



The problem of vicarious and other categories of species of *Euonymus* L. (Celastraceae) from Northern Eurasia: The carpological approach

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ABSTRACT

Among the species of *Euonymus* L. of the flora of Russia and adjacent territories, various scholars identify vicarious, endemic and relict species; their arguments and proofs are often incomplete and controversial. The present paper is dedicated to the critical analysis of all available data used for the substantiation of the status (category) of a given species. The authors employ both original and literature data on morphology, anatomy, chromosome numbers, DNA sequences, geography and ecology of species of *Euonymus*. The complex of morphological and anatomical traits of fruits instrumental for the existence of closely related species in different conditions is analyzed. Special focus is paid to the correlation between the size of geographical range, fruit and seed structure and dispersal type is discussed, as well as other factors (historical, ecological) affecting taxa migration. This determines the resolving capabilities of carpological approach developed by the authors. As a result of our research, we came to the following conclusions: *E. europaeus*, *E. maackii*, *E. sieboldianus* and *E. bungeanus* are geographic vicariants; *E. hamiltonianus* and *E. sieboldianus* are ecological vicariants; *E. velutinus* is not a vicarious species; *E. verrucosus* and *E. pauciflorus* are not vicarious; *E. alatus* and *E. sacrosanctus* are hereby considered ecological vicariants; *E. nanus* and *E. koopmannii* are geographic vicariants; *E. leiophloeus* are apparently not vicarious; *E. latifolius*, *E. sachalinensis* and *E. maximowiczianus* are hereby treated as geographic vicariants. *E. leiophloeus* appears to be a regional endemic; we consider *E. maximowiczianus* and *E. velutinus* to be subendemic species. Additionally, *E. nanus* is considered as relict taxon.

Key words: vicarious species, range, endemism, relicts, morphological and anatomical analysis, carpological approach, adaptation, Northern Eurasia

РЕЗЮМЕ

Савинов И.А., Трусов Н.А., Ембатурова Е.Ю. Проблема викарных и других категорий видов *Euonymus* L. (Celastraceae) из Северной Евразии: карпологический подход. Среди бересклетов флоры России и сопредельных стран разные авторы различают викарные (викарирующие), эндемичные и реликтовые виды, при этом приводимые ими доводы (доказательства) являются неполными и нередко противоречивыми. Статья посвящена критическому анализу всех имеющихся данных, использованных при обосновании статуса (категории) того или иного вида. Авторы оперируют данными (включая оригинальные) из области морфологии и анатомии, числа хромосом, анализа ДНК, сведений о географии и экологии видов. Проанализирован комплекс морфолого-анатомических характеристик плодов, которые способствуют существованию близких видов в различных условиях. Особое внимание уделено обсуждению связи размера ареала видов с особенностями строения их плодов и семян и типом диссеминации (это определяет разрешающие способности развиваемого авторами карпологического подхода), а также других факторов (исторических, экологических), способствующих расселению отдельных таксонов. В результате нашего исследования мы пришли к следующим выводам: *E. europaeus*, *E. maackii*, *E. sieboldianus* и *E. bungeanus* являются географическими викарантами; *E. hamiltonianus* и *E. sieboldianus* – экологические викаранты; *E. velutinus* не является викарным видом; *E. verrucosus* и *E. pauciflorus* не являются викарными видами; *E. alatus* и *E. sacrosanctus* – считаются нами экологическими викарантами; *E. nanus* и *E. koopmannii* – географические викаранты; *E. leiophloeus* не является викарным видом; *E. latifolius*, *E. sachalinensis* и *E. maximowiczianus* рассматриваются как географические викаранты. *E. leiophloeus* является региональным эндемиком; а *E. maximowiczianus* и *E. velutinus* – субэндемичными видами. Кроме того, *E. nanus* является реликтовым таксоном.

Ключевые слова: викарные виды, ареал, эндемизм, реликты, морфолого-анатомический анализ, карпологический подход, адаптации, Северная Евразия

INTRODUCTION

Species typology with respect to ranges is one of the key problems of modern biology. When the ranges are classified, their size and the taxon's distribution type are taken

into account along with aspects of its allo- and sympatry. Historical conditions of the range formation are important for the solution of the problem, as well as morphological and physiological, biological, biochemical and genetic and

caryological features (Timofeeff-Ressovsky et al. 1977:142). Often, the scholars appear to be too keen on analysis of variability and on searching for differences in natural populations. This results in “species splitting”, so they end up treating numerous species as endemic to certain territories, or relic taxa, etc.

Experts have no common opinion in understanding the term “vicarious species”. Seemingly, it was Darwin (1872) in his “On the origin of species” who first used the term “substitute species” in the evolutionary context. He emphasized the difficulty of choosing the criteria on the basis of which we allocate a species to a certain category (local race, subspecies or species); this being said, this concept in his understanding is tightly connected with the divergence of traits in different parts of a spacious range and with the principle of divergence. This logical idea was further developed by Komarov (1940:60), who pointed out splitting of an “old” species into a number of younger ones, associated with new, strictly defined ranges. Expanding this approach, Komarov suggested a method of phylogenetic series (Komarov 1940:62), enabling us to infer the evolution of closely related taxa. And further: “the species’ spatial position, its territory, its range and, of course, the outcome of its history. ... A species is unconceivable outside of space and time” (Komarov 1940:160, 161). According to Tolmachev (1962:32, 1974:48), racial differentiation of the primary parent species results in only one of its races being able to develop in each part of the initial species’ range. Having achieved complete genetic isolation, or separation, these races transform into substitute (vicarious) species. Usually, the term “vicariant” serves to describe closely related species, substituting each other throughout the entire range. In addition, their ranges are different but can connect (geographical vicariant), or, if they interconnect within one range but in different environmental conditions – ecological vicariant (Dudka 1984:40). The treatment of vicarious, or vicariing species, in plant geography, appears to change from time to time. Thus, Timonin & Ozerova (2002) completely renounce the interpretation of geographic and ecological (ecotopic) vicariants, since this kind of treatment does not show their peculiarity but rather the subjective scale of mapping, used by a researcher (large-scale mapping reveals their spatial isolation).

The species of *Euonymus* in northern Eurasia

A good illustration of the above stated problems (the connection between the species’ range type and its geography and ecology, and most importantly, its morphology) are spindle tree (*Euonymus*) species from northern Eurasia. However, this issue is very rarely brought up in botanical literature and therefore, is poorly studied. The genus *Euonymus* L. comprises, according to different estimations, from 130 to 200 species (Blakelock 1951, Leonova 1974, Ma 2001, Savinov & Baikov 2007), among which 15 (16) species are presented in Russian flora (Savinov 2009). Many authors believe there are vicarious, endemic, sub-endemic and relic taxa. To reflect the circle of close affinity between species with the genus, Komarov’s method of phylogenetic series (Prokhanov 1949, Leonova 1974, Savinov & Baikov 2007)

has been used previously, but lately was not supported by contemporary botanists.

Jurkevich (1950) recognizes 4 centres (loci) of distribution of *Euonymus* species within the former USSR borders: European, Caucasian, Central (Middle) Asian and Far Eastern. Related literature provides rather contradictory information regarding the number of species and the interpretation of their ranges within northern Eurasia. Bukshtynov (1957) considers the following species as vicarious: *E. verrucosus* Scop. and *E. pauciflorus* Maxim.; *E. europaeus* L. and *E. maackii* Rupr.; *E. latifolius* (L.) Mill. and *E. sachalinensis* (Fr. Schmidt) Maxim.; *E. leiophloeus* Steven and *E. macropterus* Rupr. Some of the above mentioned statements are more than questionable. In her survey, Leonova (1974), a representative of Komarov’s “botanical school”, avoided using the term “vicarious species”, even though in a number of cases that was exactly what she meant in her interpretation (e.g. for *E. verrucosus* and *E. pauciflorus*; less conspicuously – also in *E. alatus* (Thunb.) Siebold and *E. sacrosanctus* Koidz., *E. nanus* M. Bieb. and *E. koopmannii* Lauche). J.-S. Ma (2001) appreciates a wide interpretation of a number of species with disjunctive ranges, ignoring morphological differences (which he recognizes as intraspecific variability) and reducing them to synonyms (*E. pauciflorus* = *E. verrucosus*; *E. bungeanus* Maxim. = *E. maackii*; *E. sieboldianus* Blume = *E. hamiltonianus* Wall.; *E. velutinus* Fisch. & C.A. Mey. = *E. europaeus*; *E. sacrosanctus* = *E. alatus*; *E. leiophloeus* = *E. latifolius*; *E. planipes* (Koehne) Koehne, *E.* (= *Kalonymus*) *maximoviczianus* Prokh., *E.* × *miniatus* Tolm. = *E. sachalinensis*). Similar treatment of these species is adopted in “Flora of China” (Ma & Funston 2008). Meanwhile, Japanese and Korean authors (Ohwi 1984, Ka 2006) treat almost all these species as independent ones.

