Turczaninowia 26, 2: 170–189 (2023)
DOI: 10.14258/turczaninowia.26.2.14
http://turczaninowia.asu.ru

ISSN 1560–7259 (print edition)
TURCZANINOWIA
ISSN 1560–7267 (online edition)

УДК 582.998.1+581.9+574(1-926.81)(680+688)

Senecioneae (Asteraceae) of the Succulent Karoo and "geography of macroevolution of higher plants": a chorological essay

A. C. Timonin[1, 4] *, L. V. Ozerova[2, 5], R. K. Eberwein[3, 6]

[1] *Lomonosov Moscow State University, Leninskiye Gory, 1(12), Moscow, 119234, Russian Federation*

[2] *Tsitsin Main Botanical Garden, Botanicheskaya St., 4, Moscow, 127276, Russian Federation*

[3] *Regional Museum of Carinthia, Liberogasse, 6, Klagenfurt am Wörthersee, 9020, Austria*

[4] *E-mail: timonin58@mail.ru; ORCID iD: https://orcid.org/0000-0002-6066-551X*

[5] *E-mail: lyozerova@yandex.ru; ORCID iD: https://orcid.org/0000-0003-4964-0298*

[6] *E-mail: roland.eberwein@landesmuseum.ktn.gv.at ; ORCID iD: https://orcid.org/0000-0003-1485-216X*

* *Corresponding author*

Keywords: allochtonous flora, archaism gradient, biogeography, center of origin, cradle and museum, out of tropics, ousted relics, progression rule, Southwestern Africa, zonal stratification.

Summary. The geographic characteristic of plant macroevolution is manifested in general in neither even, nor random distribution of the archaic and advanced representatives of a higher taxon in its range. The explanatory concepts proposed are still contradictory. Besides, they are poorly testable, because they concern too long-time intervals during which multiple major changes in both the environment and the ranges of taxa can have occurred; these changes usually continue untraceable in fossil records. The tribe *Senecioneae* in the Succulent Karoo is best suited for studying the geographic patterns of plant macroevolution for the following reasons: i) the environment of the Succulent Karoo has resulted from unidirectional climate change over 10 million years (accordingly, large fluctuations of the taxon ranges there are highly unlikely); ii) the phylogeny of the tribe *Senecioneae* is quite fully recognized (and it is not distorted by extinctions, at least at the level of genera); iii) *Senecioneae* are completely allochthonous in the Succulent Karoo (accordingly, interpretation of results becomes easier and simpler). The archaic genera of *Senecioneae* are as numerous in the Succulent Karoo as the highly advanced ones, whereas the mid-advanced genera are completely absent there. Such a genus composition of the tribe in the area concerned cannot be explained by the *cradle and museum* concept, since this area is outside of center of origin/diversification of *Senecioneae*. The *zonal stratification* concept is inapplicable to this case, since the climate of the Succulent Karoo was changing unidirectional all the time without noticeable fluctuations. All other concepts proposed are also inapplicable, as they treat the emerging of archaism gradient(s) in the taxon range, but not a deficiency/absence of mid-advanced representatives of a higher taxon in a territory occupied by its archaic and highly advanced members. The absence of mid-advanced members of *Senecioneae* in the Succulent Karoo could be explained as follows. Any higher taxon very rarely and at long time intervals acquires traits that enable it to spread to areas which greatly differ in their environments from the center of origin/diversification of this taxon. All new subordinate taxa that originate during these time intervals remain confined in the center of origin/diversification of the higher taxon. Accordingly, only archaic and most advanced representatives of this higher taxon would be found faraway its center of origin/diversification.

Поступило в редакцию 03.06.2022
Принято к публикации 25.06.2023

Submitted 03.06.2022
Accepted 25.06.2023

Senecioneae (Asteraceae) Суккулентного Кару и «география макроэволюции высших растений»: хорологическое эссе

А. К. Тимонин[1], Л. В. Озерова[2], Р. К. Эбервайн[3]

[1] *Московский государственный университет им. М. В. Ломоносова, Ленинские горы, д. 1(12), г. Москва, 119234, Россия*

[2] *Главный ботанический сад им. Н. В. Цицина РАН, ул. Ботаническая, д. 4, г. Москва, 119234, Россия*

[3] *Региональный музей Каринтии, ул. Либерогассе, д. 6, г. Клагенфурт, 9020, Австрия*

Ключевые слова: аллохтонная флора, биогеография, градиент архаичности, зональная стратификация, концепция «колыбель и музей», оттесненные реликты, правило прогрессии, центры происхождения, экваториальная помпа, Юго-Западная Африка.

Аннотация. Географическая специфика макроэволюции проявляется в том, что высшим таксонам в целом свойственно упорядоченное размещение в ареале архаичных и продвинутых представителей. Предложенные объяснения этой упорядоченности противоречивы и к тому же плохо тестируемы, поскольку оперируют слишком длительными временными интервалами, в течение которых могли происходить неоднократные преобразования как среды, так и ареалов, не выявляемые в палеонтологической летописи. Парциальная флора *Senecioneae* Суккулентного Кару наилучшим образом подходит для изучения географических закономерностей макроэволюции: 1) природные условия Суккулентного Кару сформировались за 10 млн лет в результате однонаправленного изменения климата, что исключает значительные флуктуации ареалов населяющих его таксонов; 2) филогения *Senecioneae* весьма полно реконструирована и не искажена вымираниями, по крайней мере, на уровне родов; 3) эта флора аллохтонна, что упрощает интерпретацию результатов. *Senecioneae* в Суккулентном Кару в равной мере представлены архаичными и высокопродвинутыми родами при полном отсутствии родов среднего уровня эволюционной продвинутости. Такую представленность невозможно объяснять концепцией «колыбели и музея», поскольку Суккулентное Кару лежит за пределами центра происхождения/диверсификации *Senecioneae*. Концепция зональной стратификации также неприложима к данному случаю, поскольку климат Суккулентного Кару формировался без выраженных флуктуаций. Все остальные концепции тоже неприложимы, поскольку интерпретируют появление пространственного градиента нарастающей архаичности, но не дефицит таксонов среднего уровня эволюционной продвинутости. Специфику флоры *Senecioneae* Суккулентного Кару возможно объяснить тем, что такие варианты организации, которые позволяют высшему таксону осваивать местообитания, существенно отличающиеся от центра его происхождения/диверсификации, возникают в ходе его эволюции редко и разделены значительными временными промежутками. Возникающие в эти промежутки новые формы таксона остаются ограниченными в своем распространении центром его происхождения/диверсификации, а за его пределами встречаются соответственно архаики и наиболее продвинутые формы.

Any taxa always evolve within their areas which are an indispensable attribute of every taxon (Geptner, 1936; Birstein, 1985; Mordkovich, 2005; Parenti, Ebach, 2009; etc.). Every area is as unique as the taxon itself (Geptner, 1936; Darlington, 1957; Ball, 1983; Mordkovich, 2005; Parenti, Ebach, 2009; etc.). Besides, the areas are mostly unstable in space and time (Hayek, 1926; Wulff, 1944; Darlington, 1957; Kafanov, 1987; Liebherr, Hajek, 1990; Jablonski et al., 2006; Jansson et al., 2013; Zullini, 2018; etc.). At the same time, it is known that archaic and advanced representatives of most of the higher taxa are not evenly neither randomly distributed (Jablonski, 1993; Eskov, 1994). Even though either of these two groups of representatives may occur across the entire area of the higher-rank taxon (Jablonski et al., 2006), they apparently gravitate to different parts of that area. Resultantly, the higher taxon would mostly be represented by its archaic members in one part of its area while by advanced ones in the other area part (Wallace, 1876a; Geptner, 1936; Hennig, 1950; Darlington, 1957; Liebherr, Hajek, 1990; Jablonski, 1993; Eskov, 1994; etc.).

Interpretations within dispersal biogeography

The patterns of distribution of archaic and advanced representatives of a higher taxon within its area were most often analyzed within the framework of dispersal biogeography and explained by specific localization of macroevolutionary transformations of their body plans (Jablonski, 1993). Two explanations for the observed phenomenon have been suggested.

Progression rule explanation

The so-called progression rule has been formulated (originally as *Progressionsregel*) (Hennig, 1950, 1960, 1966) within phylogenetic biogeography which is dating back to Darwin's views (Crisci, Katinas, 2009). According to this rule, the formation of a new taxon is initiated by the expansion of the range of the original taxon and the settlement of its representatives in territories with different environment. When adapting to this environment, they become more and more different from their ancestral species and transform into new species (Darwin, 1872). The now prevailing cladistics proclaims that the origin of every new species at the periphery of expanded area implies that the members of its ancestral species that stayed in the original area are also changed into a new species (Hennig, 1966). Meanwhile, the environment in the original area has hardly changed, if at all. Accordingly, the new species having formed there is only minimally different from the ancestral one (Hennig, 1950; Zunino, Zullini, 2010). Resultantly, evolving higher taxon tends to accumulate its minimally changed archaic representatives in its original area whereas its advanced representatives successively originate at the periphery of its expanding area (Fig. 1); the further from the center of origin of a higher taxon,[1] the more advanced are its members (Hennig, 1950, 1966; Brundin, 1972; Morrone, Crisci, 1995; Morrone, 2009; Zunino, Zullini, 2010; Looney et al., 2016; Zhirkov, 2017).

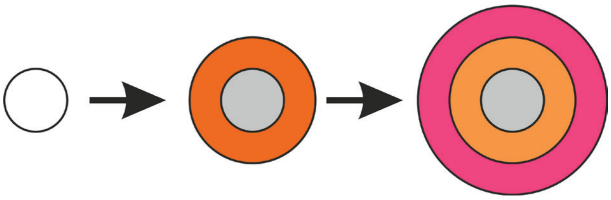

Fig. 1. Centrifugal gradient of taxon advancement; Phylogenetic biogeography, *progression rule* concept. *White* – early-divergent (= archaic) taxon; *Orange* – mid-advanced taxon; *Magenda* – late-divergent (= advanced) taxon.

Ousted relics explanation

Wallace (1876a, b) believed that new, more advanced representatives of a higher taxon permanently emerged in its center of origin, replaced their more archaic predecessors therein and gradually spread outwards this center. His idea has become a key concept of the evolutionary biogeography[2] (Geptner, 1936; Darlington, 1957; Liebherr, Hajek, 1990; Jablonski, 1993; Morrone, Crisci, 1995; Kafanov, Kudryashov, 2000; Morrone, 2009; Zunino, Zullini, 2010; Zhirkov, 2017; etc.). It has also generally been confirmed by paleontological data (Martynov, 1938; Meyen, 1987b; Jablonski, 1993; Naimark, 2001; Jablonski et al., 2006, 2013; Harnik et al., 2010; Brown, 2014). Especially eurybiontic *bridge species* spread beyond their centers of origin/diversification without further speciation (Jablonski et al., 2013). In other cases, the taxon spreading outside its center of origin/diversification entails the origin of new low-rank taxa (species or genera) (Stehli et al., 1969; Krug et al., 2008) which have hardly changed their original bauplan (Wallace, 1876a; Geptner, 1936; Wulff, 1933; Zarenkov, 2017). Therefore, members of the higher taxon that spread out of its center of origin/diversification retain the advancement level they had at the time of their origin. Accordingly, the most advanced representatives of a higher taxon inhabit its center of origin/diversification, whereas its primitive members are ousted to the periphery of this taxon area (Fig. 2); the more primitive is the representative, the more distantly it is ousted (Hillenius, 1964).

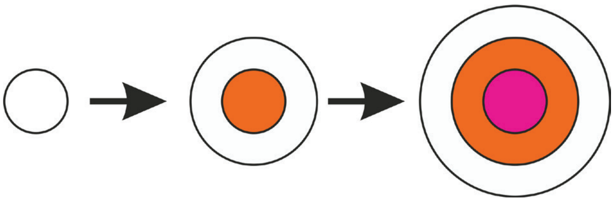

Fig. 2. Centripetal gradient of taxon advancement; Evolutionary biogeography, *ousted relics* concept. *White* – early-divergent (= archaic) taxon; *Orange* – mid-advanced taxon; *Magenda* – late-divergent (= advanced) taxon.

