, KONONENKO 2010).

The descriptions of the three subspecies from the Western Palaearctic are based on wing patterns and colouration. The nominotypical subspecies *C. l. ligustri* is described from Austria, Vienna region. Since the type specimen has been destroyed (POOLE 1989), reference can only be provided for the specimens of the NHMW from this region (figured e.g. in LÖDL *et al.* 2012, pp. 26–27). *C. l. carbolucana* Hartig, 1968 (from South Italy, Mt. Vulture), according to the original description, mostly differs from the nominotypical subspecies by its constantly deep blackish colouration of the forewings with finely whitish defined orbicular and only externally lighter marked reniform maculae, with dark fuscous hindwings and underside of wings. The *C. l. hyrcanica* Hacker & Ebert, 2002 (from North Iran, Mt. Elburs) is characterised by its average smaller size, from greyish to dark greyish ground colour with some ochreous shading and less contrasting colouration of the medial field of forewings.

However, these external differences should not be overestimated since it is known that external morphology, especially wing colouration and body size could be influenced by environmental factors (SHAPIRO 1974, CESARONI *et al.* 1994, ROSKAM & BRAKEFIELD 1999, DAPPORTO 2008, TÓTH & VARGA 2011, SANZANA *et al.* 2013, MEGA 2014).

Generally, the genital characters are known more stable and informative in taxonomic aspect than the wing patterns (SHAPIRO & PORTER 1989, MUTANEN 2005, DAPPORTO 2008, TÓTH & VARGA 2010, 2011). During the past half of the century, morphometrics has become a widely used method in taxonomy, with a special respect to geometric morphometrics (ROHLF & MARCUS 1993, ADAMS *et al.* 2004, ZELDITCH *et al.* 2004, MUTANEN *et al.* 2007, DAPPORTO 2008, 2010, TÓTH *et al.* 2014). Geometric morphometrics proved to be suitable to uncover and quantify small intra- or interspecific differences (e.g. GARNIER *et al.* 2005, DAPPORTO 2008, TÓTH & VARGA 2011).

Unfortunately, the variability of the genitalia of *C. ligustri* is poorly known. Although the description of the genitalia of *C. ligustri* is detailed by FIBIGER *et al.* (2009), however, the figured vesica and valvae do not belong to the same specimen. The vesica belongs to the type specimen of *C. ligustri gigantea* Draudt, 1937. HARTIG (1968) described *C. l. carbolucana* based on wing pattern without considering genitalia characters. EBERT and HACKER (2002) also described *C. l. hyrcanica* based on wing pattern elements. However, they have figured the genitalia of the type specimen. To our knowledge, detailed analysis on the genitalia of *C. ligustri* has not been carried out yet.

The aim of this paper is to survey the shape variation of the male valvae by geometric morphometric method in the Western Palaearctic and Russian Far East populations of *C. ligustri* including subspecies *C. l. carbolucana* and *C. l. hyrcanica*, to reveal the possible geographical pattern. We also give some biogeographical interpretation of our findings.

## MATERIAL AND METHODS

In this survey, 206 male specimens of *C. ligustri* were examined to reveal the possible geographical differences among the Western Palaearctic populations.

Specimens, based on the collecting sites, were classified as follows: South England (Eng, N = 14), Denmark (Den, N = 15), Finland (Fin, N = 15), North Alps (AlpN, N = 14), South Alps (AlpS, N = 15), Spain (Spa, N = 13), South Italy (Italy, N = 16), Croatia (Cro, N = 16), Bulgaria (Bulg, N = 20), Hungary (Hun, N = 14), Ukraine (Ukr, N = 13), Caucasus (Cauc, N = 14), North Iran (Iran, N = 14), Russian Far East (RussE, N = 13). To estimate the level of inter-specific variability of the valvae we used *Craniophora pontica* (pont, N = 14) as outgroup.