Species distribution and historical conditions

There are three large centers of distribution of most representatives of *Euonymus* species of northern Eurasia: European part of Russia together with Crimea and the Caucasus (1), Central (Middle) Asia (2) and Far East (3). This species distribution can be explained by the history of the genus’s range formation; it is tightly connected with temperate-warm and subtropical forests (so-called mesophyllic forest subtropical flora) distribution in the past. Discontinuous, disjunctive ranges of many species were formed resulting from the geographic differentiation of thermophilic “Arctic-tertiary” (Torgay) flora, coming into power in Miocene due to profound aridization of the climate in Central Asia as well as the disjunction of the continuous preboreal broadleaf Eurasian forest belt and subsequent reduction of eastern Asian elements in it early in Pliocene (Popov 1963, Kamelin 1998). Torgay flora’s legacy is still recognized in refugia (Balkan, Carpatian, Black Sea, Talysh, Eastern Asian, etc.). In late Miocene, in the course of further climatic cooling and enhanced climatic differentiation, Torgay flora disappeared across much of the Boreal region, superseded by a new type of boreal flora, which involved cryophilic plants (Akhmetiev 1987). Thus, modern *Euonymus* species of northern Eurasia are successors of so-called Torgay flora.

Paleobotanical data on the Eurasian species of *Euonymus* and environmental conditions

Paleobotanical data on the genus *Euonymus* (survey: see Leonova 1974) do not contribute much to the understanding of its migration from the primary centre and further transformation of certain species' ranges influenced by the climate aridization and glaciation in the Northern Hemisphere. Fossil record is known from the territory of North America, Western Europe, China, Japan (dated Eocene–Miocene, Oligocene). Seemingly, this is the time when *Euonymus* species first appeared within Eurasian continent in one of the periods of climatic warming. In early to middle Miocene within eastern Asia, the last invasion of subtropical plants northward took place, being followed by the largest marine transgression in Neogene (Akhmetiev 1993), along with extensive species formation within many woody plant genera. All of the above facilitated the ingression of *Euonymus* species north- and westward, along sea coasts and large river valleys. Widespread distribution of spindles from refugia, especially in Western Eurasia, started 10–11 thousand years ago, in early Holocene, which is consistent with the latest data on the distribution dynamics of species of the main forest-forming species in Europe (Birks 2019).

One of the most widespread species in Europe, *Euonymus europaeus*, is known for its exceptional trait polymorphism in natural populations; this peculiarity is more pronounced in southern regions, and the greatest diversity of forms in this species can be observed in Crimea and in the Balkan peninsula (Grosset 1975). Actually, Crimean montane gorges, as well as those of the Caucasus, the Balkan peninsula and Central Asia, could serve as glacial refugia for broadleaf forests during the latest ice age (Grosset 1967, 1975). We suppose that the relict character of Colchian-type forests in the Caucasus (Dolukhanov 1980) is also related to the events of this kind, this being said, Caucasian species of *Euonymus* could be preserved in these very conditions. Additionally, one must note, that they often have prostrate evergreen life forms, known for their vegetative mobility, just like other representatives of the Colchian forest understorey.

Life form polymorphism and prostrate shoot formation are important adaptive advantages for survival in extreme climatic conditions (Udra & Khokhryakov 1992). Currently, the concept of Pleistocene macrorefugia in the mountains around the Mediterranean and microrefugia in different areas of Europe (Birks 2019) has been accepted, which, apparently, contributed to the preservation and survival of *Euonymus* species in Europe during LGM. Additional advantages for some deciduous *Euonymus* species in their northward move were the phenomena of polyploidy and hybridization mentioned in the literature record (Bowden 1940, 1945, Schepotiev 1941, Darlington & Wylie 1955, Nath & Clay 1972), although modern research in molecular caryology and genome size can hardly come to consensus regarding the role of these processes in the enlargement of ranges. In recent molecular phylogenetic investigations of some *Euonymus* species, no solid evidence of interspecific hybridization was found (Li et al. 2014:157), however, this fact does not seem to rule it out.

There is a certain correlation between the plant range size and seed dispersal type. All studied species are representatives of the broadleaf forest understorey. They grow mainly in moderately lit conditions, particularly on forest margins; compared to close southern species, north Eurasian ones have later phenological timing of bud burst and foliage expansion, flowering and end of fruiting, persisting even in cultivation; they are associated chiefly with river valleys, sunlit forest margins with fertile soils. If they “hide” under the forest canopy, one can observe a rapid decrease in seed regeneration up to its complete absence; this circumstance prevents genetic traits from being transferred to the offspring.

The correlation between range size and dissemination of diaspores

There is a certain correlation between the range size and dispersal mode, however, the rate and distance of dissemination depend on many factors, including niche breadth, diversity of habitats occupied, colonization dynamics, dispersal ability, involvement of dispersal agents, diaspore mass, life form types, etc. (Oakwood et al. 1993, Lowry & Lester 2006). Bright aril coloration and its fleshy consistency in *Euonymus* species facilitates dispersal by herbivorous birds – warblers, robins, hazel hens and grouses, thrushes (blackbirds), as well as mammals – yellow-necked field mice, bank voles, etc. (Levina 1957, 1987). Synzoochorous (dragging the seeds away for storage) and endozoochorous (thanks to nutritious tissue of fleshy arils) dispersal in spindle trees has been reported. The seeds with arils detach from the capsules, the latter remaining pending on the tree, less often the capsules drop together with the seeds. Autobarochory is particularly noticeable in *E. macropterus* and *E. maximowiczianus* (authors' data).

Performance evaluation for the dispersal of diaspores is important from the standpoint of plant distribution and their range enhance. Out of natural agents, the most long-distance diaspore transfer is done by birds (epiornithochory), but its effect is seen slowly, over centuries. In addition to the diaspore distribution, the range size and type are determined (Levina 1957) by soil, climatic and orographic factors, phytocoenotic conditions (the plant community's resistance to the invasion of new components), the species' ecological plasticity (competitive opportunities). The phenomenon of species migration along river valleys, known for any species, was discovered long ago. Seemingly, it applies to European and Far-Eastern *Euonymus* species, because their association particularly with river valleys, where soil and climatic conditions are more favourable, has long been known. This phenomenon was described, in particular, for *E. verrucosus*, the seed dispersal in which is actively facilitated by herbivorous birds (robin redbreasts, etc.). Expansions of northernmost distribution limits of the species along rivers are believed to be a factor of its range expansion (Jurkevich 1949, 1950). In the meantime, Stratonovich (1955), followed by Leonova (1974), on the contrary, considered those protrusions along rivers to be signs of range reduction (as a typical companion of the oak tree), and its association with river systems was related to certain favourable soil conditions.

Contemporary studies present criteria to assess the effectiveness of various zoochory types (Schupp 1993), both quantitative – the number of visits by a disperser and the number of diaspores dispersed per visit, and qualitative – treatment given a seed in the disperser’s digestive tract and the quality of seeds after this treatment in terms of their germination rate and subsequent seedling survival. Modern data pools and methods to analyze them (including simulation, or mathematical modeling) enable us to consider the role of various factors in the dispersal processes and their effectiveness in different plants (Nathan & Muller-Landau 2000), including analysis of two zoochory types and their effect on spatial genetic structure (Gelmi-Candusso et al. 2017). Thus, present-day investigations of paleoecology and paleobiogeography of plants appear to embrace a wide range of plant traits and environmental factors influencing their distribution, as well as to implement modelling methods, even though one has to admit that the data we operate are of limited representativeness due to so-called “data gaps” (Kattge et al. 2020). Bridging these gaps remains a key challenge for this kind of research and efforts and initiatives should be joined to find a solution.

In relation to seeds, their shape and size were stabilized thanks to specific functions, e.g. seed dispersal type (Berg 1964, cited by the edition of 1993). Anemochory and especially zoochory do not allow the production of larger seeds, so the plants are forced to strictly regulate the seed size. Testing new geographic locations and ecological habitats, appearing due to seed dispersal by birds, is important. Zoochory, promoting the seed size stabilization, is a factor of plant evolution. However, spindle tree seeds cannot be called small (average length 0.5–0.6 cm, width in the middle part 0.3–0.4 cm). Because of it, the seed dispersal rate in *Euonymus* trees and their expansion to the new habitats seems to take place quite slowly.

A great role of various dispersal modes and means together with the distance of diaspore spreading (plus the presence of suitable habitats for their germination and further survival) in the range formation has been emphasized by Tolmachev (1974).

Molecular phylogenetic data

The issues of fruit and seed dispersal and their connection with the range were also raised in molecular phylogenetic analysis (Li et al. 2014), where only 8 species of *Euonymus* from North Eurasia were included (and there are 48 species in the total of the analysis). However, these studied species are very remote from each other phylogenetically and there is no possibility of their pairwise comparison, except *E. europaeus*, *E. maackii* and *E. hamiltonianus*, nested in limit of two sister subclades. In the article, adaptive mechanisms for dispersal of *Euonymus* species have also been considered, especially among representatives with spined and winged capsules. As a result, spined or winged capsules could be dispersed by animals, wind, and/or water. But the authors do not provide a detailed description of the fruit and seed dispersal in the studied species in the nature, probably, due to insufficient direct observations. Additionally, no special comparison of the range sizes of the spe-

cies possessing ordinary capsules without outgrowths with species having winged or spined capsules has ever been carried out by anyone.