Location of the centers of origin/diversification of taxa

Centers of origin/diversification of higher-rank taxa are as numerous and unique as the taxa themselves (Patterson, 1983). However, their

---

[1] Every taxon inevitably arises in a specific area and has therefore its own center of origin (Patterson, 1983; Santos, 2007; Zunino, Zullini, 2010; Zullini, 2018). However, its location is accurately identifiable neither from the modern areas of subordinate taxa, nor from paleontological data (Hayek, 1926; Geptner, 1936; Croizat et al., 1974; Nelson, 1983; Patterson, 1983; Newman, 1991; Bremer, 1992; Santos, 2007; Zunino, Zullini, 2010). Therefore, the researchers actually operate with observed or reconstructed centers of dispersion (Lemée, 1976), or ancestral areas (Bremer, 1992; Morrone, 2009; Ladiges et al., 2012), or centers of diversification (Naimark, 2001), which are not considered to coincide exactly with the actual centers of origin of taxa concerned.

[2] This concept has also been known as Taylor's principle (Geptner, 1936), or the *ousted relics* theory (Chernov, 1988; Kafanov, Kudryashov, 2000; Eskov, 2008; Zarenkov, 2017), or else the *diversity pump* concept (Valentine, 1969) in its simplified later version (Buzas, 1972; Jablonski, 1993; Gage, 2004; Leighton, 2005; Schüller et al., 2013; etc.).

reconstructed locations show their latitudinal coincidence. The centers of origin of higher taxa are thought to be in extratropical (even high-latitude) zones of the Northern Hemisphere (Wallace, 1876a, b; Mathew, 1915; Wulff, 1933; Geptner, 1936; Lemée, 1967), or of the Southern one (Schüller et al., 2013), or else of both Hemispheres (Wulff, 1933; Valentine, 1969; Fedonkin, 1996) as well as in the tropics (Darlington, 1957; Vtorov, Drozdov, 1978; Van der Spoel, 1983; Goldberg et al., 2005; Krug et al., 2008; Jansson et al., 2013; Rolland et al., 2014) and either in low or high latitudes according to a taxon under consideration (Valentine, 1984).

The inference that most of higher taxa originate in tropics and spread later towards higher latitudes is in a good agreement with the paleontological data (Thorne, 1977; Kafanov, 1987; Meyen, 1987b; Doyle et al., 1990; Zherikhin, 1992; Jablonski, 1993; Harnik et al., 2010; Jablonski et al., 2013; Brown, 2014; Coiro et al., 2019). It is a cornerstone of both Darlington's (1957) *out-of-the-tropics* concept and Meyen's (1987a) *equatorial pump* concept[3] (Fig. 3). The emerging new taxa replace the more archaic representatives of their embracing higher taxon to result not only in ousting of these archaic members towards the high-latitude periphery of the area of embracing taxon but in *extraequatorial persistence* of the archaic forms (Meyen, 1987b), this persistence being the longer the further from the equatorial zone they dwell.

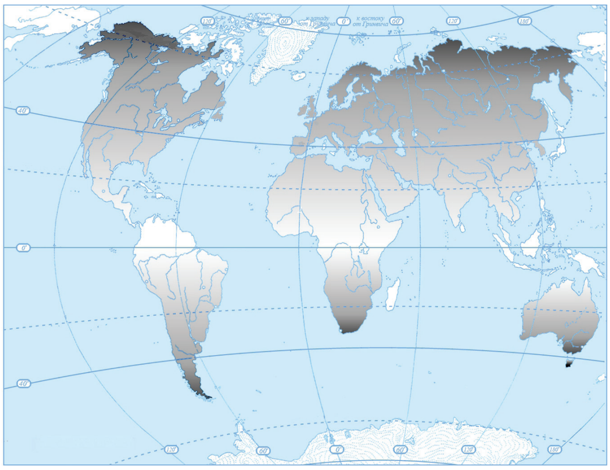

Fig. 3. Unidirectional poleward archaism gradient; *Out of tropics/equatorial pump* concept. More gray means more archaism.

Causes of the extraequatorial persistence of archaics

Many taxa managed to spread from the tropics they had arisen to high latitudes in their lifespan (Ross, 1988; Jablonski et al., 2013). As the advanced representatives of a taxon emerge in some time lag after the archaic ones, they arrive at high latitude areas also in some time lag to result in latitude positive gradient of archaic forms and their extraequatorial persistence (Wallace, 1876a; Geptner, 1936). However, the potential rate of species expansion is very high (see Eskov, 1984; Sauer, 1988). Therefore, successive emergences and expansions of more advanced members of a taxon would facilitate the latitudinal positive gradient of archaic forms only of lower taxa, *viz.* the species and perhaps also the genera (Timonin, 2011), while this gradient is also found in taxa of a higher ranks (Darlington, 1957; Meyen, 1987b; Chernov, 1988; Jablonski, 1993).

Not all taxa emerging in the tropics move to higher-latitude areas. Most middle rank taxa emerging within the tropics stay therein (Stehli et al., 1969; Chernov, 1988; Leighton, 2005; Jablonski et al., 2006, 2013; Arita, Vásquez-Domínguez, 2008; Krug et al., 2008; Harnik et al., 2010; Brown, 2014) either due to purely stochastic processes (Arita, Vásquez-Domínguez, 2008), or because they are unable to develop adaptations to the extratropical climates (Chernov, 1988; Harnik et al., 2010; Brown, 2014; Azovsky et al., 2016)[4]. Therefore, the archaic representatives of a higher taxon gradually accumulate in the tropics as the more advanced ones emerge (Jablonski et al., 2006, 2013). The tropics are thus both the *cradle* for new forms of the higher taxon and the *museum*[5] which preserves its archaic representatives (Gaston, Blackburn, 1996; Mordkovich, 2005; Jablonski et al., 2006, 2013; Moreau, Bell, 2013). The archaic forms of the higher taxon do not actually displace towards the extratropical periphery of its area (Jablonski et al., 2006), so the latitudinal archaism gradient of the higher taxon should be attributed to the fact that the diversity of its archaic forms decreases much slower with the latitude than the diversity of its advanced forms. Some deficiency of the advanced forms of a higher taxon is resultantly observable at high lati-

---

[3] Some higher taxa have most probably emerged in extratropical regions as evidenced by the paleontological data (Meyen, 1987b; Jablonski, 1993; Leighton, 2005; Eskov, 2008; Jansson et al., 2013; Rolland et al., 2014). The number of such taxa seems to increase during periods of reduced climate zonality (Eskov, 2008), but such taxa are still few in number and rather represent exceptional cases that do not refute the general pattern (see Fischer, 1960) described by the concepts of the *equatorial pump* and *out-of-the-tropics*.

[4] Jansson et al. (2013) speculate that taxon expansion to a different climatic zone is fairly frequently and is not that challenging; however, the subsequent diversification of the taxon in this zone is drastically restricted which creates the impression that there are some obstacles to latitudinal expansion of lower rank taxa.

[5] The tropics are asserted to be only a museum of the archaic forms but no way the cradle of new forms (Stebbins, 1974; Endress, 1990). This statement largely ignores the paleontological evidence.

tudes (Chernov, 1988; Mordkovich, 2005; Jablonski et al., 2006, 2013).

The outlined *cradle and museum* concept implicitly assumes the universal and essentially unidirectional orthogenetic narrowing of the adaptive capabilities of a higher taxon in the course of its evolutionary advancing, the assuming seeming highly questionable. In addition, the fact that the high-latitude decreasing of the diversity of advanced forms of a higher taxon hardly affects it's the most advanced members is unexpected and inexplicable within the framework of this concept (Chernov, 1978).

Interpretations within contracting area reasoning

Both *Progressionsregel* and *diversity pump* concepts are completely dispersal; they accordingly reason the taxon archaism gradient with expansion of taxon areas. However, the development of the taxon areas is equally affected by their expansion and contraction (Geptner, 1936; Wulff, 1944; Van der Spoel, 1983; Eskov, 1984; Newman, Foster, 1987; Leighton, 2005; Arita, Vásquez-Domínguez, 2008; Jablonski et al., 2013; etc.). Contractions of the taxon areas have also been named as the major, if not the only reason for the latitudinal archaism gradients within higher taxa.

Inverse latitudinal archaism gradient

The latitudinal archaism gradient of avian tribes (Gaston, Blackburn, 1996) and families of woody dicotyledons (Kerkhoff et al., 2014) has been attributed to the contraction of their areas and their relocation to lower latitudes caused by Late Tertiary and Quaternary cooling in the high latitudes and succeeded by recolonization of high latitudes with the subsequent climate warming. Contractions of their areas were total, but recolonizations of high latitudes turned out selective: only advanced representatives of higher taxa were able to recolonize high latitudes, as they considerably surpassed the archaic forms as regards to their *colonizing potential* (Gaston, Blackburn, 1996; Kerkhoff et al., 2014). Resultantly, archaic representatives of higher taxa are now concentrated in the tropics, while evolutionary advancement and youth of their representatives increase with the latitude (Fig. 4). Thus, latitudinal archaism gradients are inverse in these taxa as regards to mostly ones described in biogeography (Gaston, Blackburn, 1996). These inverse latitudinal gradients of taxon archaism have been concluded from the modern distribution of the taxa concerned. So, these gradients characterize just the present distribution of archaic and advanced representatives of these taxa. Such a distribution could be a short-term pattern which could show the specifics of area transformations during periods of rapid (as compared to the rate of evolutionary processes) climate fluctuations, the pattern being principally different from the geographic modes of macroevolution under long-term, rather stable abiotic environment (Emeljanov, 2004).

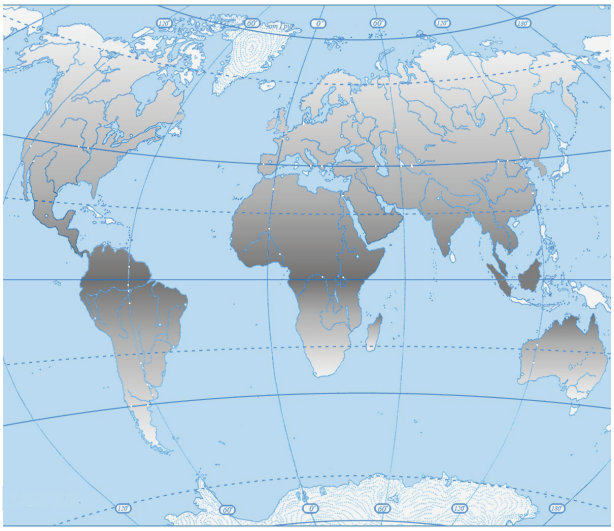

Fig. 4. Inverse unidirectional archaism gradient. More gray means more archaism.

Zonal stratification concept

The latitudinal archaism gradient of higher taxa is attributed to contractions of areas of previously cosmopolitan/subcosmopolitan taxa in the framework of Zherikhin–Eskov's concept of zonal stratification (Zherikhin, 1978; Eskov, 1994, 2008). The tropics are traditionally interpreted broadly in biogeography (Darlington, 1957; Fischer, 1960; Stehli et al., 1969; Buzas, 1972; Valentine, 1984; Meyen, 1987b; Newman, Foster, 1987; Jablonski, 1993; Leighton, 2005; Mordkovich, 2005; Jablonski et al., 2006, 2013; Arita, Vásquez-Domíngez, 2008; Krug et al., 2008; Harnik et al., 2010; Jansson et al., 2013; Brown, 2014; Kerkhoff et al., 2014; Rolland et al., 2014; Zarenkov, 2017), but the authors of the *zonal stratification* concept follow Razumovsky (1971) and Vakhrameev (1991) and clearly distinguish the tropical zone *per se*[6] and two subtropical ones[7]. Maximal number of archaic forms has been encountered specifically in the subtropical zones and not in the tropical one (Fig. 5) (Razumovsky, 1971, 1999; Zherikhin, 1978; Valentine, 1984; Eskov, 1994, 2008).

---

[6] "Equatorial" in Kafanov, Kudryashov (2000).

[7] "Tropical" in Kafanov, Kudryashov (2000).

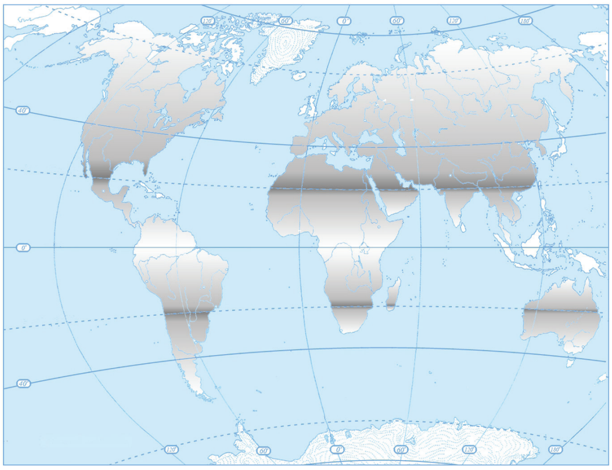

Fig. 5. Bidirectional archaism gradient; *zonal stratification* concept. More gray means more archaism.