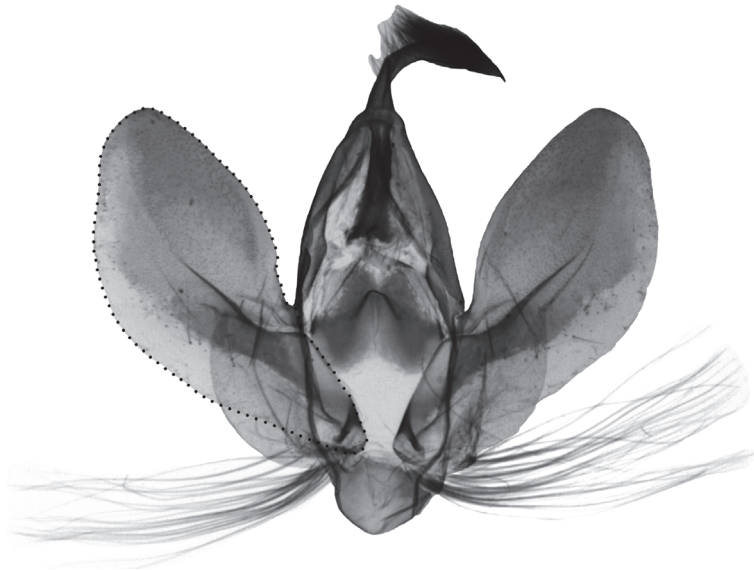
A representative sample of the South Italian and North Iranian populations was collected from the type localities and nearby territories of the subspecies *carbolucana* and *hyr-*

*canica*. The North Iranian sample included also one of the paratypes of *hyrcanica* from the Talysh Mts.

The examined specimens belong to the following collections: Hungarian Natural History Museum, Budapest, Hungary (HNHM), Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy (MSMG), Museo di Storia Naturale di Milano, Italy (MSNM), Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), Natur-Museum Luzern, Switzerland (NML), Naturhistorisches Museum Wien, Austria (NHMW), Zoological Collection of the University of Debrecen, Hungary (UD, coll. Z. Varga deposited here), Zoological Museum, University of Copenhagen, Denmark (ZMUC), Zoological Museum, University of Oulu, Finland (ZMUO), Zoologische Staatssammlung München, Germany (ZSM), Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK), E. Derzhinskij (Vitebsk, Belarus), P. Gyulai (Miskolc, Hungary), G. Ronkay (Budapest, Hungary), Sz. Szanyi (Velyka Dobron, Ukraine), J. L. Yela (Toledo, Spain) and the private collection of the first author.

Genitals were dissected following mainly the techniques recommended by ROBINSON (1976) with minor modifications adapted to larger noctuid moths. A 15% potassium hydroxide (KOH) solution was used to macerate the full abdomen. Eosin dye was used to stain the weakly sclerotized structures. After dehydrating in 96% ethanol, the genital apparatus was mounted to Euparal. Photos of the slides were taken by an Olympus DP 70 digital microscope camera connected to an Olympus SZX12 zoom stereo microscope.

The outlines of the left valvae (Fig. 1) were digitalised by tpsDig 2.16 (ROHLF 2010). PAST 2.17c (HAMMER *et al.* 2001) software package was used to calculate Hangle Fourier harmonics. Fourier shape analysis use digitalised xy-coordinates from the outline of the given shape to reconstruct the outline using harmonically related trigonometric curves. The produced Fourier coefficients, two per harmonic, describe the size ('amplitude') and



**Fig. 1.** Genital capsule of *Craniophora ligustri* with the 100 semi landmarks (black dots) of left valvae

angular offset relative to the starting position ('phase angle') of each harmonic curve. In this way, and using some appropriate number of harmonics, it is possible to describe even extremely complex shapes (for more detail see: HAINES & CRAMPTON 2000). The first 11 harmonics capture more than 96% of the total integrated power of the shape. Fourier coefficients were analysed by CVA using the MASS package. Wilks'  $\lambda$  was used to measure the discriminatory power of the CVA model with values ranging from 0 (perfect discrimination) to 1 (no discrimination). To test the statistical significance of the visible pattern obtained by CVA plot and UPGMA trees, MANOVA (Multivariate Analysis of Variance) was used. We also interested the classification success of the main groups, thus Jackknife classification was carried out using PAST. In this test one known specimen is sequentially omitted at a time, and assigned using the discriminant function the calculation of which is based on all cases except that particular individual. The number of correct assignments was used to evaluate the predictive power of the discriminant function of CVA.