Molecular data and current models for species migration

Lately, models based on molecular data and characterizing possible plant migration to the regions further north in the periods of climatic warming, have been created. McLachlan et al. (2005) show that migration rate of two north American trees (*Fagus grandifolia* Ehrh., *Acer rubrum* L.) in the post-glacial period was a lot lower than it was estimated before, in research based on pollen analysis (less than 100 m a year versus 100–1000 m a year). Molecular records also indicate the presence of several refugia, located closer to the glacier and serving as the starting point of the post-glacial plant migration (Pearson 2006). The dispersal rate of certain species apparently depends on distance and successfulness of the dispersal, including rare occasions of long-distance dispersal events (Bennett 1998, Clark 1998). With regard to *Euonymus* species, effectiveness of different zoochory types, ornithochory in particular, should be taken into account. Research of this kind (qualitative) have not been performed to date. The migration and spread of European species (including *E. europaeus*) from the refugia in eastern and southern Europe is discussed in Bennet et al. (1991), where the authors actively operate the data on pollen composition change in different epochs of the interglacial period and the glacial retreat. Such research, based on molecular record and taking pollen data into consideration, could potentially be very advisable for other Eurasian *Euonymus* species. That would allow us to reconstruct the migration of particular species in the post-glacial period.

Thus, various approaches to the solution of the vicarious species (taxa) problem exist nowadays. Firstly, data on fossil record and plant geography are of crucial importance here, along with those of morphology and environmental science. In the recent years, molecular methods and modeling are increasingly implemented. The correlation of the species’ range size with dispersal modes and adaptations to them, which, in their turn, depend on the fruit and seed structure, become more and more significant. As we believe, this determines the “target resolution capability” of the carpological approach, which still appears to be under-represented in the related scientific record.

MATERIAL AND METHODS

The study is based on the critical analysis of herbarium materials from LE, MW, MHA, MOSP, KW, MSUD, VLA, NS, Sakhalin regional museum of natural history (mainly from Moneron island), personal collections from different regions – European Russia, Ukraine, Crimea, Caucasus (Russian, Armenia, Georgia, Azerbaijan), in some countries of East and West Europe (Austria, Bulgaria, Croatia, Denmark, France, Germany, Greece, Italy, United Kingdom), Russian Far East (three field trips: 2007, 2017, 2019, to Sakhalin Island and Primorye Territory: Sikhote-Alin mountain, Khanka Lake region, southern part of Khassan District),

China and Nepal (deposited in MHA) and morphology and anatomical analysis of some species in the lab. The total number of studied herbarium specimens is over 4000.

Original carpological characters (structure of fruits and seeds) were discovered for the following species: *Euonymus alatus*, *E. bungeanus*, *E. europaeus*, *E. hamiltonianus*, *E. latifolius*, *E. maackii*, *E. maximowiczianus*, *E. nanus*, *E. pauciflorus*, *E. sachalinensis*, *E. sacrosanctus*, *E. sieboldianus*, *E. velutinus*, *E. verrucosus*. We used freshly harvested (in nature and in cultivation) samples of fruits and seeds.

The sections were made freehand using a razor blade. Temporary water- or glycerol-based micropreparations were made. A binocular lens MBC-1 and Biomed C-2 microscope were used. Lipids were identified by means of staining with Sudan III. Suitable sections were photographed with Canon videocamera.

To identify the environmental affinity of the studied taxa, as well as effective seed protection, a number of parameters are used, namely: fruit morphology, pericarp thickness and number of sclerenchyma cell layers in the endocarp, endocarp thickness as related to the overall pericarp thickness, exocarp cells structure, presence and topography of druses in mesocarp cells. To evaluate successful dispersal in similar environmental conditions, the following characters are used: carpel number, number of seeds in a fruit, the degree to which the aril covers the seed, the number of cell layers in the aril, presence of oil inclusions in the aril cells, seedcoat thickness.

North Eurasia is considered here as territory to the north of 40°N. It mainly coincides with the state borders of the former USSR.

The nomenclatural information for the scientific names follows to International plant name index (<https://www.ipni.org/>); when establishing priority species names – to World Flora Online (WFO), www.worldfloraonline.org.

Definitions of basic concepts and terms

Vicarious (or vicariant/vicariad) species: closely related species (taxa), substituting each other throughout the entire range.

Geographical vicarious species: species (taxa) with different but possibly connected (interconnected) ranges.

Ecological vicarious species: species (taxa) which are interconnected within one range but occur in different environmental conditions.

Resolving capability of carpological approach: connection between area size, fruit/seed structures and dispersal mode.

The plant adaptation to certain environmental conditions is reflected in morphology and anatomy of their organs and tissues. If the conditions are not optimal, the plant's external appearance and sizes of vegetative organ can vary quite significantly. Reproductive structures are more constant and conservative; it especially relates to fruits and particularly, their anatomy. Meanwhile, fruit morphology and anatomy is directly connected with the species' ecological niche size, as in the course of development, the fruit protects the enclosed seeds, and at maturity, it facilitates the germination. Therefore, a comparative morphological and anatomical study of fruits in species of a genus can resolve

not only the question of their affinity and relation, but also their adherence to the same or different environmental conditions. Of the carpological characters, the greatest attention should be paid to the thickness of the pericarp and seed coat, the thickness of the sclerenchyma in them, which provides seed protection, as well as the characteristics that ensure successful dissemination. For representatives of *Euonymus*, this is first of all the nutritional value of the aril: its thickness, the presence of abundant oil inclusions (drops) in the cells, as well as the number of seeds in the fruit.

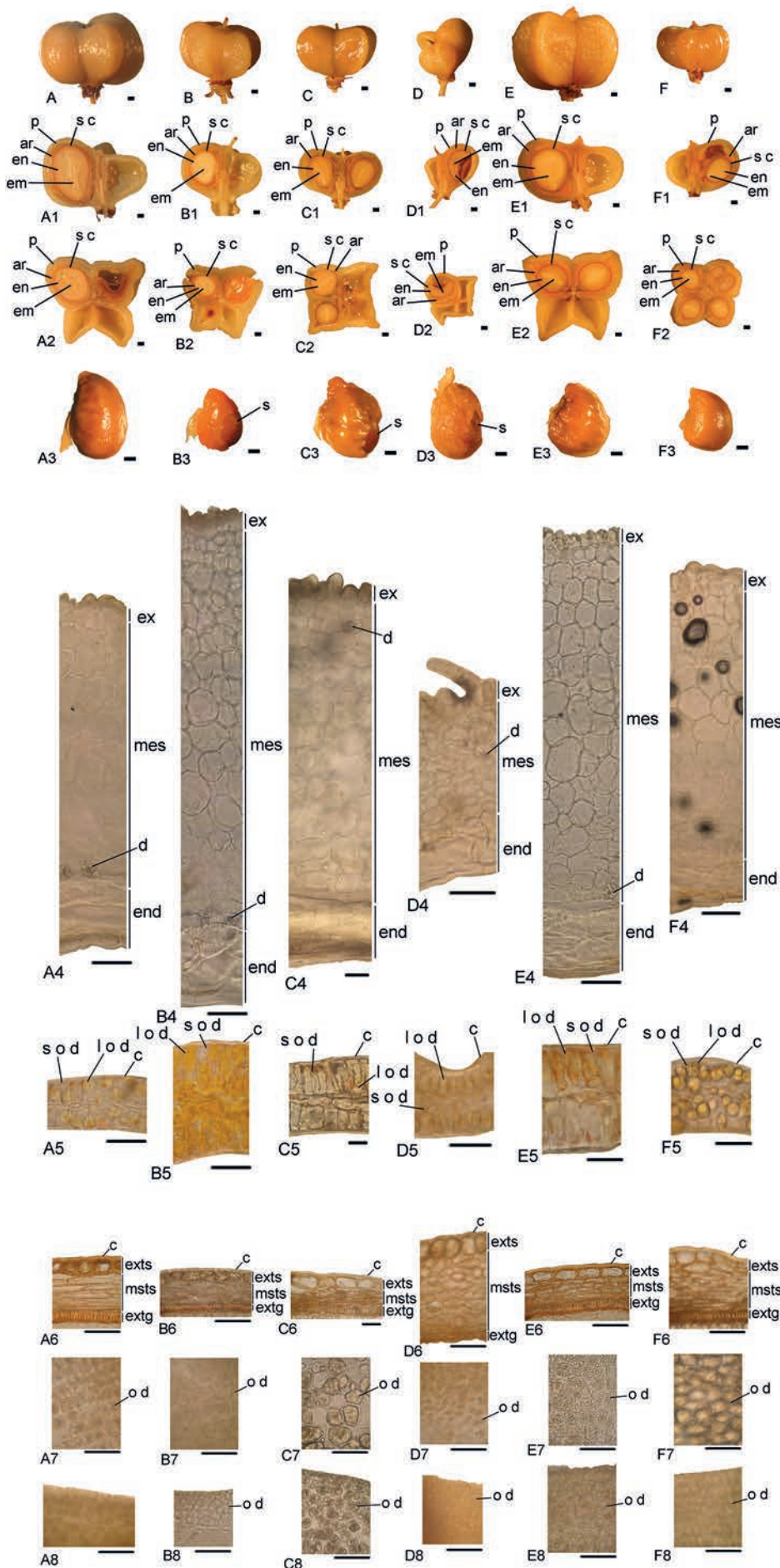
RESULTS AND DISCUSSION

According to the record available in literature (mainly to Bukshytynov 1957 and Leonova 1974) and on the basis of a preliminary analysis (taking the studied taxa's degree of affinity, geographical distribution, fruit and seed structure, dissemination type into consideration), a number of species groups were identified and consecutively described below.