Zherikhin (l. c.) and Eskov (l. c.) proceed from the idea of the low thermal gradient and evenness of the Earth climate in the Mesozoic–Early Cenozoic (Théel, 1911–1912; Hayek, 1926; Razumovsky, 1971; Zherikhin, 1978; Newman, Foster, 1987; Eskov, 1994, 2008; Kafanov, Kudryashov, 2000; Krassilov, 2006) or even earlier (Valentine, 1969; Vakhrameev, 1991). The climate of that time is assumed to have been very similar with the modern subtropical climate in rather wide zone that stretched from the equator to fairly high latitudes (Zherikhin, 1978; Vakhrameev, 1991; Eskov, 1994, 2008)[8].

Such an evenness of the environment is thought to have resulted in that centers of origin/diversification of the higher taxa were scattered disorderly on the Earth, the taxon archaism gradients were numerous and multidirectional, and not only higher taxa but also very many lower-rank ones were cosmopolitan (Eskov, 2008). The thermal gradient on the Earth began to grow from the mid-Tertiary due to high-latitude cooling and contemporal warming in the subequatorial (tropical *sensu stricto*) zone (Razumovsky, 1971, 1999; Zherikhin, 1978; Valentine, 1984; Newman, Foster, 1987; Raymond et al., 1989; Newman, 1991; Eskov, 1994, 2008). The area of the formerly global climate and areas of taxa adapted to that climate contracted to the modern subtropical zones; accordingly, the new biotas of more advanced forms emerged within the equator zone as well as in temperate and high latitudes, where the climate significantly changed (Zherikhin, 1978; Eskov, 1994, 2008). The latitudinal archaism gradient resultantly became two-directional, *viz.* from the equator to the subtropics and from the poles to the subtropics.

Resumptive concept and its drawbacks

Increasing of latitudinal thermal contrast is a long-term but transitory transformation of the Earth's climates. Epochs of clear latitudinal zones of climate alternate with epochs of a globally equalized warm (subtropical) climate. Accordingly, the regimes of zonal stratification and equatorial pump, which determine the geographic pattern of macroevolution, also alternate (Eskov, 1994, 2008).

While there is now a general consensus regarding past cardinal changes of the Earth's climates, but the existence of globally equalized subtropical climates during the Phanerozoic which is *a sine qua non* prerequisite for the zonal stratification, is highly contestable (Hayek, 1926; Chernov, 1988; Emeljanov, 2004; etc.). Warming and cooling of climates were often accepted to be global against the background of maintained steep latitudinal thermal gradient (see Chumakov, 1993)[9]. Climate transformations of this kind resulted in irregular shifts, widening, and narrowing of climate zones, and also in appearance and disappearance of the polar climate (Hayek, 1926; Geptner, 1936; Fischer, 1960; Chernov, 1975; Gladenkov, 1995; Kafanov, Kudryashov, 2000; Leighton, 2005; Jansson et al., 2013; etc.). Those climate transformations must have been accompanied by appropriate changes of taxa areas. However, no such changes in taxon areas could result in concentration of their archaic representatives precisely in subtropical zones.

Test model

The fact that macroevolutionary processes are geographically structured (Jablonski, 1993) seems to be taken for granted. Nevertheless, any concrete distribution patterns of archaic and advanced representatives of higher taxa as well as the causes of these patterns have been described variably. These disagreements are possibly attributable to the diversity of the taxa *per se* (Buzas, 1972; Jablonski, 1993;

---

[8] The climate was even suggested to have been tropical everywhere from the equator up to Polar Regions during the early Paleogene (Théel, 1911–1912).

[9] Cosmopolitanism of Cretaceous taxa under steep thermal gradient was once attributed to their exceeding eurythermy, while their Cenozoic descendants were ascribed to progressing stenothermy (Szafer, 1952). Eurythermy and latitudinal cosmopolitanism are also known in some modern genera and even species of water organisms (Ross, 1983; Jablonski et al., 2013). Both may well have been inherent in Cretaceous taxa (although the universal cosmopolitanism of the Cretaceous biotas is bewildering, if only this phenomenon were real). However, no progressing stenothermy could have concentrated archaic representatives of taxa in any latitudinal zone under clear climate zonality.

Gage, 2004; Leighton, 2005; Rolland et al., 2014) or to differences in geographic patterns of macroevolution at different levels of the taxonomic hierarchy (Emeljanov, 2004). Since all biogeographical patterns are of statistical nature (Jablonski et al., 2013), then further studies of geographic distribution of both archaic and advanced representatives of various higher taxa are required to distinguish between spatial-temporal patterns of macroevolution and mere statistical deviations[10].

Model selection

As a matter of fact, the current area of any modern taxon can be revealed in much detail. However, observed current areas of taxa are a result of their expansion and regional extinction (Wulff, 1944; Darlington, 1957; Leighton, 2005; Jablonski et al., 2006; Jansson et al., 2013; etc.) which could have happened repeatedly in many cases (Jablonski et al., 2006). The temporal dynamics of taxon areas can be reconstructed on the base of their modern distribution, but such reconstructions are fraught with gross mistakes if not checked against paleontological data (Liebermann, 2002; Jablonski et al., 2006; Eskov, 2008)[11].

The application of paleontological data for reconstructing dynamics of taxon areas is also highly restricted due to their limited availability and fragmented nature (Haeckel, 1866; Liebermann, 2002). Of Phanerozoic organisms, there are only all classes of skeletal invertebrates (Prothero, 2013), many orders of vascular plants (Meyen, 1987a), and probably also all families of terrestrial tetrapods (Chernykh, 1986; Kalmar, Currie, 2010) that seem to be represented as fossils. On contrary, some 90 % of the total species and genera did not leave any trace in the paleontological record (see Foote, Raup, 1996)[12]. This makes our knowledge of the areas of higher taxa that include these genera and species certainly incomplete; moreover, the extent of this data gap can hardly be accurately estimated. Even when fossils are preserved, they merely evidence the existence of a certain taxon at a certain time in certain site, but they do not allow us to assess confidently the whole taxon area, let alone its temporal changes (Hayek, 1926; Zunino, Zullini, 2010; Jablonski et al., 2013; Zullini, 2018). Therefore, the paleobotanists are doomed to operate with more or less justified reconstructions even when collecting paleobiogeographical data (Makridin, Meyen, 1988).

In addition, the use of paleontological data to study the geographical patterns of macroevolution is hampered by the fact that the time sequence of the appearance of representatives of higher taxa in the fossil record often does not correspond to the sequence of their actual appearance (Morrone, 2009). Moreover, many characters of organisms are lost in course of their fossilization to result in that rather many fossil genera as well as taxa of other ranks are really paraphyletic groups (Foote, Sepkoski, 1999), thereof the usability of such taxa for studying geographic patterns of macroevolutionary processes further decreases (Brundin, 1972; Parenti, Ebach, 2009; Ladiges et al., 2012).

The above discussion clearly shows that special selection of a model object is necessary for studying geographical features of macroevolution when working either with neontological or with paleontological data.

Suggested perspective

Biogeographic patterns are inextricably linked with the ecological ones (Simpson, 1953a; Morrone, 2009) and are ultimately reduced to the latter[13] (Valentine, 1969; Wiens, Donoghue, 2004; Brown, 2014; Azovsky et al., 2016). Whatever been interpreted, the latitudinal archaism gradient of higher taxa, which has been catching biogeographers mind for a century and a half, shows the manner the taxa colonize regions that are very different ecologically from the centers of taxon origin/diversification. Along with the well-known latitudinal ecological gradient, there is also a gradient of aridity in the tropical (in a broad sense) zone (Fischer, 1960; Brown, 2014). This aridity gradient is coincided by the diversity gradient quite similar with the latitudinal diversity gradient (Fischer, 1960; Wiens, Donoghue, 2004; Brown, 2014). The arid diversity gradient obviously also shows the manner the taxa colonize the territories that sharply differ ecologically from the center of taxon origin/diversification, where the archaic rep-

---

[10] That is, in order to discriminate between the so-called general pattern and paradoxical distribution (Parenti, Ebach, 2009).

[11] According to Donoghue, the distribution of taxa can be reconstructed with the desired accuracy by rigorously recording the time of the clade occurrence using a molecular clock (Donoghue et al., 2001; Donoghue, Moore, 2003). However, the suitability of the molecular clock for this purpose is disputed (Sanmartin, 2012).

[12] Only some 1–2.5 % of species that ever existed on the Earth are assessed to have been preserved in the paleontological record (Durham, 1967). On the other hand, Paul (2009), basing on the results of speculative calculations, believes that all species whenever existed have left fossilized remains, but most of their remains are either not yet found, or not identified due to diagenetic transformations. While this estimation looks inspirational, it is hardly usable now.

[13] "…evolution is essentially an ecological process operating with genetic machinery" (Valentine, 1969: 905).

resentatives of taxa can also accumulate (Cowling, Hilton-Taylor, 1999); therefore, the arid diversity gradient is also suitable for studying the geographical patterns of macroevolution.

Senecioneae **of Succulent Caroo as a test model**

During the expedition work in Southern Africa, Lyudmila V. Ozerova realized that the recent flora of *Senecioneae* in the Succulent Karoo could serve a promising model object for study of geographical patterns of macroevolution.

Succulent Karoo as a perspective region

The Succulent Karoo (Fig. 6) stretches from NNW to SSE as rather long belt in western Republic of South Africa and extreme (south)western Namibia (Jürgens, 1991; Hilton-Taylor, 1996; Mucina et al., 2006). This area has been constantly connected with (modern) Africa since the Proterozoic; it has never been completely covered by the sea since the mid-Jurassic and has therefore been retained land-based connections with the rest of southern Africa since then (Meadows, Watkeys, 1999). Therefore, plant migrations thereto from neighboring territories must have significantly prevailed over long-distance dispersal. Accordingly, the long-distance dispersal must have hardly affected the formation of the modern terrestrial biota of the Succulent Karoo, if any. Then, this accidental and unverifiable (Parenti, Ebach, 2009) dispersal can be safely ignored as a factor of development of Succulent Karoo flora.

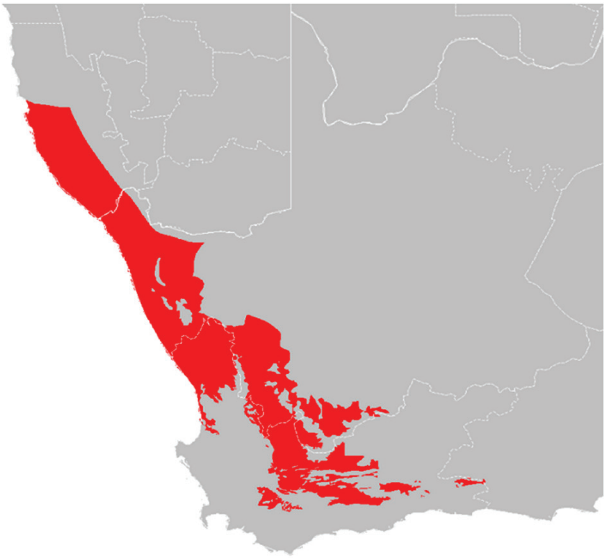

Fig. 6. Succulent Karoo. Taken from open sources: https://en.wikipedia.org/wiki/Succulent_Karoo#/media/File:AT1322_map.png (Free accessed)

The climate of the Succulent Karoo is the most arid variant of the South African Mediterranean climate with regular, total, albeit weak winter rains and summer drought (Hilton-Taylor, 1996; Desmet, Cowling, 1999; Burke, 2004; Mucina et al., 2006; Verboom et al., 2009), with fogs as significant factor of maintaining the humidity regime. This climate began to form about 10 mya in the Middle Miocene (Goldblatt, Manning, 2002; Verboom et al., 2009) and was completely formed by the early Pliocene 5 mya (Goldblatt, Manning, 2002; Mucina et al., 2006; Verboom et al., 2009) or perhaps even later, about 3 mya (Linder, 2005). Thus, the duration of the existence of this climate is quite comparable with the average duration of the existence of species and is much shorter than the average duration of the existence of genera (4 and 12 million years, respectively) of animals (Alekseev et al., 2001), whereas taxa of higher plants of the same ranks are considered even more long-lived (Vassiliev, 1965). Therefore, traceless extinctions of taxa are unlikely to have taken place during the formation of the modern flora of the Succulent Karoo (see also: Goldblatt, Manning, 2002; Linder, 2005)[14]. Added to that is a great stability of climate of the Succulent Karoo during the Pliocene and even Pleistocene (Goldblatt, 1997; Goldblatt, Manning, 2002; Van der Niet, Johnson, 2009). Some characters of Pleistocene climate fluctuations are clearly discernible only in the eastern border regions of the Succulent Karoo (Meadows, Watkeys, 1999; Mucina et al., 2006; Potts et al., 2013). However, even in these regions, the climate fluctuations caused just fragmentation of species areas in mountainous terrains and fluctuations of area boundaries within about 100-kilometer distance, while not a single species seems to have got locally extinct in the Succulent Karoo and re-colonized it (Potts et al., 2013).