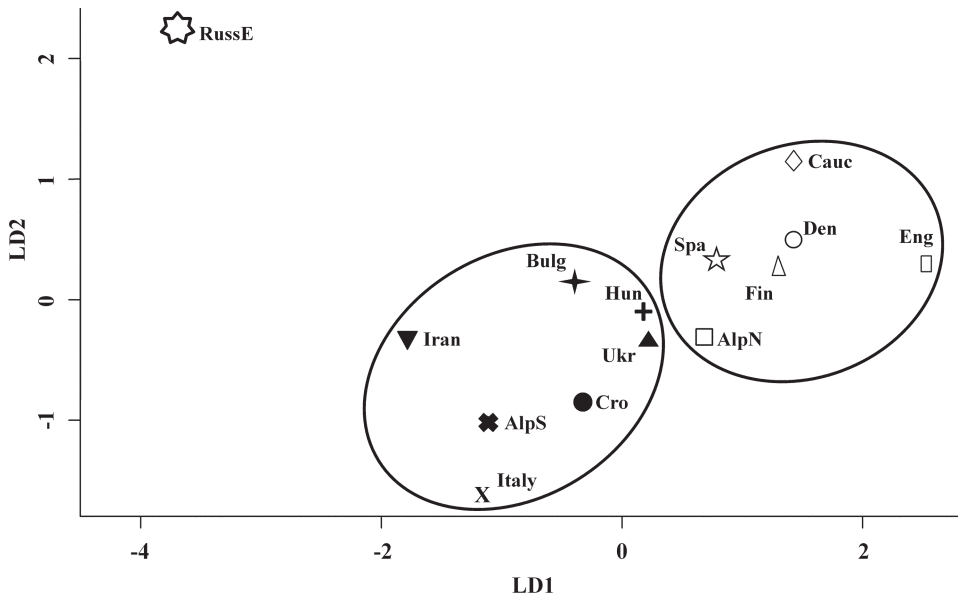
Cluster analysis was applied using the 'pvclust' package of the R 3.0.3 computing environment (R CORE TEAM 2014). *P*-values (%) for Hierarchical Clustering were computed via multiscale bootstrap resampling (SUZUKI & SHIMODAIRA 2011). The UPGMA tree was built using Mahalanobis distances. The 'pvclust' package provides two types of *p*-values: AU (Approximately Unbiased) *p*-value and BP (Bootstrap Probability) value. AU *p*-value, which is computed by multiscale bootstrap resampling, is a better approximation to unbiased *p*-value than BP value computed by normal bootstrap resampling. The number of bootstrap replications was set to 10.000. To visualise the morphological variability of the genitalia in geographical space, the first CV axis was interpolated using Inverse Distance Weighting (IDW) method in Quantum GIS 2.0.1 (QGIS DEVELOPMENT TEAM 2014).

Measurement error (ME) was computed by using one-way ANOVA (BAILEY & BYRNES 1990, GARNIER *et al.* 2005). All individuals were measured twice and the percentage of ME was defined for each shape variable, independently. The ME values were less than 20% in all cases, 10% on average.