Group 1 (vicarious species): *E. europaeus*, *E. velutinus*, *E. maackii*, *E. sieboldianus*, *E. hamiltonianus* and *E. bungeanus*

Geographical distribution and environmental conditions. *E. europaeus* – Europe, Crimea, the Caucasus; in the understorey of light broadleaf and mixed forests, in coastal bush thickets. *E. velutinus* – Transcaucasia, Iran, Turkmenistan, in light forests and bush thickets along river valleys and mountain slopes. *E. maackii* – Dahuria, Mongolia, Russian Far East, China; among bushes in floodplain meadows, less often in sparse broadleaf forests. *E. sieboldianus* – Far East: Sakhalin, the Kuril Islands, Japan; among bushes in floodplain meadows, in river valleys, lowlands, less often on mountain slopes. *E. hamiltonianus* – China, India, Japan, Cashmir, Korea, Myanmar, Nepal, Pakistan, Afghanistan, Bhutan, Thailand; sparse forests, including alpine ones. *E. bungeanus* – northern and northeastern China.

Morphological and anatomical characters. In all examined species, fruits are pink globose lobed capsules (Fig. 1, A–F; Table 1), formed by 4 carpels (Fig. 1, A2–C2, E2–F2; Table 1), in *E. velutinus* – often only 2 ovary locules are developed (Fig. 1, D2; Table 1). The capsules are 7–11 mm in length and 9–14 mm wide, in most species the pericarp thickness is around 1 mm (0.85 to 1.25 mm), in *E. sieboldianus* – over 1.5 mm, in *E. velutinus* – about 0.4 mm (Fig. 1, A–F, A1–F1, A2–F2; Table 1). The exocarp is single-layered, its cells being dome-shaped, with more or less developed cuticle (Fig. 1, A4–C4, E4–F4). In *E. velutinus*, uniseriate multicellular trichomes are found (Fig. 1, D4). The mesocarp consists of 10–14 layers of parenchymal cells, in *E. maackii* – 15–18, in *E. velutinus* – 7–8. The cells contain druses (Fig. 1, A4–F4; Table 1). The endocarp is composed of 3 to 4 layers of sclerenchymal radially elongated cells (Fig. 1, A4–F4). The endocarp relative thickness ranges from 14 % (*E. bungeanus*) to 22.5 % (*E. velutinus*) of the overall pericarp thickness (Table 1). In each locule, up to 2 seeds are developed (one in *E. velutinus*) (Fig. 1, A1–F1, A2–F2). Each seed is fully covered by an orange-coloured aril, or a small part is left uncovered (Fig. 1, A3–F3; Table 1). The aril is composed of 2–4 cell layers: 2 epidermal layers and 2 layers of deteriorating parenchyma, or just the epidermal part is present. The aril cells comprise oil inclusions of two types: small ones of the same size and large ones of varying size (Fig. 1, A5–F5; Table 1). The seed coat is of many layers, with pronounced exotesta of large thick-walled, cutinized cells, and exotegmen of fibers, elongated along the seed axis (Fig. 1, A6–F6). The seedcoat thickness ranges from 0.12 mm (*E. maackii*) to 0.27 mm (*E. sieboldianus*) (Table 1). The seeds



possesses an endosperm and a well-developed embryo with the radicle, plumule and large cotyledons (Fig. 1, A2–F2, A3–F3). Oil appears to be the predominant storage substance. Both endosperm and embryo cells in mature seeds are found to contain copious oil inclusions (oil drops) (Fig. 1, A7–F7, A8–F8). For *E. velutinus* (immature seeds were studied), data on mature seedcoat structure are lacking, therefore it cannot be compared to other studied species in relations to its thickness and other traits. However, we may note that *E. velutinus* is similar to other species in terms of its histological topography. The same applies to the seed and endosperm structure.

Notes. Far-Eastern species are often treated as *E. europaeus* L. var. *hamiltonianus* (Wall. ex Roxb.) Maxim. f. *maackii* (Rupr.) Maxim. and f. *sieboldiana* (Blume) Maxim. or as *E. hamiltonianus* Wall. in Roxb. var. *maackii* (Rupr.) Kom. and var. *sieboldianus* (Blume) Kom. Via *E. hamiltonianus*, growing in the Himalayas, species of the series clearly demonstrate Himalayan relations. *E. velutinus* was also previously considered to be a subvariety of

Figure 1 Fruit morphology and anatomy in *Euonymus* species of Group 1.

A–A8 – *E. europaeus* L., B–B8 – *E. maackii* Rupr., C–C8 – *E. sieboldianus* Blume, D–D8 – *E. velutinus* Fisch. & C.A. Mey., E–E8 – *E. hamiltonianus* Wall., F–F8 – *E. bungeanus* Maxim.

A–F – fruit, side view. A1–F1 – fruit, longitudinal section, A2–F2 – fruit, transverse section, A3–F3 – seed covered by the aril. A4–F4 – pericarp, cross section in the median zone, A5–F5 – aril, cross section in the median zone, A6–F6 – seedcoat, cross section in the median zone of the seed, A7–F7 – endosperm, cross section in the median zone of the seed, A8–F8 – embryo, cross section in the median zone of the seed.

ar – aril, c – cuticle, d – druse, em – embryo, en – endosperm, end – endocarp, ex – exocarp, extg – exotegmen, exts – exotesta, lod – large oil drop, mes – mesocarp, msts – mesotesta, od – oil drop, p – pericarp, s – seed, sc – seedcoat, sod – small oil drop.

Scale bar – 1 mm.

Table 1. Morphological, anatomical and morphometric characters in fruits of 6 *Euonymus* species groups

Group	Species	Fruit				Flowering / fruiting*	Pericarp						Ariol				Seed			
		Shape		Pericarp thickness, mm	Number of carpels		Exocarp thickness, mm	Mesocarp			Endocarp		Part of seed is covered by ariol	Number of layers		Oil inclusions (drops)		Number per locule	Size, mm	Seedcoat thickness, mm
		Globose, lobed	Obovate (oblong), lobed					Globose, winged	Number of cell layers	Thickness, mm	Druses	Number of cell layers		Thickness, mm	Completely	Not entirely, with a "window" on antiraphe	by 1/2-2/3			
	<i>E. europaeus</i>	+		10×14	0.85	4	V-VI / VII-VIII	0.07	12-14	0.64	+	3-4	0.18	+	+	+	+	up to 2	10×5×4	0.19
	<i>E. maackii</i>	+		8×12	1.25	4	V-VI / IX-X	0.05	7-8	1.02	+	3-4	0.19	+	+	+	+	up to 2	5×3.5×3	0.12
	<i>E. sieboldianus</i>	+		7.5×11	1.57	4	V-VI / IX-X	0.04	12-14	1.22	+	3-4	0.28	+	+	+	+	up to 2	5.5×4.5×4	0.27
1	<i>E. velutinus</i>	+	+	9×7	0.4	2 (4)	VI / IX	0.09	10-11	0.26	+	3	0.09	+	+	+	+	1	-	-
	<i>E. hamiltonianus</i>	+		11×14	1.06	4	V-VI / VIII-IX	0.03	10-12	0.84	+	3-4	0.18	+	+	+	+	up to 2	7×4.5×4	0.14
	<i>E. bungeanus</i>	+		7×12	0.91	4	V-VI / IX-X	0.03	7-9	0.69	+	3-4	0.13	+	+	+	+	up to 2	5×3.5×3	0.21
2	<i>E. pauciflorus</i>	+	+	9×9	0.57	4	V-VI / VIII-IX	0.02	5-6	0.34	+	6-7	0.20	+	+	+	+	up to 4	4.5×3.5×3	0.15
	<i>E. verrucosus</i>	+		9×13	0.30	4	VI / VIII-IX	0.02	5-6	0.19	+	2-3	0.08	+	+	+	+	up to 2	5×3.5×3	0.20
3	<i>E. alatus</i>	+		5×4	0.3	1 (4)	VII / VIII-IX	-	9	0.16	+	3-4	0.12	+	+	+	+	1	4×3.5×3	0.14
	<i>E. sacrosanctus</i>	+	+	6.5×4.5	0.31	1 (4)	IV-VI / VII-IX	0.04	6-7	0.14	+	3-4	0.15	+	+	+	+	1	5.5×5×4.0	0.14
4	<i>E. koopmannii</i>	+		15×15		4	V-VI / IX	-	9-11	-	-	5	-	-	-	-	-	up to 2	4×3.5×3.5	-
	<i>E. nanus</i>	+	+	12×11	0.36	4	V-VI / X	0.02	11-12	0.21	+	3-4	0.11	+	+	+	+	up to 2	4×3×2.5	0.06
5	<i>E. leiophloeus</i>	+	+	10×26		4	V / VII-IX	0.01	24-28	-	-	6-7	-	-	-	-	-	up to 2	5×4.5×4.5	-
	<i>E. macropterus</i>	+	+	9×26	0.52	4-5	V-VI / VII-IX	0.02	16-20	0.41	+	2-3	0.09	+	+	+	+	up to 2	5.5×3.5×3	0.09
	<i>E. maximowiczianus</i>	+	+	11×14	1.36	4-5	V-VI / VII-IX	0.02	24-28	1.23	+	2-3	0.12	+	+	+	+	up to 2	4.5×3.5×3	0.10
6	<i>E. latifolius</i>	+	+	14×24	0.91	3-5	V-VI / VII-IX	0.02	16-20	0.81	+	2	0.08	+	+	+	+	up to 2	6×4.5×4	0.17
	<i>E. sachalinensis</i>	+	+	14×30	1.81	3-5	V-VI / VII-IX	0.02	26-30	1.75	+	2-3	0.04	+	+	+	+	up to 2	5.5×5×4.5	0.11

* - data taken from literature (Shukhobodskij 1958)

∅ - no information

E. europaeus – *E. europaeus* var. *velutinus* (E. Mey.) Fisch. & C.A. Mey. Vicariousness of *E. europaeus*, *E. velutinus*, *E. sieboldianus*, *E. hamiltonianus*, *E. maackii*, *E. przewalskii* Maxim. was acknowledged by Kleopov (1990).