Thus, the composition and initial distribution of the species of flowering plants that settled the Succulent Karoo seem to be quite fully detectable in the modern flora of this region. This makes it possible to use this recent flora to analyze the geographic patterns of macroevolution.

Composition and genesis of the flora of *Senecioneae* in the Succulent Karoo

Consideration of recent flora has an advantage over the study of paleontological material, since it

---

[14] The vast majority of species of this flora is believed to have recently resulted from *in situ* speciation in Pliocene–Pleistocene (Goldblatt, 1997; Burke, 2005; Linder, 2005; Mucina et al., 2006; Verboom et al., 2009; Potts et al., 2013).

makes it possible to most fully and accurately take into account the composition and distribution of taxa. In addition, it also makes it possible to study areas of low-rank higher taxa, whose distribution most clearly manifest their ecological specificity, whereas the connection between the area of a taxon and its ecological features is significantly “blurred” for families and is virtually imperceptible for orders and higher-ranked taxa (Chernykh, 1986; Roy et al., 1996). However, the primitive low-rank taxa are extremely difficult to be distinguished from the advanced ones. That is why we follow Platnick (1981) and take early-divergent and late-divergent taxa (as nested in cladogram) for substitutes of archaic and advanced taxa, respectively.

The Succulent Karoo adjoins from the north and northeast to the Fynbos region, with which it is most closely associated floristically (Gibbs Russell, 1987; Jürgens, 1991; Hilton-Taylor, 1996; Cowling, Hilton-Taylor, 1999). Both regions are so similar floristically that they are sometimes combined into a Greater Cape Floristic Region (Jürgens, 1991; Mucina et al., 2006; Verboom et al., 2009; Potts et al., 2013). It is noteworthy that the Fynbos flora is generally represented by much more ancient supra-generic taxa (Cowling, Hilton-Taylor, 1999; Verboom et al., 2009). Consequently, the flora of the Succulent Karoo should be recognized as a depleted aridized derivative of the Fynbos flora (Verboom et al., 2009) and, more broadly, of the Cape flora (Cowling, Hilton-Taylor, 1999).

Asteraceae are one of the main constituents of the flora of the Succulent Karoo (Gibbs Russell, 1987). It is represented by almost 100 genera there and is second only to Mesembryanthemaceae (= Aizoaceae) in such taxa (Hilton-Taylor, 1996)[15]. *Senecioneae*, one of the largest tribes in family Asteraceae, is monophyletic (Pelser et al., 2007; McDonald-Spicer et al., 2019). Phylogenetic relations between its genera and species groups have been revealed in sufficient detail (Pelser et al., 2007). This makes this tribe quite usable for testing concepts on geographic patterns of macroevolution.

The tribe *Senecioneae* is cosmopolitan (Bremer et al., 1994; Nordenstam et al., 2009); in southern Africa, it has its center of origin (Coleman et al., 2003) or center of diversification featuring a number of monophyletic endemic lineages, even including the subtribe *Othonninae* (Bremer et al., 1994; Funk et al., 2005; Nordenstam et al., 2009; McDonald-Spicer et al., 2019). Nevertheless, Ozerova’s field observations and published data (Gibbs Russell et al., 1984; Goldblatt, Manning, 2000, 2002; Germishuizen, Meyer, 2003; Burke, Mannheimer, 2004; Mucina et al., 2006; Manning, Cron, 2011; Nordenstam, 2012; Nordenstam, Pelser, 2012; Cron, 2013; African Plant Database, 2022) show that *Senecioneae* are rather poorly represented in the Succulent Karoo at the generic rank: there are only genera *Bertilia*, *Bolandia*, *Cineraria*, *Curio*, *Crassothonna*, *Kleinia*, *Euryops*, *Hertia*, *Lopholaena*, *Othonna*, and *Senecio*[16]. Some of them are represented by just a single species barely entering the very periphery of the Succulent Karoo, which could hardly be attributed to insufficient dissemination ability of these species. Attention is drawn to the fact that both early-divergent and the late-divergent genera are equally represented in the flora concerned (4 each), while mid-advanced genera clearly avoid the Succulent Karoo (Fig. 7).

All the genera mentioned are the most diverse outside the Succulent Karoo. This fact and the recent emergence of this biome indicate that the centers of origin/diversification of these genera were located outside the Succulent Karoo in the Great Cape Floristic Region, the flora of the latter having been mainly formed *in situ* (Fenner et al., 1997). As the Succulent Karoo is the most aridized area of this Region, then settling of the concerned genera there should be considered a colonization of extreme (arid) habitats by some their species.

Since the Succulent Karoo biome has recently emerged *in situ*, the composition of the genera of *Senecioneae* therein probably demonstrates a minimally distorted sequence of the colonization of this area by differently advanced genera. Therefore, the data obtained are suitable for considering the basic concepts of the geography of macroevolution.

Geography of macroevolution as evidenced by the case study of *Senecioneae* of the Succulent Karoo

The *Senecioneae* of the Succulent Karoo has shown that the early-divergent (archaic) and the late-divergent (most advanced) genera are the most successful in colonization of the extreme arid biotopes, while the deficiency of mid-advanced ones is clearly detectable there. Other biotopes can also be

---

[15] There are 90 genera listed in this work; however, the author accepts genera *Senecio* s. latiss. and *Kleinia* s. lat. not accounting later segregated genera *Bertilia* (Cron, 2013), *Bolandia* (Manning, Cron, 2011), *Caputia* (Nordenstam, Pelser, 2012), *Crassothonna* (Nordenstam, 2012) and *Curio* (Heath, 1997).

[16] Segregation of monophyletic genera from the polyphyletic conglomerate currently designated as *Senecio* is still far from its completion. Therefore, the number of genera of tribe *Senecioneae* in the flora of the Succulent Karoo is expected to grow, but this is unlikely to change their early-divergent-to-late-divergent taxa ratio within this region.

extreme for a higher taxon, because the initial ecological specifics of the taxon determine which environment is extreme for it (Geptner, 1936; Gibert, Deharveng, 2002; Wiens, Donoghue, 2004; Zavarzin, 2012). Such habitats are also occupied mostly by the archaic and the most advanced representatives of higher taxa as evidenced by many taxa of flowering plants of high latitudes and high altitudes (Mazurenko, Khokhryakov, 1984); Hexapoda of polar deserts (Chernov, 1978); fresh-water Isopoda (Hessler, Wilson, 1983); synanthropic Insecta (Zherikhin, 1978); deep-sea Teleostei (Rass, 1959).

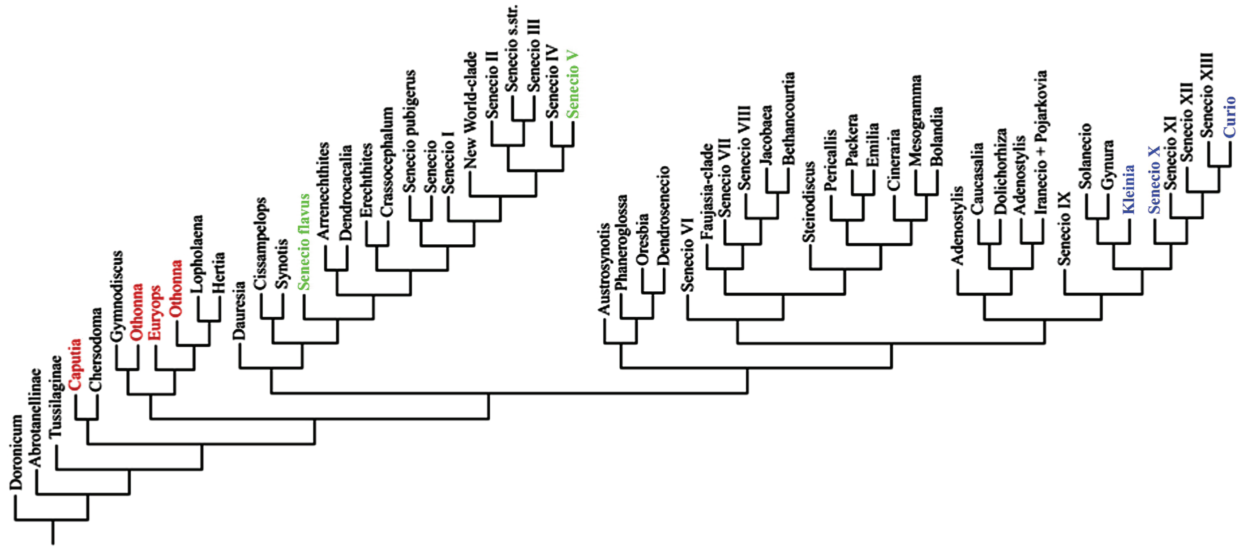

Fig. 7. Phylogeny of the genera of *Senecioneae*, presented in the Succulent Karoo (red). The cladogram is reproduced from Pelser et al. (2007) with great simplifications. Red – early-divergent, Green – mid-advanced, Blue – late-divergent.

Nobody knows yet how widespread is the phenomenon of the colonization of extreme habitats predominantly by archaic and most advanced representatives of a higher taxon, but it is certainly not unique to the *Senecioneae* of the Succulent Karoo. This phenomenon appears to be a fairly general pattern of the geography of macroevolution.

The flora of *Senecioneae* of the Succulent Karoo has almost certainly descended from the Cape flora of higher latitudes, which looks like sharp contradiction to the *phytospreading* from the equatorial region adopted in both *out-of-the-tropics* concept and *equatorial pump* one. However, both concepts ultimately attribute the evolutionary advancing (= progressive semophilesis) in the tropics to the presence of the most favorable environment there, which makes possible the existence of more numerous populations, more taxa, greater variety of selection vectors (Zarenkov, 2017), weakened selective control over the structure of organisms (Vtorov, Drozdov, 1978; Rasnitsyn, 1989; etc.).

The region of the Cape flora is similar to the Succulent Karoo in terms of thermal conditions, but it is more humid. It is thus a region with more favorable environments. Therefore, the spreading of *Senecioneae* genera descendant from the Cape ancestors into the Succulent Karoo is a colonizing of pessimal/extreme habitats by them which is quite comparable with the colonizing thermally pessimal higher-latitude habitats by the taxa of tropical origin. The discrepancy between our data and the predictions of the *out-of-the-tropics* and *equatorial pump* concepts reflects the different localization of optimal and pessimal biotopes in which different taxa evolve. This discrepancy is purely geographical in nature, while there is no controversy between them in terms of biological causality.

The *equatorial pump* concept implies a continuous action of its machinery. More and more advanced representatives of a higher taxon constantly originate in the center of its origin under characteristically favorable environments. Emerging representatives competitively replace their more archaic predecessors and gradually spread from the center of origin of the taxon to regions with pessimal conditions and exclude archaics on their ways. Temporal lag in the colonization of regions outside the center of origin of the taxon by its advanced forms results in a centrifugal archaism gradient and long-term persistence of archaic forms far away from the center of taxon origin (this is essentially a complete reproduction of Wallace's (1876a) reasoning). However, our data show no archaism gradient in the Great Cape Floristic Region. Instead, the early-divergent (archaic) and late-divergent (advanced) genera are represented in equal proportions (ca. 45.5 % for either) in the pessimal Succulent Karoo, while the mid-advanced ones are nearly absent. Acute deficiency of the mid-advanced forms there must be caused by some factor that prevents them from spreading out of the center of diversification of the higher taxon.