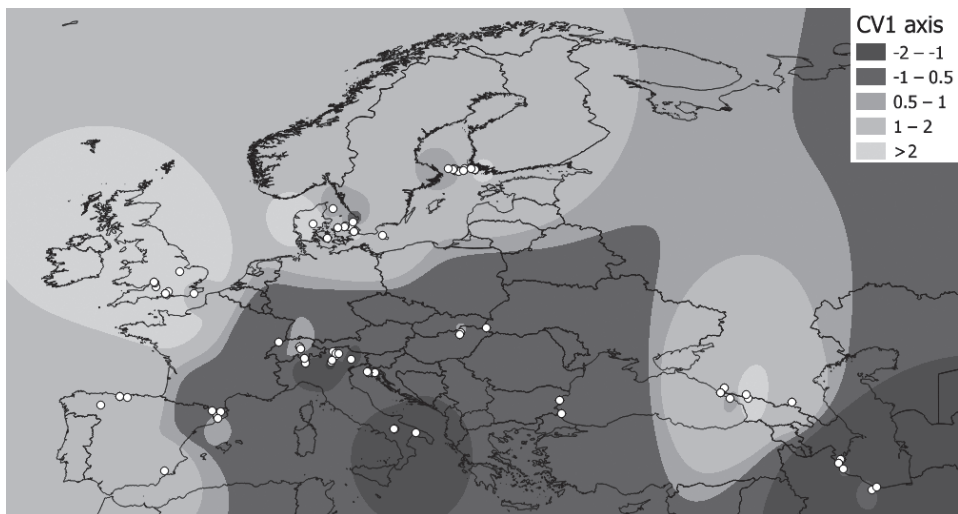
## RESULTS

The first 11 harmonics were used as variables in CVA (canonical variate analysis). In the first step, *C. pontica* was set as outgroup. In this case, the first CV axis explained 60.64% of the variance and the second CV axis 13.69% of the variance (Wilks'  $\lambda = 0.004$ ,  $p < 0.05$ ). When only the groups of *C. ligustri* were tested, the first CV axis explained 40.91 % of the total variance and the second CV axis 15.2 % of the variance (Wilks'  $\lambda = 0.02$ ,  $p < 0.05$ ). The pairwise MANOVA showed that *C. pontica* was significantly different from all other groups. The Russian Far East population was also significantly different from all groups of *C. ligustri* except the North Iranian sample.

The centroids of the *C. ligustri* groups are illustrated on Figure 2. The most separated group is the Russian Far East, as it was expected based on the significance tests. The rest of the *a priori* assemblages were combined into a Northern group and a Southern one. The UPGMA tree (Fig. 3) was constructed on hierarchical clustering via multiscale bootstrap resampling based on Mahalanobis distances. It shows a very similar result to the CVA plot. *C. pontica*



**Fig. 2.** Scatter plot of the group centroids. The filled symbols mark the Southern group, the empty symbols mark the Northern group. Further explanation of the legends, see 'Material and methods'



**Fig. 4.** Inverse distance weighting (IDW) interpolation of the first CV axis. The CV1 axis can explain 40.91 % of the total variance between groups. Two main group are visible on the map: Northern group (brighter grey) and Southern group (darker grey). White dots indicate the collecting sites of the examined specimens



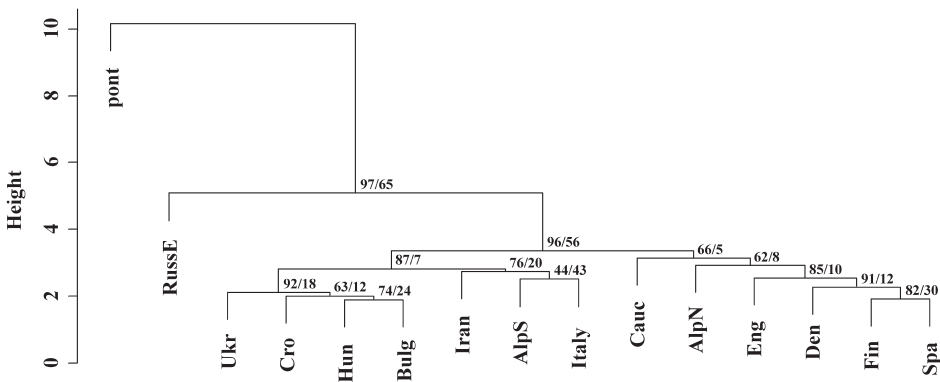
**Table 1.** Results of Jackknife grouping. The groups based on the suggestion of centroids and UPGMA tree. Original groups along rows, CVA groups along columns.

	Southern group	Northern group	Russian Far East	Specimens
Southern group	81.7%	16.5%	1.8%	109
Northern group	13.1%	86.9%	0	84
Russian Far East	7.7%	0	92.3%	13
Specimens	101	91	14	206

is clearly separated from *C. ligustri* and the sample from the Russian Far East is also separated from the remaining groups. The Northern deme of *C. ligustri* includes the English, Danish, Finnish, North Alpine, Spanish and Caucasian samples, while the Southern deme contains the South Alpine, South Italian, Croatian, Bulgarian, Hungarian, Ukrainian and North Iranian samples.