Group 2 (non-vicarious species): *E. verrucosus* and *E. pauciflorus*

Geographical distribution and environmental conditions. *E. verrucosus* – Europe, the Caucasus; in the understorey of broadleaf and coniferous forests. The northern range border in the European part of Russia reaches 58°N, some “protrusions” extending northward along the river valleys in Kostroma, Nizhny Novgorod and Kirov Regions, Udmurtian Republic and Perm Territory. This being stated, the species is completely absent in Leningrad and Novgorod Regions and in Estonia, in all northern and northwestern districts of Tver Region, that is, in the majority of the Valdai Hills; whereas it is commonly found in western and southern districts of Pskov Region (record from the literature and personal observations). *E. pauciflorus* – Far East, northeast China; in shaded habitats in broadleaf, mixed or rarely coniferous forests; the species can be found as high as 1000 m above sea level, therefore, can apparently grow in more extreme conditions. The authors have observed *E. pauciflorus* on well-lit slopes near Dalnegorsk (Primorye Territory).

Morphological and anatomical characters. Fruits of *E. verrucosus* and *E. pauciflorus* seem to be similar at first glance, since the seeds in both species are covered by the aril by 1/2 or 2/3 (Fig. 2, A3, B3; Table 1). However, the fruits have multiple traits of difference. In *E. verrucosus*, the capsule is large (9×13 mm), globose, lobed, formed by 4 carpels (Fig. 2, B–B2; Table 1). Each locule holds up to 2 seeds (Fig. 2, B2; Table 1). The capsule of *E. pauciflorus* is different in shape (obovate), smaller in size (9×9 mm) and has up to 4 seeds in each locule (Fig. 2, A–A2; Table 1). The pericarp in *E. pauciflorus* exceeds that of *E. verrucosus* in thickness almost twice, 0.57 mm versus 0.30 mm (Table 1). The exocarp in both species is one-layered and of cutinized tabular cells, but in *E. pauciflorus* the cell walls are thickened (Fig. 2, A4–B4; Table 1). The mesocarp in *E. verrucosus* consists of 7–9

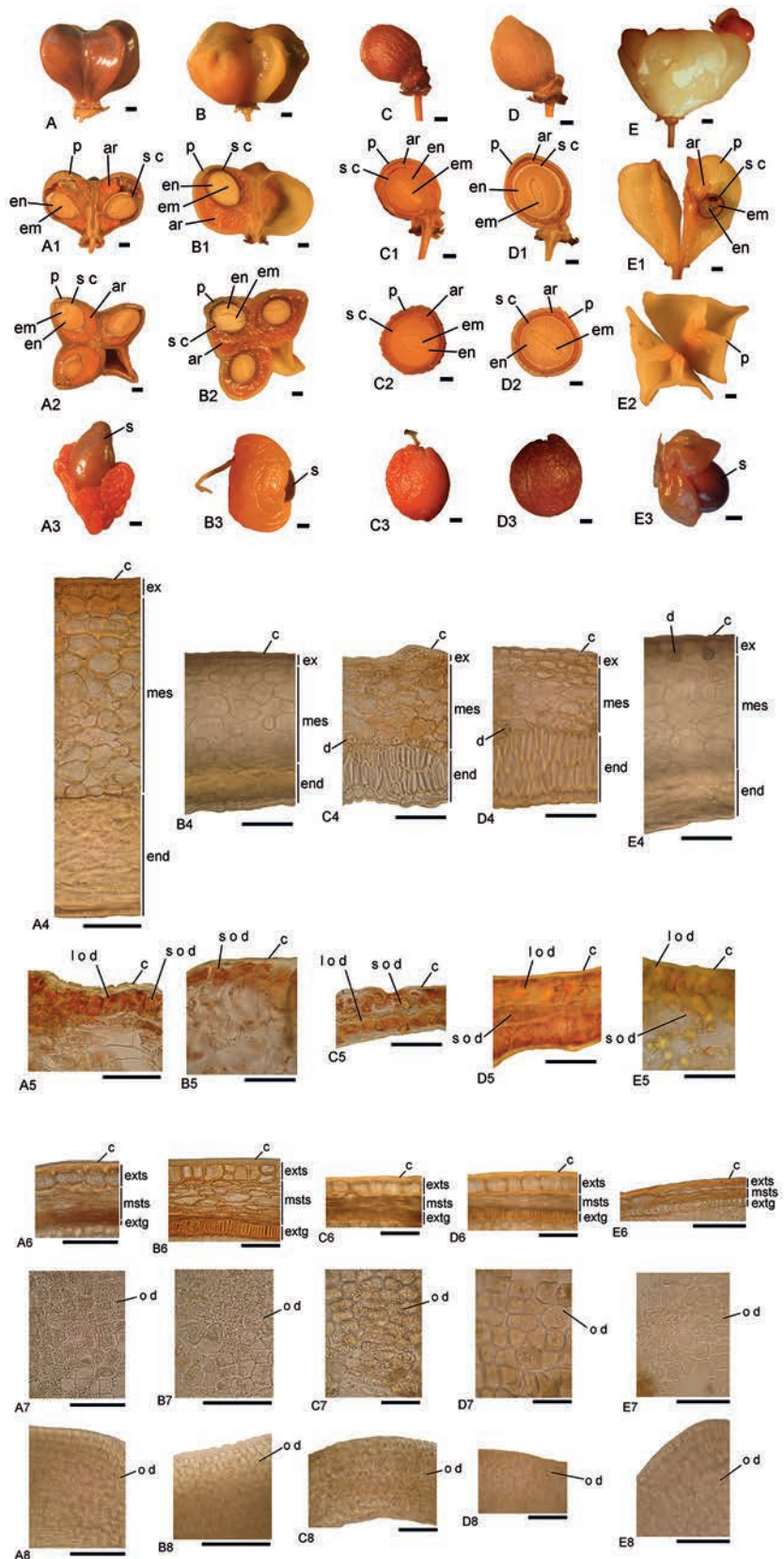


Figure 2 Fruit morphology and anatomy in *Enonymus* species of Groups 2, 3 and 4.

A–A8 – *E. pauciflorus* Maxim., B–B8 – *E. verrucosus* Scop., C–C8 – *E. alatus* (Thunb.) Siebold, D–D8 – *E. sacrosanctus* Koidz., E–E8 – *E. namus* M. Bieb.

A–E – fruit, side view, A1–E1 – fruit, longitudinal section, A2–E2 – fruit, transverse section, A3–E3 – seed in the aril. A4–E4 – pericarp, transverse section in the median zone, A5–E5 – aril, transverse section in the median zone, A6–E6 – seedcoat, transverse section in the median zone of the seed, A7–E7 – endosperm, transverse section in the median zone of the seed, A8–E8 – embryo, transverse section in the median zone of the seed. Captions same as in Figure 1.

Scale bar – 1 mm.

druse-containing parenchymal cell layers, in *E. pauciflorus* – of 10 to 12 layers of parenchymal cells, no druses are found (Fig. 2, A4–B4; Table 1). The endocarp of *E. pauciflorus* is built of 6–7 layers of tangentially elongated sclereids, and, compared to the overall pericarp thickness, it is thicker in this species than in *E. verrucosus* (35 % and 27 %, respectively) (Fig. 2, A4–B4; Table 1). In both species, arils are thick, multiple-layered, possessing a single epidermal layer and parenchyma of many layers. But in *E. pauciflorus*, the aril cells comprise both small oil inclusions of the same size and large ones varying in size, while in *E. verrucosus*, only small ones are present (Fig. 2, A5–B5; Table 1). The crude fat content in the arils of *E. pauciflorus* is shown to be high (46.64 %), whereas in *E. verrucosus* it is low (7.4 %) (Trusov 2005). The seed coat is multiple-layered, with pronounced exotesta of large thick-walled cutinized cells and exotegmen of fibers elongated along the seed axis. The exotegmen is particularly pronounced in *E. verrucosus* (Fig. 2, A6–B6). The seed coat thickness in *E. verrucosus* is 0.20 mm, in *E. pauciflorus* it is less – 0.15 mm (Table 1). The seeds possess endosperm and a well-developed embryo with the radicle, the plumule and large cotyledons (Fig. 2, A1–B1, A2–B2). Fatty oil is found to be the main storage substance in the seed. In mature seeds, endosperm and embryo cells contain numerous oil drops (Fig. 2, A7–B7, A8–B8).