Just the *out-of-the-tropics* concept in its *cradle and museum* version implies that the majority of subordinate taxa which emerge within the center of diversification of their embracing higher taxon never leave this center and that only some few of them spread beyond the center limit (Stehli et al., 1969; Leighton, 2005; Jablonski et al., 2006, 2013; Krug et al., 2008). Hence, the deficiency of the advanced forms of a taxon develops in the regions that are pessimal/extreme for this taxon (Chernov, 1978; Kafanov, Kudryashov, 2000), which manifests itself as a centrifugal gradient of increasing archaism. However, the deficiency of just the mid-advanced forms in pessimal/extreme habitats, as evidenced by the *Senecioneae* of the Succulent Karoo and some other cases, is by no way explicable within the framework of either *out-of-the-tropics* concept or its *cradle and museum* version.

Corrected model of geography of macroevolution: a suggestion

Some amendments in the concept of geography of macroevolution are thereof necessary as follows (Timonin, 2011).

Any higher taxon, like a species, is maximally adapted to a certain range of environments alias the adaptive zone of a taxon (Simpson, 1953b, as restricted by Van Valen, 1971). These environments define the area of ecological optimum for this taxon, in which it diversifies in course of time. A higher taxon can forever remain in the area of its ecological optimum, in spite of it can continue diversifying and advancing evolutionary therein; or else, a taxon, as it evolves, can develop an organization that will allow its members to adapt to the environment beyond its ecological optimum. Having thus evolved, the taxon would expand its adaptive zone and become able to spread to areas outside its diversification center, the areas where the environment was pessimal/extreme for it. Any evolutionary transformation causes temporal unbalancing of the adaptive compromise organization of living beings and inevitably diminishes their fitness; the more profound is the transformation, the stronger is decreasing of the fitness (Rasnitsyn, 1989). Accordingly, evolutionary transformations are mostly feasible under reduced selection pressure (Meyen, 1987b). The pessimal/extreme environment causes additional selection pressure. That is why the pessimal/extreme environment makes therefore possible only some minimal changes of the organization of living beings, while any drastic changes are eliminated; such environment virtually preserves the evolved organization (Timonin, 2011; Grandcolas, Trewick, 2016). Hence, speciation is still possible in pessimal/extreme habitats, though it is much impeded (Jansson et al., 2013), but any significant changes of the original organization of living beings are efficiently eliminated and the appearance of more advanced members of the higher taxon is effectively hampered therein.

The adaptive compromise is looser within the area of the ecological optimum of a higher taxon (= center of taxon diversification) and selection control over the organization of living beings is reduced (Rasnitsyn, 1989). More significant restructuring of the organization and progressive semophilesis become accordingly possible within the taxon in such area. Evolutionarily advancing does not always allow emerging subordinate taxa to develop adaptations to pessimal/extreme environments (Timonin, 2011). Semophyletic advancing usually limits opportunity for adapting to pessimal/extreme habitats (Chernov, 1988) and cause the advanced representatives of a taxon remain "locked" within the (ecologically optimal) center of taxon diversification. Such a limitation is by no means permanent. Subsequent evolutionary advancing can over time result in an organism structure that would be adaptable to pessimal/extreme environment and thus would make it possible for the most advanced at that time members of the taxon to spread outside its diversification center. The "diversity pump" would still be functional, but as any pump, it would work in batch and from time to time "push out" the most advanced representatives of higher taxon away from the center of its diversification[17].

Successive pumping out of taxon members from the diversification center is likely to be intermittent by time intervals sufficiently long for subordinate taxa to be significantly transformed[18]. Such

---

[17] This line of reasoning resembles the *taxon cycle* concept (Wilson, 1959 – cited by: Liebherr, Hajek, 1990), but it does not include the requirement for cyclical specialization/despecialization of species.

[18] For example, the clade containing *Caputia* is estimated to have originated about 10 mya and the clade containing *Curio* is estimated to have originated 7 to 5 mya (Pelser et al., 2010); both clades have their representatives in the Succulent Karoo.

advanced forms would be quite different from their archaic counterparts not only in taxonomic characters but also in their reactions to the environment and ways of adaptation to pessimal/extreme environments. These differences would cause that when populating pessimum/extreme areas, the advanced representatives of a higher taxon are more likely to co-exist with, not exclude the archaic ones that had settled therein earlier (Timonin, 2011). As a result, the higher taxon would be represented by its primitive and most advanced members in habitats which are pessimal/extreme for this taxon.

The emerging more advanced forms of a higher taxon would either exclude their archaic counterparts in the center of diversification of this taxon, as the Darlington's (1957) *diversity pump* concept and the Meyen's (1987a) *equatorial pump* concept proclaim, or they would partition an adaptive zone of this taxon (Simpson, 1953a) and coexist with the archaics therein, as the Gaston, Blackburn's (1996) *cradle and museum* concept proclaims. In the latter case, a higher taxon would accumulate its archaic representatives in its diversification center[19].

Repeated 'pumping out" the most advanced forms of a higher taxon from the center of its diversity would result in a gradual accumulation of less and less archaic representatives of this taxon in the pessimal/extreme areas and filling the gap between the archaic and the most advanced forms therein. However, as such "pumpings out" are likely to be separated by long lapses of time, then, the less and less archaic forms of a higher taxon would accumulate in its pessimal/extreme areas at a rather low rate and the contrast between its variously advanced representatives therein would also decrease slowly and become conspicuous only in very long-term pessimal/extreme areas. Sharp contrast between differently advanced representatives of a higher taxon would be inherent in young biomes of ecologically pessimal/extreme regions, where (relatively) significant representation of archaic and most advanced forms concurs with clear deficiency of mid-advanced ones. This is exactly the situation observed in the flora of *Senecioneae* in the Succulent Karoo and also in the fauna of Hexapoda in Arctic deserts (Chernov, 1978).

Most taxa feature their centers of diversification near the Equator (Darlington, 1957; Kafanov, 1987; Meyen, 1987b; Jablonski, 1993; Harnik et al., 2010; Jablonski et al., 2013; Brown, 2014; etc.). Accordingly, the centrifugal gradients of the increasing archaism of representatives of higher taxa take the form of Poleward latitudinal gradients (the further from the Equator, the more archaic forms). If the center of differentiation of a higher taxon is located differently, then the archaism gradient of its representatives still remains centrifugal, but it must inevitably deviate from the Poleward latitudinal direction. Therefore, even the archaism gradient in birds and arboreal dicotyledons directed towards the Equator (Gaston, Blackburn, 1996; Kerhoff et al., 2014), i. e. opposite to the prevailing direction, cannot be considered a refutation of either *out-of-the-tropics* and *equatorial pump* concepts without additional confirmation.

Successively emerging more advanced forms of a higher taxon are undoubtedly unequal in their dispersal and adaptive capabilities to colonize the ecologically pessimal/extreme areas of this taxon. These different capabilities would geographically be expressed in different rate and distance of their spreading out of the center of taxon diversification. If a form with especially large dispersal and adaptive abilities arises at some point in time, it would be able to inhabit areas located much further from the center of differentiation of its embracing taxon than those populated by its more archaic predecessors. If the latter ones are replaced in the center of higher taxon differentiation by subsequent advanced forms, then the archaic representatives of a higher taxon would take areas outside of the center of taxon differentiation and just between those occupied by more advanced representatives (Fig. 8). We do not assert that the concentration of archaics in the subtropics and the predominance of more advanced forms of higher taxon in the equatorial zone and higher latitudes (Zherikhin, 1978; Eskov, 1994, 2008) are just such a case. But we believe it is quite possible, that the location of archaic representatives of a higher taxon between its advanced ones could

---

[19] The accumulation of archaic representatives of a higher taxon at the center of its diversification may in fact be illusory. The archaic taxa are known to settle mountains, sea depths, and other very specific 'marginal' habitats which are often small-sized and ephemeral (Geptner, 1936; Belyaev, 1966; Lemée, 1967; Birstein, 1985; Erwin, 1985; Newman, 1991; Eskov, 1994; Gibert, Deharveng, 2002; Van Dover et al., 2002; Ricklefs, 2005; Moreau, Bell, 2013; Schüller et al., 2013); the archaic forms may also persist as coenophobic ruderals outside complexes of co-adapted species or as pioneer members of successions (Zherikhin, 1979; Dlusskiy, 1981; Kalandadze, Rautian, 1992; Kalandadze et al., 1995; Rautian, Zherikhin, 1997; Markov, Naymark, 1998). The actual distribution of taxa is customary reduced to two-dimensional contours on small-scale maps in biogeography (Makridin, Meyen, 1988), so that very different habitats, including the very specific ones are superposed as if they were one common habitat. Archaic forms populating these habitats in fact exist outside the area of ecological optimum for their higher taxon, i. e. outside the area of evolutionary advancing of this higher taxon. Such archaic forms are biologically in the same relations with the advanced relatives as the archaic forms that persist out of the diversification center of their higher taxon are with the advanced ones populating it.

be a result of the ordinary mechanism of the *equatorial pump* and does not unavoidably require *zonal stratification of climates* to be attributed to.

Concluding remarks

Specific traits of the flora of *Senecioneae* in the Succulent Karoo have allowed us to somewhat adjust the *equatorial pump*/*out-of-the-tropics* concepts. The suggested version of these concepts is consistent with a wider range of biogeographic data. It makes possible to recognize a unified cause for a wider range of phenomena (Poleward latitudinal archaism gradient, reverse latitudinal archaism gradient, bi-directional archaism gradient, variously oriented archaism gradients). We think this version to be promising enough to spend time testing it with other research objects.

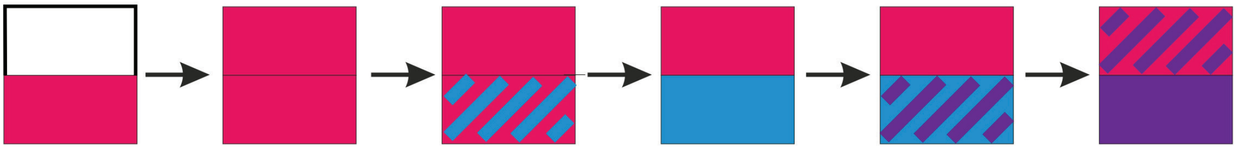

Fig. 8. Suggested corrected model of geography of macroevolution. Some taxon (*Magenda*) arises in region of taxon optimum and then spread into the pessimal/extreme area. More advanced representative of this taxon (*Blue*) evolves in the region of taxon optimum in time and replaces its original counterpart therein. However, it is unable to populate the pessimal/extreme area and remains in the region of optimum. Then, in the region of the optimum, another, even more advanced representative of the taxon (*Violet*) arises, which replaces its once-fortunate predecessor. It is able to adapt to the pessimal environment and spreads therefore into the pessimal/extreme area, where the original representative of the taxon still exists. This latest representative is too different from the original one for the two forms to compete with each other. Resultantly, the pessimal/extreme area is occupied by the primitive and most advanced representatives of the taxon.

Acknowledgements

We are deeply indebted to Dr. E. van Yaarsveld and Dr. D. Gilgenhuys for the organization of expeditions to study the flora of South Africa, and Dr. I. Kadis for her help with translation of the text into English and criticism. A. C. Timonin's work was carried out in accordance to Government order for the Lomonosov Moscow State University (project No. 121032500084-6). L. V. Ozerova's investigation was carried out in accordance to Government order for Tsitsin Main Botanical Garden of Russian Academy of Sciences (project No. 122042700002-6. "Unique Scientific Installation Fund Greenhouse").

REFERENCES / ЛИТЕРАТУРА

African Plant Database (version 4.0.0). [2022]. Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, "Retrieved [set month and year]". URL: http://africanplantdatabase.ch (Accessed 26 May 2023).

Alekseev A. S., Dmitriev V. Yu., Ponomarenko A. G. 2001. Evolution of the taxonomic diversity. In: A. Yu. Rozanov, I. S. Barskov (eds.). *Ekosistemnyye perestroyki i evolyustiya biosfery* [*Ecosystem restructures and the evolution of biosphere*]. Iss. 5. Moscow: GEOS. Pp. 1–126. [In Russian] (***Алексеев А. С., Дмитриев В. Ю., Пономаренко А. Г.*** Эволюция таксономического разнообразия // Экосистемные перестройки и эволюция биосферы. Вып. 5. Под ред. А. Ю. Розанова, И. С. Барскова. М.: ГЕОС, 2001. С. 1–126).