The CVA plot and the UPGMA tree support the three main branches (i.e., the Russian, the Northern and the Southern ones). These groups were set for Jackknife groupings (Table 1). The 84.5% of the specimens were well classified. 13.1% of the specimens of the Northern deme and 16.5% of the specimens of the Southern deme were overlapping. Only one specimen from the Russian Far East group was misclassified (7.7%) to the Southern deme and only two specimens from the Southern deme (1.8%) to the Russian Far East group are misidentified.

To visualise the morphological variability of the genitalia in geographic space, the first CV axis was interpolated using Inverse Distance Weighting (IDW) method (Fig. 4). The result of the interpolation also suggests that the Western Palaearctic populations of *C. ligustri* are forming two main clades.



**Fig. 3.** UPGMA tree based on Mahalanobis distances with AU/BP *p*-value (%). Further explanation of the legends see 'Material and methods'

## DISCUSSION

Our findings show that geometric morphometrics based on the outline of valvae proved to be suitable to separate *Craniophora pontica* from *C. ligustri*, and also distinguished some different geographical population groups in *C. ligustri*. However, these differences are rather small due to the simplified shape of the valvae. The value of the Wilks'  $\lambda$  is larger by one order of magnitude than for *C. pontica*, indicating that this is a clearly separated species. Within *C. ligustri*, only populations of the Russian Far East could have been separated from the Western Palaearctic population groups (Fig. 1 & Table 1). This difference seems to coincide with their disjunct distribution. There are numerous comparable examples in which temperate nemoral species with disjunct distributions show subspecific differentiation (e.g. *Stauropus fagi fagi* – *S. fagi persimilis*, *Apamea aquila aquila* – *A. a. discrepans* – *A. a. substriata*, *Brachionycha nubeculosa nubeculosa* – *B. n. kullbergi* – *B. n. jezoensis*, *Orthosia gothica gothica* – *O. g. jezoensis*) or they are split to vicariant sister-species (e.g. *Spatalia argentina* – *S. doerriesi*, *Harpya milhauseri* – *H. umbrosa*, *Dicranura ulmi* – *D. tsvetajevi*, *Drymonia dodonaea* – *D. dodonides*, *Catocala sponsa* – *C. dula*, *Jodia croceago* – *J. sericea*) (SCHINTLMEISTER 1989, RONKAY *et al.* 2001, SCHINTLMEISTER & FANG 2001, GOATER *et al.* 2003, ZILLI *et al.* 2009, RONKAY *et al.* 2011). Most of the examined species in the Russian Far East have paler greyish hindwings suffused with lighter fuscous or greyish scales. It seems that the Russian Far Eastern populations constitute a distinct subspecies. However, it is necessary to compare with other populations from Japan, Korean Peninsula and China, especially with *C. l. gigantea* Draudt, 1937 (white hindwings with blackish marginal band).

Our results suggest that the Western Palaearctic populations of *C. ligustri* can be subdivided into two (a Northern and a Southern) main population groups (see Results and Figs 2 & 4). The transitional zone between these demes is likely broad and continuous. This pattern is clearly expressed on the Figure 4.

The grouping of samples on the UPGMA tree (Fig. 3) does not correspond exactly to their actual geographic distribution with incongruencies in relation to the IDW map (Fig. 4), see e.g. the Spanish sample. The IDW strongly suggests the duality of the Spanish individuals but the low number of the samples (six-six specimens in each 'subgroup') did not allow their separation in the cluster analysis. Thus, we have to conclude that the IDW provide more information than the UPGMA tree.