Notes: Maximowicz (1881), having originally described the species *E. pauciflorus*, later treated it as *E. verrucosus* Scop. var. *pauciflorus* Regel. Leonova (1974) considers these two species to be genetically close, originating from a common ancient form, but differing well by a series of morphological traits. Ma (2001) does not differentiate between these two species, uniting them in *E. verrucosus*. The difference in the species' ecological niches and traits of their fruit morphology and anatomy allow us to conclude they are not vicarious, yet closely related.

Group 3 (vicarious species): *E. alatus* and *E. sacrosanctus*

Geographical distribution and environmental conditions. *E. alatus* – Far East: Sakhalin, the Kuril Islands, Japan, Korea, China; open slopes. *E. sacrosanctus* – eastern Siberia – the Irkut river gorge, western Khamar-Daban, Dahuria; mainland of the Russian Far East, Korea, China; mixed and broadleaf forests, bush thickets, meadows, floodplains, mountain slopes. In oak forests near Khanka Lake, it is the most commonly found *Euonymus* species.

Morphological and anatomical characters. Fruits of *E. alatus* and *E. sacrosanctus* are quite similar in their morphological and anatomical structure (Fig. 2, C–C8, D–D8; Table 1). The capsule of *E. alatus* is globose, while that of *E. sacrosanctus* is slightly oblong. 4 carpels, most often only one of them develops and the locule contains a single seed (Fig. 2, C–C2, D–D2; Table 1). The pericarp thickness is almost the same, around 0.30 mm (Table 1). The exocarp is one-layered, of tabular cutinized cells. The mesocarp is composed of 5–6 layers of druse-bearing parenchymal cells. The endocarp consists of 3–4 layers of sclerenchymal fibers, elongated along the fruit axis. In both species, the endocarp makes up for almost half of the pericarp in thickness (Fig. 2, C4, D4; Table 1). Arils in both species fully cover the seeds and are formed by 2 epidermal cell layers and 2 layers of residual parenchyma cells, less often only epidermis is present. Aril cells possess oil inclusions of both above mentioned types (Fig. 2, C3, C5, D3, D5; Table 1). The seed coat in both species is about 0.14 mm thick (Table 1). Its most pronounced parts are the exotesta of large tabular cells with thickened walls, especially the outer and the inner ones, and cuticle, as well as the exotegmen of sclerenchymal fibers, elongated along the seed axis (Fig. 2, C6, D5). The seeds possess endosperm and a well-developed

embryo with the radicle, the plumule and large cotyledons (Fig. 2, C1–C2, D1–D2). Fatty oil is found to be the main storage substance in the seed. In mature seeds, endosperm and embryo cells contain numerous oil drops (Fig. 2, C7–C8, D7–D8).

Notes. These closely related species caused great confusion, which, to a certain extent, forces some scholars not to acknowledge *E. sacrosanctus* as an independent species, reducing it to a synonym of *E. alatus*. Their differences are not so pronounced and conspicuous, and geographically, their ranges partly overlap (in the south of the Korean peninsula and in eastern China). Apparently, it is worthwhile to consider *E. sacrosanctus* a mainland species (eastern Siberia, Khabarovsk and Primorye Territories), whereas *E. alatus* should be treated as primarily an island-bound species (Sakhalin, southern Kurils, Japan, Korean peninsula, eastern China), and only along the shoreline of Bo Hai Gulf in Northeast China and in the extreme south of the Korea Peninsula, both species, *E. alatus* and *E. sacrosanctus*, occur, according to Leonova (1974). Samples from Moneron Island, interpreted by Leonova (1974:75) as those of *E. sacrosanctus*, but with traits transitional to *E. alatus*, require further investigation. In Kiseleva's (1988) paper, the range maps show that both species discussed are found at Moneron Island. Data to support a similar pattern among populations of *E. sacrosanctus* in the southern districts of Primorye, are present (original data).

Group 4 (vicarious species): *E. nanus* and *E. koopmannii*

Geographical distribution and environmental conditions. *E. nanus* is a small evergreen shrub with a disjunctive range comprising eastern Europe, the Caucasus, China; occurs in deciduous lowland bush thickets and in mountainous coniferous forests and in brushwood. *E. koopmannii* – small evergreen shrub growing in Central Asia (Pamir-Alay, Tian-Shan); on the slopes of alpine gorges, in bush thickets and walnut (*Juglans regia* L.) forests. The second species has a very limited range in the upper part of the Syr-Darya basin.

Morphological and anatomical characters. In *E. nanus*, the fruit is an obovate, slightly lobed capsule (12×11 mm), formed of 4 carpels. Each locule may possess up to 2 seeds (Fig. 2, E–E2; Table 1). The pericarp is around 0.36 mm in thickness (Table 1). One-layered exocarp is made of tabular cutinized cells. The mesocarp is of 6–7 layers of druse-bearing parenchymal cells. The endocarp consists of 3 to 4 layers of tangentially elongated sclereids; its thickness takes up about 30 % of the pericarp (Fig. 2, E4; Table 1). The seed is covered by the aril by 1/2–2/3, the latter is thick, multiple-layered, with a single epidermal layer and many layers of parenchyma underneath. The cells possess oil inclusions (drops) of both types (Fig. 2, E3, E5; Table 1). Large oil drops are not very numerous. The seeds are reddish-brown in colour, 4×3×2.5 mm (Table 1). The seed coat is relatively thin – about 0.6 mm. In it, the most pronounced are the exotesta of large tabular cells with thickened walls (in particular, the outer ones) and cuticle, and the exotegmen of sclerenchymal fibers, elongated along the seed axis (Fig. 2, E6; Table 1). Seeds of *E. nanus* possess endosperm and a well-developed embryo with the radicle, the plumule and large cotyledons (Fig. 2, E1, E2). Its main storage substance is fatty oil. In mature seeds, both embryo and endosperm cells are found to contain copious oil inclusions (drops) (Fig. 2, E7–E8; Table 1). In *E. koopmannii*, fruits and seeds are larger in size: 15×15 mm and 4.0×3.5×3.5 mm, respectively. The pericarp consists of 9 cell layers, 5 of which belong to the endocarp. Seeds are covered with an orange aril by 1/2–2/3 (Table 1). Regrettably, there is not have enough morphometric data as well as data on fruit and seed anatomy and morphology of *E. koop-*

mannii, to compare these two species in relation to their quantitative and some qualitative traits of fruits and seeds. However, these species are shown to have similar histological topography of the pericarp and the seedcoat.

Notes. On the basis of the occupied ecological niche, similar habitat and evergreen habit, as well as similar fruit morphology, one can consider these taxa geographical vicariants.

Group 5 (vicarious species): *E. macropterus* and *E. leiophloeus*

Geographical distribution and environmental conditions. *E. macropterus* is a deciduous tree up to 9 m high or a large shrub, growing in Khabarovsk and Primorye Territories, Sakhalin Region, Japan, Korea and northeastern China; in coniferous and mixed forests, along streams, on slopes, side slopes and cliffs, on the sea coast. *E. leiophloeus* is a low semievergreen shrub found in Transcaucasia; shady forests, mountain slopes and valleys.

Morphological and anatomical characters.

The fruit of *E. macropterus* is a globose winged capsule (9×9 mm without the wing-like projections, with the projections – 9×26 mm), formed by 4 to 5 carpels. In each locule, up to 2 seeds may develop (Fig. 3, A–A2; Table 1). The pericarp is 0.52 mm thick (Table 1). Single-layered exocarp consists of tabular cells covered by the cuticle. The mesocarp is made of 11–12 parenchymal druse-containing cells; cells of middle layers are larger in size. The endocarp is composed of 2–3 layers of tangentially elongated sclereids, taking up to 17 % of the pericarp thickness (Fig. 3, A4; Table 1). The aril does not cover the seed completely, leaving a small “window” uncovered; the aril is thick, multi-layered, with many layers of parenchyma under the single epidermal layer. The cells contain oil inclusions (drops) of both types (Fig. 3, A3, A5; Table 1). The seed is 5.5×3.5×3 mm. The seed coat is around 0.9 mm thick (Table 1). The most pronounced layer is exotesta made of large tabular cells with thickened walls (especially the outer one) and cuticle, and exotegmen of sclerenchymal fibers, elongated along the seed axis (Fig. 3, F6). Seeds of *E. macropterus* possess endosperm and a well-developed embryo with the radicle, the plumule and large cotyledons. Fatty oil appears to be the main storage substance. In mature seeds, both embryo and endosperm cells are found to possess copious oil inclusions