Arita H. T., Vásquez-Domínguez E. 2008. The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. *Ecol. Lett.* 11(7): 653–663.

Azovsky A., Garlitska L., Chertoprud E. 2016. Multi-scale taxonomic diversity of marine harpaticoids: Does it differ at high and low latitudes? *Mar. Biol.* 163(5): article number 94.

Ball I. R. 1983. Planarians, plurality, and biogeographical explanations. In: R. W. Sims, J. H. Price, P. E. S. Whalley (eds.). *Evolution, time, and space: The emergence of the biosphere*. The Systematics Association Special Vol. 23. London: Academic Press. Pp. 409–430.

Belyaev G. M. 1966. *Donnaya fauna naibolshikh glubin (ultraabissali) Mirovogo okeana* [*Bottom fauna of the ultraabyssal depth of the world ocean*]. Moscow: Nauka. 248 pp. [In Russian] (***Беляев Г. М.*** Донная фауна наибольших глубин (ультраабиссали) Мирового океана. М.: Наука, 1966. 248 с.).

Birstein J. A. 1985. *Genesis presnovodnoy, peshchernoy i glubokovodnoy faun* [*Genesis of freshwater, cave and deep-water faunas*]. Moscow: Nauka. 248 pp. [In Russian] (***Бирштейн Я. А.*** Генезис пресноводной, пещерной и глубоководной фаун. М.: Наука, 1985. 248 с.).

Bremer K. 1992. Ancestral areas: a cladistic reinterpretation of the center of origin concept. *Syst. Zool.* 4(4): 436–445.

Bremer K. with assistance of ***Anderberg A. A., Karis P. O., Nordenstam B., Lundberg J., Ryding O.*** 1994. *Asteraceae: Cladistics and classification*. Portland: Timber Press. 752 pp.

Brown J. H. 2014. Why are there so many species in the tropics? *J. Biogeogr*. 41(1): 8–22.

Brundin L. 1972. Phylogenetics and biogeography, reply to Darlington's "practical criticism" of Hennig–Brundin. *Syst. Zool.* 21(1): 69–79.

Burke A. 2004. A preliminary account of patterns of endemism in Namibia's Sperrgebiet – the Succulent Karoo. *J. Biogeogr*. 31(10): 1613–1622.

Burke A. 2005. Endemic plants of the arid Succulent Karoo in Namibia: Towards hypotheses for their evolution. *Ecography* 28(2): 171–180.

Burke A., Mannheimer C. 2004. Plant species of the Sperrgebiet (Diamond Area I). *Dinteria* 29: 79–109.

Buzas M. A. 1972. Patterns of species diversity and their explanation. *Taxon* 21(2/3): 275–286.

Chernov Yu. I. 1975. *Prirodnaya zonalnost i zhivotnyy mir sushi* [*Natural zonation and the terrestrial animal world*]. Moscow: Nauka. 222 pp. [In Russian] (***Чернов Ю. И.*** Природная зональность и животный мир суши. М.: Наука, 1975. 222 с.).

Chernov Yu. I. 1978. *Struktura zhivotnogo naseleniya Subarktiki* [*Structure of the animal population in the Subarctic*]. Moscow: Nauka. 167 pp. [In Russian] (***Чернов Ю. И.*** Структура животного населения Субарктики. М.: Наука, 1978. 167 с.).

Chernov Yu. I. 1988. Philogenetic level and geographic distribution of taxa. *Zool. Zhurn*. 67(10): 1445–1458. [In Russian] (***Чернов Ю. И.*** Филогенетический уровень и географическое распределение таксонов // Зоол. журн. 1988, Т. 67, № 10. С. 1445–1458).

Chernykh V. V. 1986. *Problema tselostnosti vysshikh taksonov: tochka zreniya paleontologa* [*Problem of integrity of higher taxa from palaeontologist's point of view*]. Moscow: Nauka. 142 pp. [In Russian] (***Черных В. В.*** Проблема целостности высших таксонов: точка зрения палеонтолога. М.: Наука, 1986. 142 с.).

Chumakov N. M. 1993. Problems of palaeoclimate in studies on the evolution of the biosphere. In: A. Yu. Rozanov (ed.). *Problemy doantropogennoy evolyutsii biosfery* [*Problems of pre-Antropogenic evolution of the biosphere*]. Moscow: Nauka. Pp. 106–122. [In Russian] (***Чумаков Н. М.*** Проблемы палеоклимата в исследованиях по эволюции биосферы // Проблемы доантропогенной эволюции биосферы. Под ред. А. Ю. Розанова. М.: Наука, 1993. С. 106–122).

Coiro M., Doyle J. A., Hilton J. 2019. How deep is the conflict between molecular and fossil evidence on the age of angiosperms? *New Phytol.* 223(1): 83–99.

Coleman M., Liston A., Kadereit J. W., Abbott R. J. 2003. Repeat intercontinental dispersal and Pleistocene speciation in disjunct Mediterranean and desert *Senecio* (Asteraceae). *Amer. J. Bot.* 90(10): 1446–1454.

Cowling R. M, Hilton-Taylor C. 1999. Plant biogeography, endemism and diversity. In: W. R. J. Dean, S. Milton (eds.). *The Karoo: Ecological patterns and processes*. Cambridge; New York: Cambridge Univ. Press. Pp. 42–56.

Crisci J. V., Katinas L. 2009. Darwin, historical biogeography, and the importance of overcoming binary opposites. *J. Biogeogr*. 36(6): 1027–1032.

Croizat L., Nelson G., Rosen D. E. 1974. Centers of origin and related concepts. *Syst. Zool.* 23(2): 265–287.

Cron G. V. 2013. *Bertilia* – a new monotypic genus in the *Senecioneae* (Asteraceae) from South Africa. *S. Afr. J. Bot.* 88: 10–16.

Darlington P. J. 1957. *Zoogeography: The geographical distribution of animals*. New York: John Wiley & Sons. Inc. xi + 675 pp.

Darwin C. 1872. *The origin of species by means of natural selection, or preservation of favoured races in the struggle for life.* 6th ed. London: John Murray. xxii + 458 pp.

Desmet P. G., Cowling R. M. 1999. The climate of the Karoo – a functional approach. In: W. R. J. Dean, S. Milton (eds.). *The Karoo: Ecological patterns and processes*. Cambridge; New York: Cambridge Univ. Press. Pp. 3–16.

Dlusskiy G. M. 1981. *Muravi pustyn* [*Ants of deserts*]. Moscow: Nauka. 230 pp. [In Russian] (***Длусский Г. М.*** Муравьи пустынь. М.: Наука, 1981. 230 с.).

Donoghue M. J., Bell C. D., Li J. 2001. Phylogenetic patterns in Northern Hemisphere plant geography. *Int. J. Plant Sci*. 162. (Suppl. 6): S41–S52.

Donoghue M. J., Moore B. R. 2003. Toward an integrative historical biogeography. *Integr. Comp. Biol.* 43(2): 261–270.

Doyle J. A., Holton C. L., Ward J. V. 1990. Early Cretaceous tetrads, zonasulculate pollen, and Winteraceae. II. Cladistic analysis and implications. *Amer. J. Bot.* 77(12): 1558–1568.

Durham J. W. 1967. The incompleteness of our knowledge of the fossil record. *J. Paleontol.* 41(3): 559–565.

Emeljanov A. F. 2004. Evolution of the terrestrial biota in the light of biogeography. In: A. F. Alimov (ed.). *Fundamentalnyye zoologicheskiye issledovaniya: teoriya i metody* [*Fundamental zoological researches: Theory and methods*]. Moscow; St. Petersburg: КМК Scientific Press Ltd. Pp. 216–242. [In Russian] (**Емельянов А. Ф.** Эволюция наземной биоты в свете биогеографии // Фундаментальные зоологические исследования: теория и методы. Под ред. А. Ф. Алимова. М.; СПб.: Тов-во науч. изд. КМК, 2004. С. 216–242).

Endress P. K. 1990. Evolution of reproductive structures and functions in primitive angiosperms (Magnoliidae). *Mem. New York Bot. Gard.* 55: 5–34.

Erwin T. L. 1985. The taxon pulse: A general pattern of lineage radiation and extinction among carabid beetles. In: G. E. Ball (ed.). *Taxonomy, phylogeny and zoogeography of beetles and ants*. Dordrecht: W. Junk Publ. Pp. 437–472.

Eskov K. Yu. 1984. Continental drift and problems in historical biogeography. In: Yu. I. Chernov (ed.). *Faunogenez i filotsenogenez* [*Faunogenesis and phylocoenogenesis*]. Moscow: Nauka. Pp. 24–92. [In Russian] (**Еськов К. Ю.** Дрейф континентов и проблемы исторической биогеографии // Фауногенез и филоценогенез. Под ред. Ю. И. Чернова. М.: Наука, 1984. С. 24–92).

Eskov K. Yu. 1994. On macrobiogeographical patterns of the phylogenesis. In: A. Yu Rozanov, M. A. Semikhatov (eds.). *Ekosistemnyye perestroyki i evolyutsiya biosfery* [*Ecosystem restructuring and the evolution of the biosphere*. Iss. 1. Moscow: Nedra. Pp. 199–205. [In Russian] (**Еськов К. Ю.** О макробиогеографических закономерностях филогенеза. Географические аспекты эволюции // Экосистемные перестройки и эволюция биосферы. Под ред. А. Ю. Розанова, М. А. Семихатова. Вып. 1. М.: Недра, 1994. С. 199–205).

Eskov K. Yu. 2008. *Udivitelnaya paleontologiya: istoriya Zemli i zhizni na ney* [*This amazing paleontology: the history of the Earth and life on it*]. Moscow: ENAS. 312 pp. [In Russian] (**Еськов К. Ю.** Удивительная палеонтология: история Земли и жизни на ней. М.: ЭНАС, 2008. 312 с.).

Fedonkin M. A. 1996. Cold water cradle of animal life. *Paleontol. J.* 30(6):669–673.

Fenner M., Lee W. G., Wilson J. B. 1997. A comparative study of the distribution of genus size in twenty angiosperm floras. *Biol. J. Linnean Soc.* 62(2): 225–237.

Fischer A. G. 1960. Latitudinal variations in organic diversity. *Evolution* 14(1): 64–81.

Foote M., Raup D. M. 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiol.* 22(2): 121–140.

Foote M., Sepkoski J., Jr. 1999. Absolute measures of the completeness of the fossil record. *Nature* 398(6726): 415–417.

Funk V. A., Bayer R. J., Keeley S., Chen R., Watson L., Gemeinholzer B., Schilling E., Panero J. L., Baldwin B. G., Garcia-Jacas N., Susanna A., Jansen R. K. 2005. Everywhere but Antarctica: Using a supertree to understand the diversity and distribution of the Compositae. *Biol. Skr.* 55: 343–374.

Gage J. D. 2004. Diversity in deep-sea benthic macrofauna: The importance of local ecology, the larger scale, history and the Antarctic. *Deep-Sea Res.* 2(51): 1689–1708.

Gaston K. J., Blackburn T. M. 1996. The tropics as a museum of biological diversity: An analysis of the New World avifauna. *Proc. R. Soc. London*. B. 263(1366): 63–68.

Geptner V. G. 1936. *Obshchaya zoogeografiya* [*General zoogeography*]. Moscow; Leningrad: Biomedgiz. 548 pp. [In Russian] (**Гептнер В. Г.** Общая зоогеография. М.; Л.: Биомедгиз, 1936. 548 с.).

Germishuizen G., Meyer N. L. (eds.). 2003. Plants of southern Africa: An annotated checklist. *Strelitzia* 14: Pp. i–vi + 1–1231.

Gibbs Russell G. E. 1987. Preliminary floristic analysis of the major biomes in southern Africa. *Bothalia* 17(2): 213–227.

Gibbs Russell G. E., Germishuizen G., Herman P., Oliver O., Perold S. M., Reid C., Retief E., Smook L., van Rooy J., Welmen W. G. 1984. List of species of southern African plants. *Mem. Bot. Survey S. Afr.* 48: Pp. i–v + 1–144.

Gibert J., Deharveng L. 2002. Subterranean ecosystems: A truncated functional biodiversity. *BioSci.* 52(6): 473–481.