The major refugia of temperate nemoral species were in the Mediterranean peninsulas of Iberia, southern Italy and Balkans during the last glaciation (e.g. HEWITT 1996, 1999, 2004, TABERLET *et al.* 1998, SCHMITT 2007). Thus



the most probable, relatively large refugia of the Southern strain may have extended from South Italy and the Balkan Peninsula across the Euxinic coast of Asia Minor to the Talysh and North Iran (Hyrcanian part of Elburs Mts) from which this strain may have populated south-eastern Central Europe and Southeast Europe, east of the Carpathians as well as, Transcaucasia and North Iran. It seems that the population extending from the South Italian refuge could not leave the peninsula because of the barrier effect of the Alps (BILTON *et al.* 1998, TABERLET *et al.* 1998) but obviously populated the southern Alps since the North Italian (South Alps sample) and South Italian (subspecies *carbolucana*) populations were shown to be identical.

According to the original description, *C. l. carbolucana* differs from *C. l. ligustri* externally by its deep blackish ground colour of the forewings (HARTIG 1968) although this form often appears also in northern Italy and Balkans samples, and sometimes even in the samples of the Northern groups. *C. l. carbolucana* (South Alps and South Italian samples) externally cannot be clearly differentiated from the other European specimens, and its genital trait suggests that this taxon is rather a darker morphotype than a subspecies. It should be re-examined, however, based on larger materials from the Provence region (France) and Sicily (Italy).

Probably several extra-Mediterranean refugia also existed in some parts of southern Central Europe, Southern Urals, Caucasus, Western Asia from which mostly Central and Northern Europe was colonized (STEWART & LISTER 2001, SURGET-GROBA *et al.* 2001, BABIK *et al.* 2004, URSENBACHER *et al.* 2006, SCHMITT & VARGA 2009, 2012, STEWART *et al.* 2010, VARGA 2010). As the re-colonization might be multidirectional (e.g. FUMAGALLI *et al.* 1996, BILTON *et al.* 1998, DEFFONTAINE *et al.* 2005, KOTLÍK *et al.* 2006, GRATTON *et al.* 2008) the Northern strain may have populated Southern Fennoscandia, the British Isles and possibly also the northern Atlantic part of Iberia from an eastern extra-Mediterranean refugial area in the very early postglacial period, before the Littorina transgression. It seems to be more probable that the slight geographical differentiation of these populations can be considered as the consequence of an early postglacial splitting due to post-expansive regression than the signal of several extra-Mediterranean refugia, although the latter possibility cannot be excluded. To explain this pattern we hypothesise that *C. ligustri* has populated the British Isles from Iberia, via the 'Lusitanian' way, similarly to *Fraxinus excelsior* (HEUERTZ *et al.* 2004, FRAXIGEN 2005), which is probably its most important food plant there. However, no evidence supports the hypothesis that the expansion of *C. ligustri* followed the same track. This question needs a revision using larger sample sizes, since the Iberian specimens from the North Atlantic coast area and from the Eastern Pyrenees seem to belong to different (Northern vs Southern) strains (Fig. 4).

A few specimens are different from their group average because of the high similarity and simplified shape of the valvae (see the different colour patches on Fig. 4). Unfortunately, our samples are clearly insufficient to decide whether (1) these are individual forms connected to the variation in food plants (distribution of the section *Ornus* vs *Fraxinus*, see WALLANDER 2008, HINSINGER *et al.* 2013), or (2) the expression of some alleles of the common, ancestral gene pool.

In contrast, *C. l. hyrcanica* (North Iranian sample) has an average smaller size, and a more uniform ground colour varying from pure greyish to dark greyish with ochreous scales. Although specimens with similar colouration were found also in the Caucasus and the Russian Far East, the medial shadow reaches the inner margin by an angle of about 45 degrees only in the North Iranian sample. These external traits seem to be unique to the population of Talysh and Hyrcanian part of Elburs Mts.

Although our present knowledge about the West Asiatic and Eastern Palearctic populations (China, Japan, Korean Peninsula) is obviously insufficient to explain completely the distribution of this species, our survey provided, however, useful preliminary information on the matter. A more comprehensive dataset would allow to gain a better understanding of the transitional zone between the two main European demes (Northern and Southern) and to unravel the re-colonization routes of Western Europe (Iberian Peninsula vs Eastern Europe).

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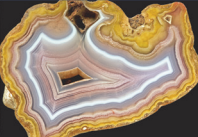
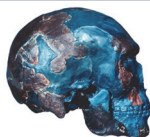


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