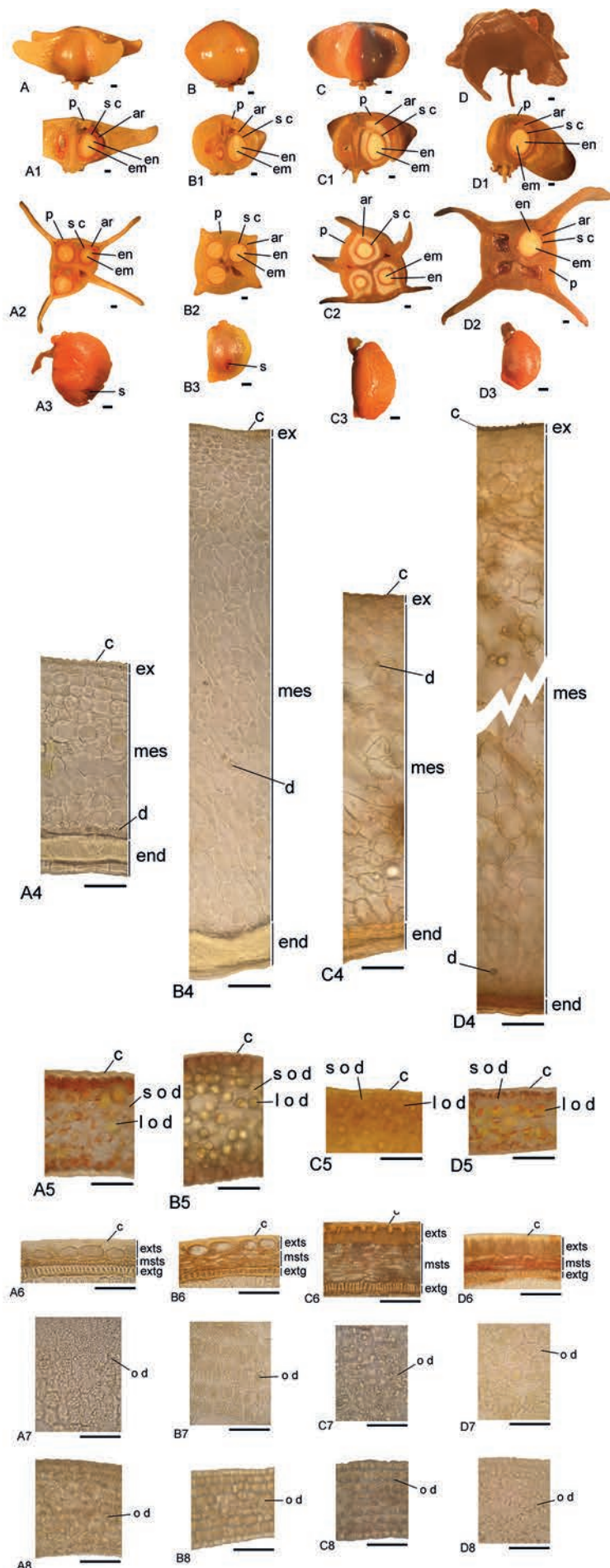


Figure 3 Fruit morphology and anatomy in *Euonymus* species of Groups 5 and 6.

A–A8 – *E. macropterus* Rupr., B–B8 – *E. maximowiczianus* Prokh., C–C8 – *E. latifolius* (L.) Mill., D–D8 – *E. sachalinensis* (Fr. Schmidt) Maxim.

A–D – fruit, side view, A1–D1 – fruit, longitudinal section, A2–D2 – fruit, transverse section, A3–D3 – seed in the aril, A4–D4 – pericarp, transverse section in the median zone, A5–D5 – aril, transverse section in the median zone of the seed, A6–D6 – seedcoat, transverse section in the median zone of the seed, A7–D7 – endosperm, transverse section in the median zone of the seed, A8–D8 – embryo, transverse section in the median zone of the seed. Captions as in Figure 1. Scale bar – 1 mm.

(drops) (Fig. 3, A7, A8). In *E. leiophloeus*, fruits are globose, with long wings. Their size with no wing-like projections is 10×10 mm, with them – 10×26 mm. The pericarp consists of 9–11 cell layers, 6 or 7 of them compose the endocarp. Seeds are 5×4.5×4.5 mm (Table 1). Unfortunately, available morphometric, morphological and anatomical data on the structure of fruits and their parts in *E. leiophloeus* are not sufficient for comparing these two species in relation to their quantitative and some qualitative fruit and seed traits. However, histological topography of their pericarp and seed coat show resemblance.

Notes. Ranges of these species are far apart (at a significant distance) from each other, due to their different life forms: a tall tree and a small shrub, and, as a consequence of having different ecological niches, as well as semi-evergreen nature of *E. leiophloeus*, one can suppose that these species are not vicarious.

Group 6 (vicarious species): *E. latifolius*, *E. sachalinensis* and *E. maximowiczianus*

Geographical distribution and environmental conditions. *E. latifolius* – western Europe, Crimea, the Caucasus, Asia Minor, Iran; in broadleaf, coniferous or mixed forests, extending to the altitude of 1800 m above sea level. *E. sachalinensis* – Sakhalin, Japan; in brushwood (bush thickets) in mixed or coniferous forests on mountain slopes at the altitude up to 800 m above sea level. *E. maximowiczianus* – Primorye Territory, northeastern China; mixed forests across mountain slopes and on the sea coast along the rocky cliffs, in bush thickets and half-grown forest.

Morphological and anatomical characters. Capsules of all these species are globose, with small wing-like projections. In *E. latifolius* and *E. maximowiczianus*, the capsules are formed by 4–5 carpels, in *E. sachalinensis* – of 3–4, rarely 5 (Fig. 3, B–B2, C–C2, D–D2; Table 1). The pericarp thickness in *E. latifolius* is 0.91 mm, in *E. maximowiczianus* – 1.36 mm, in *E. sachalinensis* – 1.81 mm (Table 1). The exocarp cells are tabular, with cutnized walls. The mesocarp is made of parenchymal cells containing druses, in all species cells of the middle layers are markedly larger. The mesocarp in *E. latifolius* consists of 16–20 cell layers (0.81 mm in thickness), in *E. maximowiczianus* – of 24–28 layers (1.23 mm), in *E. sachalinensis* – of 26–30 layers (1.75 mm). The endocarp comprises 2–3 layers of tangentially elongated sclereids (Fig. 3, B4–D4; Table 1). In *E. latifolius* and *E. maximowiczianus*, it takes up around 9 % of the overall pericarp thickness, while in *E. sachalinensis* – only 2 % (Table 1). Each locule bears up to 2 seeds (Fig. 3, B2–D2; Table 1). The seeds are either entirely covered by the aril (*E. sachalinensis*) or a small area is left uncovered (*E. latifolius*, *E. maximowiczianus*) (Fig. 3, B3–D3; Table 1). The arils are composed of multiple cell layers, multi-layered parenchyma is located underneath the single epidermal layer. The cells possess oil inclusions of both types (Fig. 3, B5–D5; Table 1). The seed coat in *E. latifolius* and *E. sachalinensis* is about 0.10 mm in thickness, in *E. maximowiczianus* – 0.17 mm (Table 1). The most pronounced zones are the exotesta of large cells with thickened walls (in *E. latifolius* – horseshoe-like thickening of the outer wall is observed) and cuticle; and the exotegmen of sclerenchymal fibers, elongated along the seed axis (in *E. sachalinensis*, the exotegmen is two-layered in some parts) (Fig. 3, B6–D6; Table 1). The seeds possess endosperm and a well-developed embryo with the radicle, the plumule and large cotyledons. Fatty oil appears to be the main storage substance. In mature seeds, endosperm and embryo cells contain copious oil inclusions (drops) (Fig. 3, B7–D7, B8–D8).

Notes. The species are distinguished well by shape and size of the capsule wings, as well as traits of leaf and flower morphology, ranges, however, sometimes they are united

as synonyms. Thus, Ma (2001) considers *E. leiophloeus* to be synonymous to *E. latifolius*, whereas *E. maximowiczianus*, *E. planipes* and *E. miniatus* – synonymous to *E. sachalinensis*.

Additional group 1: relict species *E. nanus*

The range, environmental conditions, traits of fruit morphology and anatomy in *E. nanus* are mentioned above.

Note 1. Almost all botanists acknowledge the relict type of *E. nanus*'s contemporary range (see Krishtofovich in Fedchenko 1914:30, with reference to Vysotsky and Pachoskij). Wulff (1944) and Pachoskij (1910) believe that *E. nanus* survived from the Tertiary period within sites of its former range, having undergone significant transformations (according to Pachoskij, it is a representative of Podolskian flora). Kleopov (1930), as well as Kleopov & Grin' (1933, cited by Leonova 1974) suggests the species' complicated migration path from the conservation areas (in the European site – from the Carpatian mountains and the Caucasus) in the course of Torgay nemoral flora dispersal (see Kleopov 1990). Leonova (1974) apparently shares Kleopov's point of view.

Note 2. The traits showing difference between Middle Asian individuals (larger sizes and profound flowering) and populations from European and Caucasian (and Mongolian) regions were already pointed out by Maximowicz & Krishtofovich (1914). Due to the disjunctive range of *E. nanus*, its Central Asian populations look quite like part of this disjunction, which makes many scholars (e.g., Ma 2001) deny the independent species status for *E. koopmannii* (taking into consideration that morphological differences are insignificant). However, carpological characters, as the results of our studies show, differ well between them. According to Kleopov (1990), these species are vicarious.

Additional group 2: endemic species *E. leiophloeus*

Geographical distribution and ecological conditions. *E. leiophloeus* – regional endemic (western Caucasus, north-western Turkey: Artvin province).