Gladenkov Yu. B. 1995. The migration of marine palaeobiotic communities: Causes and consequences. In: A. Yu. Rozanov, M. A. Semikhatov (eds.). *Ekosistemnyye perestroyki i evolyutsiya biosfery* [*Ecosystem restructures and the evolution of biosphere*]. Iss. 2. Moscow: Palaeontologicheskiy institut RAN. Pp. 129–132. [In Russian] (**Гладенков Ю. Б.** Миграции морских палеобиотических сообществ: причины и следствия // Экосистемные перестройки и эволюция биосферы. Под ред. А. Ю. Розанова, М. А. Семихатова. Вып. 2. М.: Палеонтол. ин-т РАН, 1995. С. 129–132).

Goldberg E. E., Roy K., Lande R., Jablonski D. 2005. Diversity, endemism, and age distribution in macroevolutionary sources and sinks. *Amer. Natur.* 165(6): 623–633.

Goldblatt P. 1997. Floristic diversity in the Cape Flora of South Africa. *Biodiv. Conserv.* 6(3): 359–377.

Goldblatt P., Manning J. C. 2000. Cape plants: A conspectus of the Cape Flora of South Africa. *Strelitzia* 9: 1–743.

Goldblatt P., Manning J. C. 2002. Plant diversity of the Cape Region of southern Africa. *Ann. Missouri Bot. Gard.* 89(2): 281–302.

Grandcolas P., Trewick S. A. 2016. What is the meaning of extreme phylogenetic diversity? The case of phylogenetic relict species. In: R. Pellens, P. Grandcolas (eds.). *Biodiversity conservation and phylogenetic systematics*. Springer Nature. Pp. 99–115.

Haeckel E. 1866. *Generelle Morphologie der Organizmen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie. Bd. 2. Allgemeine Entwickelungsgeschichte der Organismen*. Berlin: Georg Reimer. clx + 462 pp.

Harnik P. G., Jablonski D., Krug A. Z., Valentine J. W. 2010. Genus age, provincial age and the taxonomic structure of marine faunas. *Proc. R. Soc. London*. B. 277(1699): 3427–3435.

Hayek A. 1926. *Allgemeine Pflanzengeographie*. Berlin: Gebrüder Borntraeger. viii + 409 pp.

Heath P. V. 1997. Three new generic names in Asteraceae: Part 1. *Calyx* 5: 136.

Hennig W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutsch. Zenralverlag. 370 pp.

Hennig W. 1960. Die Dipteren-Fauna von Neuseeland als systematisches und tiergeographisches Problem. *Beitr. z. Entomologie* 10(3/4): 221–329.

Hennig W. 1966. *Phylogenetic systematics*. Urbana: Chicago: Univ. Illinois Press. 263 pp.

Hessler R. R., Wilson G. D. F. 1983. The origin and biogeography of malacostracan crustaceans in the deep sea. In: R. W. Sims, J. H. Price, P. E. S. Whalley (eds.). *Evolution, time, and space: The emergence of the biosphere*. The Systematics Association Special. Vol. 23. London: Academic Press. Pp. 227–254.

Hillenius D. 1964. Periphery and archaic forms. *Beaufortia* 11(138): 78–83.

Hilton-Taylor C. 1996. Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. In: L. J. G. van der Maesen, X. M. van der Burgt, J. M. van Medenbach de Rooy (eds.). *The biodiversity of African plants: Proc. XIVth AFTFAT Congress, 22–27 August 1994*. Wageningen; Dordrecht: Kluwer Acad. Publ. Pp. 58–72.

Jablonski D. 1993. The tropics as a source of evolutionary novelty through geological time. *Nature* 364(6433): 142–144.

Jablonski D., Belanger C. L., Berke S. K., Huang S., Krug A. Z., Roy K., Tomasovych A., Valentine J. W. 2013. *Out of tropics*, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *PNAS* 110(26): 10487–10494.

Jablonski D., Roy K., Valentine J. W. 2006. Out of tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science* 314(5796): 103–106.

Jansson R., Rondríguez-Castañeda G., Harding L. E. 2013. What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution* 67(6): 1741–1755.

Jürgens N. 1991. A new approach to the Namib Region. I: Phytogeographic subdivision. *Vegetatio* 97(1): 21–38.

Kafanov A. I. 1987. The Willis' "age and area" rule and latitudinal heterochrony of marine biota. *Zhurn. obsch. Biol.* 48(1): 105–114. [In Russian] (***Кафанов А. И.*** Правило «age and area» Дж. Виллиса и широтная гетерохронность морской биоты // Журн. общ. биол., 1987. Т. 48, № 1. С. 105–114).

Kafanov A. I., Kudryashov V. A. 2000. *Morskaya biogeografiya* [*Marine biogeography: A text-book*]. Moscow: Nauka. 176 pp. [In Russian] (***Кафанов А. И., Кудряшов В. А.*** Морская биогеография: Учебное пособие. М.: Наука, 2000. 176 с.).

Kalandadze N. N., Rautian A. S. 1992. Heuristic model of evolution of community and its taxonomical and ecological diversity. In: B. A. Yurtsev (ed.). *Biologicheskoye raznoobraziye: podkhody k izucheniyu i sokhraneniyu* [*Biological diversity: The approaches to the study and conservation*]. St. Petersburg: Zoologicheskiy institut RAN. Pp. 65–80. [In Russian] (***Каландадзе Н. Н., Раутиан А.С.*** Эвристическая модель эволюции сообщества и его таксономического и экологического разнообразия // Биологическое разнообразие: подходы к изучению и сохранению. Под ред. Б. А. Юрцева. СПб.: Зоол ин-т РАН, 1992. С. 65–80).

Kalandadze N. N., Rautian A. S., Rautian G. S. 1995. Ecogenesis of carnivorous tetrapods of Southern America. In: V. A. Krassilov, A. Yu. Rozanov (eds.). *Evolutsiya ekosistem: Mezhdunarodnyi simpozium (g. Moskva, 26–30 sentyabrya 1995 g.): tesisy dokladov* [*Ecosystem evolution: Abstracts Intern. Symp. Moscow, 26–30 Sept. 1995*]. Moscow: Palaeontologicheskiy institut RAN. P. 54. [In Russian] (***Каландадзе Н. Н., Раутиан А. С., Раутиан Г. С.*** Экогенез плотоядных тетрапод Южной Америки // Эволюция экосистем: Междунар. симпоз. (г. Москва, 26–30 сентября 1995 г.): тез. докл. Под ред. В. А. Красилова, А. Ю. Розанова. М.: Палентол. ин-т РАН, 1995. С. 54).

Kalmar A., Currie D. J. 2010. The completeness of the continental fossil record and its impact on patterns of diversification. *Paleobiol.* 36(1): 51–60.

Kerkhoff A. J., Moriarty P. E., Weiser M. D. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *PNAS* 111(22): 8125–8130.

Krassilov V. A. 2006. Paleontology and paradigms of modern natural sciences. In: S. B. Rozhnov (ed.). *Evolutsia biosfery i bioraznoobraziya: k 70-letiyu A. Yu. Rozanova* [*Evolution of the biosphere and biodiversity. To the 70th anniversary of A. Yu. Rozanov*]. Moscow: KMK Scientific Press Ltd. Pp. 7–19. [In Russian] (***Красилов В. А.*** Палеонтология и парадигмы современного естествознания // Эволюция биосферы и биоразнообразия: К 70-летию А. Ю. Розанова. Под ред. С. В. Рожнова. М.: Тов-во науч. изд. КМК, 2006. С. 7–19).

Krug A. Z., Jablonski D., Valentine J. W. 2008. Species–genus ratios reflect a global history of diversification and range expansion in marine bivalves. *Proc. R. Soc. London*. B. 275(1639): 1117–1123.

Ladigies P. Y., Bayly M. J., Nelson G. 2012. Searching for ancestral areas and artifactual centers of origin in biogeography: With comment on East-West patterns across Southern Australia. *Syst. Biol.* 61(4): 703–708.

Leighton L. R. 2005. The latitudinal diversity gradient through deep time: Testing the "Age of the Tropics" hypothesis using Carboniferous productidine brachiopods. *Evol. Ecol.* 19(6): 563–581.

Lemée G. 1967. *Précis de biogéographie*. Paris: Masson et Cie. 358 pp.

Liebermann B. S. 2002. Phylogenetic biogeography with and without the fossil record: Gauging the effect of extinction and paleontological incompleteness. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 178(1–2): 39–52.

Liebherr J. K., Hajek A. E. 1990. A cladistic test of the taxon cycle and taxon pulse hypotheses. *Cladistics* 6(1): 39–59.

Linder H. P. 2005. Evolution of diversity: The Cape flora. *Trends in Plant Sci.* 10(11): 536–541.

Looney B. P., Ryberg M., Hampe F., Sánchez-García M., Matheny P. B. 2016. Into and out of tropics: Global diversification patterns in a hyperdiverse clade of ectomycorrhizal fungi. *Mol. Evol.* 25(2): 630–647.

Makridin V. P., Meyen S. V. 1988. Paleobiogeographic studies. In: V. V. Menner, V. P. Makridin (eds.). *Sovremennaya paleontologiya. T. 2. Metody, napravleniya, problemy, prakticheskoye prilozheniye* [*Modern paleontology. Vol. 2. Methods, research directions, problems, practical application: Reference manual*. Moscow: Nedra. Pp. 5–32. [In Russian] (***Макридин В. П., Мейен С. В.*** Палеобиогеографические исследования // Современная палеонтология. Т. 2. Методы, направления, проблемы, практическое приложение: справочное пособие. Под ред. В. В. Меннера, В. П. Макридина. М.: Недра, 1988. С. 5–32).

Manning J. C., Cron G. V. 2011. The genus *Bolandia* (Asteraceae: *Senecioneae*) expanded to include three discoid taxa previously treated as *Senecio scapiflorus*, and a note on the typification of *Brachyrrhynchos*. *S. Afr. J. Bot.* 77(1): 203–215.

Markov A. V., Naymark E. B. 1998. *Kolichestvennyye zakonomernosti makroevolyutsii: opyt primeneniya sistemnogo podkhoda k analizu razvitiya nadvidovykh taksonov* [*Quantitative regularities of macroevolution: An attempt of systemic analysis of the development of taxa of above-species rank*]. Moscow: GEOS. 318 pp. [In Russian] (***Марков А. В., Наймарк Е. Б.*** Количественные закономерности макроэволюции: опыт применения системного подхода к анализу развития надвидовых таксонов. М.: ГЕОС, 1998. 318 с.).

Martynov A. [V.] 1938. Etudes sur l'histoire géologique et de phylogénie des ordres des insectes (Pterýgota). 1-e Partie. Palaeoptera et Neoptera – Polyneoptera. In: *Trav. Inst. Paléontol.* T. 7. Livr. 4. Moscow; Leningrad: Edit. Acad. Sci. URSS. 149 pp. [In Russian] (***Мартынов А. В.*** Очерки геологической истории и филогении отрядов насекомых (Pterygota). Часть I. Palaeoptera и Neoptera – Polyneoptera // Тр. Палеонтол. ин-та. Т. VII , вып. 4. М.; Л.: Изд-во АН СССР, 1938. 149 с.).

Mathew W. D. 1915. Climate and evolution. *Ann. New York Acad. Sci.* 24(6): 171–318.

Mazurenko M. T., Khokhrjakov A. H. 1984. Features of evolutionary transformations of plants in high latitudes and highlands. In: A. L. Janshin (ed.). *Makroevolyutsiya* [*Macroevolution: Materials of 1st All-Union Conference on problems of evolution*]. Moscow: Nauka. Pp. 155–156. [In Russian] (***Мазуренко М. Т., Хохряков А. П.*** Особенности эволюционных преобразований растений высоких широт и высокогорий // Макроэволюция: Материалы I Всес. конф. по проблемам эволюции. Под ред. А. Л. Яншина. М.: Наука, 1984. С. 155–156).

McDonald-Spicer C., Kner N. J., Encinas-Viso F., Schmidt-Lebuhn A. N. 2019. Big data for a large clade: Bioregionalization and ancestral range estimation in the daisy family (Asteraceae). *J. Biogeogr.* 46(2): 255–267.

Meadows M. E., Watkeys M. K. 1999. Palaeoenvironments. In: W. R. J. Dean, S. Milton (eds.). *The Karoo: Ecological patterns and processes*. Cambridge; New York: Cambridge Univ. Press. Pp. 27–41.

Meyen S. V. 1987a. *Fundamentals of paleobotany*. London; New York: Chapman and Hill. xxi + 432 pp.