Notes. The species occupies a rather insignificant range (approximate area 60000 sq. km), which can be connected with limited renewal by seed in natural populations (plants with prostrate stems, common for the species growing in moist gorges, fruiting rarely and scarcely), natural boundaries such as the Greater and the Minor Caucasus and, possibly, inconsiderable bird contribution to its seed dispersal.

Additional group 3: subendemic species *E. maximowiczianus* and *E. velutinus*

E. maximowiczianus occurs in southern Primorye Territory north up to 44–45°N, border areas of northeastern China and North Korea. Its range size is quite comparable with that of Caucasian *E. leiophloeus*. These plants have no problems fruiting both in the wild and in cultivation. The range limitation by 45°N in Primorye Territory is seemingly related to the absence of more suitable soil and climatic conditions.

E. velutinus – subendemic of the Caucasus (+ Central Asia). The species is also known to have a restricted range (yet larger than that of *E. leiophloeus* and *E. maximowiczianus*), which could be, primarily, due to external factors: boundaries such as the sea and mountains, insignificant bird contribution to the seed dispersal. The formation of a discontinuous range can be explained by historical reasons, such as changes in the area of salt-water basin, formed during the Thetys sea reduction and mountain range formation. Moreover, it is noteworthy that, when introduced in Moscow region, *E. velutinus* flowers in mid-July, not every year and scarcely; fruits do not reach maturity (Trusov & Sozonova 2011).

Carpological approach outcome

So, the carpological characters identified in the article were compared with the nature of the ranges of the studied species and their dispersal modes, which made it possible to conclude that they were interpreted as vicarious or non-vicarious. In endemic species (especially in narrowly local endemics), we discuss specific features in the structure of their fruits and seeds that contribute to the existence of restrictive mechanisms in dispersal: a decrease in the number of carpels and seeds in a fruit, a decrease in total pericarp and seed coat thickness, as well as sclerenchymal layers, fewer oil drops in arils. This is primarily related to the embryo protection, the successfulness of dispersal and the involvement of biotic agents into this process, as well as the existence of physical barriers. Thus, in *E. nanus*, the amount of large oil inclusions (drops) in the aril cells is low; *E. maximowiczianus* has the smallest exocarp thickness among the representatives of the *Kalonymus*; in *E. velutinus* – small fruit, reduction of two pericarp locules, development of only one seed per locule, thin pericarp.

How many relict and endemic species are there?

According to the existing criteria of relict species (see Tolmachev 1974, Elenevskij & Radygina 2002), only *E. nanus* can be assigned to them, for its discontinuous range (reducing currently due to the decrease in population) and loss of ability for regeneration by seed. Schepotev (1941) also noted its ability for autogamy, even though, e.g., *E. europaeus* and *E. verrucosus* are typical cross-pollinated species (Sapankevich 1953). Our data show that *E. nanus* has quite a thick pericarp with well-developed endocarp, yet its seed coat appears to be rather thin. Supposedly, the thin seedcoat has negative impact on seed preservation and, as a result, on the renewal by seed. Vegetative mobility (formation of prostrate runner-like shoots) can be considered to possibly compensate for the loss of seed renewal.

One also must add, that many other species of the genus growing in extreme conditions (heavy shading and competition with other plants) show similar behavior. It makes no sense to discuss here 9 local endemic species from Eastern Europe, excluded from *E. europaeus* by Klokov (1959), which are said to testify the “autochton (indigenous) development of thermophilic flora at the given territory, at least from early Neogene” – they were felicitously called “paper species” by Grosset (1975).

This problem really demonstrates wide polymorphism of shoot, leaf and inflorescence pubescence traits, leaf blade size and shape, and the variability itself appears to be clinal in the natural populations (Savinov 2009). Many other species can be assigned to the group of “ancient taxa” (Arctic Tertiary, according to Engler & Popov, e.g., *E. leiophloeus* in the Caucasus), their range having undergone considerable changes from the Miocene period, however, to date they remain prominent representatives of European, Caucasian and Central (Middle) Asian forests and montane gorges. Ranges of Far Eastern species, apparently, have undergone changes to a much lesser extent as inland glaciation in the far northeastern part of Asia was much less pronounced than in Europe and almost never extended to southern latitudes (Monin & Shishkov 1979).

Our understanding of the status of certain *Euonymus* species outlined here well correspond with contemporary data on climate change and vegetation dynamics over the last 2.6 million years, in particular, the contrasting Pleistocene era along with the subsequent interglacial period – the Holocene (Birks 2019).

Chorological groups of Northern Eurasian species of *Euonymus*

We have analyzed distribution patterns of studied *Euonymus* species, considering not only present-day ranges but also historical conditions of their formation. The following geographical elements (chorological groups) characterizing the range type, were identified. I. European elements: 1 – European-Caucasian-Asia Minor (*E. europaeus*), 2 – Eastern European (*E. verrucosus*), 3 – Mediterranean-Balkan-Asia Minor (*E. latifolius*); II Caucasian and Central Asian elements: 4 – Western Caucasian (*E. leiophloeus*), 5 – Iranian and Turanian (*E. velutinus*), 6 – Central (Middle) Asian (*E. koopmannii*, *E. semenovii* Regel & Herder); III Disjunctive Eurasian elements: 7 – Disjunctive European-Caucasian-Asian (*E. nanus*). IV Eastern Asian elements: 8 – Manchurian (*E. maximowiczianus*, *E. maackii*, the latter reaching Eastern Dauria in the west, *E. pauciflorus*), 9 – Sakhalin and Hokkaido (*E. sachalinensis*, *E. miniatus*), 10 – Japanese and Korean (*E. planipes*, *E. sieboldianus*), 11 – Japanese and Manchurian, or continental and islander (*E. macropterus*, *E. sacrosanctus*), 12 – Sakhalin-Japanese-Chinese (with eastern and south-eastern China, as in *E. alatus*). V. Himalayan elements: 13 – Himalayan (*E. hamiltonianus*).

Thus, conducted morphological and anatomical analysis of 17 species, represented in northern Eurasia, allowed us to clarify modern concepts of vicarious and non-vicarious species as well as endemics and relicts.

The following species of the **group 1** are believed to be vicarious:

Geographic vicariants (*E. europaeus*, *E. maackii*, *E. sieboldianus*, *E. bungeanus*). They grow in similar conditions, are part of the forest understorey and are associated with river and stream banks. Also, fruit morphological and anatomical traits facilitating seed protection and dispersal, show similarities.

Ecological vicariants (*E. hamiltonianus* and *E. sieboldianus*). They occur within the same range but in different environmental conditions. Meanwhile, their fruit morphology and anatomy show resemblance.

E. velutinus, as we believe, is not a vicarious species, despite the fact that it grows in similar ecological conditions. Traits of its fruit morphology and anatomy, connected with seed protection and dispersal, differ greatly from those of other species. Its fruit structure could possibly be connected with its range limitation.

Species from the **group 2**, as we believe, are not vicarious. Habitats of *E. verrucosus* and *E. pauciflorus* differ environmentally and geographically are set apart. Also, morphological and anatomical structure of their fruits demonstrates a number of significant differences.

Species of the **group 3** – *E. alatus* and *E. sacrosanctus* – are hereby considered ecological vicariants. They are found to grow in different environmental conditions, yet their ranges overlap. As well, they show much resemblance in fruit structure.

Species of the **group 4**, as we think, are geographic vicariants. Some morphological and morphometric characteristics of fruit structure in *E. koopmannii* require further clarification.

Species of the **group 5** are apparently not vicarious, as they are found to have remote ranges and different habitus; *E. leiophloeus* is known for its semi-evergreen nature. Further clarification of some morphological and morphometric characters of fruit structure in *E. leiophloeus* is required.

Species of the **group 6** are hereby treated as geographic vicariants. *E. latifolius*, *E. sachalinensis* and *E. maximowiczianus* occur in similar conditions but their ranges are set apart. Morphological and anatomical peculiarities, related to seed protection and dissemination, resemble in these species.

E. leiophloeus appears to be a regional endemic; we consider *E. maximowiczianus* and *E. velutinus* to be subendemic species. The main reasons for the limitation of their ranges and the species' incapability of active dispersal and migration seem to be as follows: 1) limited renewal by seed in natural populations; 2) presence of natural boundaries; 3) insignificant bird contribution to the dispersal; 4) no suitable soil and climatic conditions. Competition with similar species for resources may also affect them.

CONCLUSIONS

So, part of *Euonymus* species from northern Eurasia corresponds to the criteria, applied to vicarious species by relevant experts. We consider the following species to be geographic vicariants: *E. europaeus*, *E. maackii*, *E. sieboldianus*, *E. bungeanus*, *E. nanus* and *E. koopmannii*, *E. latifolius*, *E. sachalinensis* and *E. maximowiczianus*. The following species are believed to be ecological vicariants: *E. hamiltonianus* and *E. sieboldianus*; *E. alatus* and *E. sacrosanctus*. *E. verrucosus* and *E. pauciflorus*, as well as *E. leiophloeus* and *E. macropterus* do not appear vicarious. *E. nanus* demonstrates a classic example of a relict species, with all traits of being relict, proven by our research materials. *E. leiophloeus* is hereby considered a regional endemic; *E. maximowiczianus* and *E. velutinus* – subendemic species.

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