Meyen S. V. 1987b. Geography of macroevolution in higher plants. *Zhurn. obshch. biol.* 48(3): 291–309. [In Russian] (***Мейен С. В.*** География макроэволюции у высших растений // Журн. общ. биол., 1987. Т. 48, № 3. С. 291–309).

Mordkovich V. G. 2005. *The basics of biogeography*. Moscow: KMK Scientific Press. 236 pp. [In Russian] (***Мордкович В. Г.*** Основы биогеографии. М.: Тов-во науч. изд. КМК, 2005. 236 с.).

Moreau C. S., Bell C. D. 2013. Testing the museum *vs.* cradle tropical biological diversity hypotheses: Phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution* 67(8): 2240–2257.

Morrone J. J. 2009. *Evolutionary biogeography: An integrative approach with case studies*. New York; Chichester: Columbia Univ. Press. xiv + 301 pp.

Morrone J. J., Crisci J. V. 1995. Historical biogeography: Introduction to methods. *Ann. Rev. Ecol. Syst.* 26: 373–401.

Mucina L., Jürgens N., Le Roux A., Rutherford M. C., Schmiedel U., Esler K. J., Powrie L. W., Desmet P. G., Milton S. J. *with contribution by* ***Boucher C., Ellis F., Lambrechts J. J. N., Ward R. A., Manning J. C., Midgley H. F.*** 2006. Succulent Karoo biome. *Strelitzia* 19: 221–299.

Naimark E. B. 2001. Change of taxonomic structure in the centers of diversification. In: A. G. Ponomarenko, A. Yu. Rozanov, M. A. Fedonkin (eds.). *Ekosistemnyye perestroyki i evolyutsiya biosfery* [*Ecosystem rearrangements* *and evolution of the biosphere*]. Iss. 4. Moscow: Palaeontologicheskiy institut RAN. Pp. 78–86. [In Russian] (***Наймарк Е Б.*** Смена таксономической структуры в центрах диверсификации // Экосистемные перестройки и эволюция биосферы. Вып. 4. Под ред. А. Г. Пономаренко, А. Ю. Розанова, М. А. Федонкина. М.: Палеонтол. ин-т РАН, 2001. С. 78–86).

Nelson G. 1983. Vicariance and cladistics: Historical perspective with implications for the future. In: R. W. Sims, J. H. Price, P. E. S. Whalley (eds.). *Evolution, time, and space: The emergence of the biosphere.* The Systematics Association Special Vol. 23. London: Academic Press. Pp. 469–492.

Newman W. 1991. Origins of Southern Hemisphere endemism, especially among marine Crustacea. *Mem. Queensland Mus*. 31: 51–76.

Newman W. A., Foster B. A. 1987. Southern Hemisphere endemism among the barnacles: explained in part by extinction of northern members of amphitropical taxa? *Bull. Marine Sci*. 41(2): 361–377.

Nordenstam B. 2012. *Crassothonna* B. Nord., a new African genus of succulent Compositae – *Senecioneae*. *Compositae Newslett*. 50: 70–77.

Nordenstam B., Pelser P. B. 2012. *Caputia*, a new genus to accommodate four succulent South African *Senecioneae* (Compositae) species. *Compositae Newslett*. 50: 56–59.

Nordenstam B., Pelser P. B., Kadereit J. W., Watson L. E. 2009. *Senecioneae*. In: V. A. Funk, A. Susanna, T. F. Stuessy, R. J. Bayer (eds.). *Systematics, evolution, and biogeography of Compositae*. Vienna: Inst. Ass. Plant Taxonomy. Pp. 503–525.

Parenti L. R., Ebach M. C. 2009. Comparative biogeography: Discovering and classifying biogeographical patterns of a dynamic Earth. Berkeley; Los Angeles; London: Univ. Calif. Press. x + 295 pp.

Patterson C. 1983. Aims and methods in biogeography. In: R. W. Sims, J. H. Price, P. E. S. Whalley (eds.). *Evolution, time, and space: The emergence of the biosphere*. The Systematics Association Special Vol. 23. London: Academic Press. Pp. 1–28.

Paul C. R. C. 2009. The fidelity of the fossil record: The improbability of preservation. *J. Palaeontol*. 52(2): 485–489.

Pelser P. B., Kennedy A. H., Tepe E. J., Shidler J. B., Nordenstam B., Kadereit J. W., Watson L. E. 2010. Patterns and causes of incongruence between plastid and nuclear *Senecioneae* (Asteraceae) phylogenies. *Amer. J. Bot*. 97(5): 856–873.

Pelser P. B., Nordenstam B., Kadereit J. W., Watson L. E. 2007. An ITS phylogeny of tribe *Senecioneae* (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56(4): 1077–1104.

Platnick N. J. 1981. The progression rule or progress beyond rules in biogeography. In: G. Nelson, D. E. Rosen (eds.). *Vicariance biogeography: A critique*. New York: Columbia Univ. Press. Pp. 144–150.

Potts A. J., Hedderson T. A., Vlok J. H. J., Cowling R. M. 2013. Pleistocene range dynamics in the eastern Greater Cape Floristic Region: A case study of the Little Karoo endemic *Berkheya cuneata* (Asteraceae). *S. Afr. J. Bot*. 88: 401–413.

Prothero D. R. 2013. *Bringing fossils to life: An introduction to paleobiology.* 3rd ed. New York: Columbia Univ. Press. 671 pp.

Rasnitsyn A. P. 1989. Phytospreading in the selectionistic perspective. *Zhurn. Obsch. Biol.* 50(5): 581–583. [In Russian] (***Расницын А. П.*** Фитоспрединг с точки зрения селекциониста // Журн. общ. биол., 1989. Т. 50, № 5. С. 581–583).

Rass T. S. 1959. Deep-sea fishes. In: L. A. Zenkevich (ed.). *Uspekhi v izuchenii okeanicheskikh glubin (biologiya i geologiya). Itogi nauki. Dostizheniya okeanologii* [*Advances in the study of ocean depths (biology and geology). Results of Science. Advances of oceanology*]. Vol. 1. Moscow: Acad. Sci. USSR Publ. Pp. 285–315. [In Russian] (***Расс Т. С.*** Глубоководные рыбы // Успехи в изучении океанических глубин (биология и геология). Итоги науки. Достижения океанологии. Т. 1. Под ред. Л. А. Зенкевича. М.: Изд-во АН СССР, 1959. С. 285–315).

Rautian A. S., Zherikhin V. V. 1997. Models of phylocoenogenesis and the lessons of ecological crises of geological past. *Zhurn. Obsch. Biol.* 58(4): 43–47. [In Russian] (***Раутиан А. С., Жерихин В. В.*** Модели филоценогенеза и уроки экологических кризисов геологического прошлого // Журн. общ. биол., 1997. Т. 58, № 4. С. 43–47).

Raymond A., Kelly P. H., Lutken C. B. 1989. Polar glaciers and life at the equator: The history of Dinantian and Namurian (Carboniferous) climate. *Geology* 17(5): 408–411.

Razumovsky S. M. 1971. On the origin and age of tropical and laurel-leaved floras. *Bull. Main Bot. Gard. Acad. Sci. USSR* 82: 43–51. [In Russian] (***Разумовский С. М.*** О происхождении и возрасте тропических и лавролистных флор // Бюл. Главн. бот. сада АН СССР, 1971. Вып. 82. С. 43–51).

Razumovsky S. M. 1999. Introduction to vegetation paleogeography. In: S. M. Razumovsky. Selected works. Moscow: KMK Scientific Press Ltd. Pp. 119–194. [In Russian] (***Разумовский С. М.*** Введение в палеогеографию растительного покрова // С. М. Разумовский. Избранные труды. М.: Тов-во науч. изд. КМК, 1999. С. 119–194).

Ricklefs R. E. 2005. Small clades at the periphery of passerine morphological space. *Amer. Natur*. 165(6): 651–659.

Rolland J., Condamine F. L., Jiguet F., Morlon H. 2014. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PloS Biol*. 12(1): e10001775.

Ross R. 1983. Endemism and cosmopolitanism in the diatom flora of the East African Great Lakes. In: R. W. Sims, J. H. Price, P. E. S. Whalley (eds.). *Evolution, time, and space: The emergence of the biosphere*. The Systematics Association Special. Vol. 23. London: Academic Press. Pp. 157–177.

Roy K., Jablonski D., Valentine J. W. 1996. Higher taxa in biodiversity studies: Patterns from Eastern Pacific marine mollusks. *Phil. Trans. R. Soc. London*. B. 351(1347): 1605–1613.

Sanmartin I. 2012. Historical biogeography: evolution in time and space. *Evol. Educ. Outreach*. 5(4): 555–568.

Santos C. M. D. 2007. On the basal clades and ancestral areas. *J. Biogeogr*. 34(8): 1470–1471.

Sauer J. D. 1988. *Plant migrations: The dynamics of geographic patterning in seed plant species*. Berkeley; Los Angeles; London: Univ. California Press. XVI + 282 pp.

Schüller M., Brandt A., Ebbe B. 2013. Diversity of Southern Ocean deep-sea benthos between cosmopolitism and cryptic speciation: New species from the ANDEEP expedition. *Zootaxa* 3692(1): 004–006.

Simpson G. G. 1953a. *Evolution and geography: An essay on historical biogeography with special reference to mammals.* Eugene: Oregon State System of Higher Education. 64 pp.

Simpson G. G. 1953b. *The major features of evolution.* New York: Columbia Univ. Press. XX + 434 pp.

Stebbins G. L. 1974. *Flowering plants: Evolution above the species level.* Cambridge (Mass.): Belknap Press of Harvard Univ. Press. xviii + 399 pp.

Stehli F. G., Douglas R. G., Newell N. D. 1969. Generation and maintenance of gradients in taxonomic diversity. *Science* 164(3882): 947–949.

Szafer W. 1952. *Zarys ogolnej geografii roslin*. 2nd ed. Warszawa: Panstwowe Wydawn Naukowe. 428 pp.

Théel H. 1911–1912. Priapulids and sipunculids dredged by the Swedish Antarctic Expedition 1901–1903 and the phenomenon of bipolarity. *Kugl. Svenska Vetenskapsakad. Handl*. 47(1): 1–36.

Thorne R. F. 1977. Where and when might the tropical angiospermous flora have originated? *Gard. Bull. Singapore*. 29: 183–189.

Timonin A. C. 2011. *Anomalnoe vtorichnoe utolshchenie tsentrosemennykh: spetsifika morfofunktsionalnoy evolutsii rasteniy* [*Anomalous secondary thickening in Centrosperms: Specificity of the morphological and functional evolution of plants*]. Moscow: KMK Scientific Press Ltd. 355 pp. [In Russian] (***Тимонин А. К.*** Аномальное вторичное утолщение центросеменных: специфика морфофункциональной эволюции растений. М.: Тов-во науч. изд. КМК, 2011. 355 с.).

Vakhrameev V. A. 1991. *Jurassic and Cretaceous floras and climates of the Earth*. Cambridge; New York; Port Chester; Melbourne; Sydney: Cambridge Univ. Press. xvii + 318 pp.

Valentine J. W. 1969. Niche diversity and niche size patterns in marine fossils. *J. Paleontol*. 43(4): 905–915.

Valentine J. W. 1984. Neogene marine climate trends: Implications for biogeography and evolution of the shallow-sea biota. *Geology* 12(11): 647–650.

Van der Niet T., Johnson S. D. 2009. Patterns of plant speciation in the Cape floristic region. *Mol. Phyl. Evol*. 51(1): 85–93.

Van der Spoel S. 1983. Mode of dispersal in plankton organisms and speciation: the dawn of pelagic biogeography. In: R. W. Sims, J. H. Price, P. E. S. Whalley (eds.). *Evolution, time, and space: The emergence of the biosphere*. The Systematics Association Special. Vol. 23. London: Academic Press. Pp. 291–334.

Van Dover C. L., German C. R., Speer K. G., Parson L. M., Vrijenhoek R. C. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295(5558): 1253–1257.

Van Valen L. 1971. Adaptive zones and the orders of mammals. *Evolution* 25(2): 420–428.

Vassilyev V. N. 1965. On longevity of species. In: E. M. Lavrenko (ed.). *Problemy sovremennoy botaniki* [*Problems in contemporary botany*]. Vol. 1. Moscow; Leningrad: Nauka. Pp. 48–51. [In Russian] (***Васильев В. Н.*** О продолжительности существования вида // Проблемы современной ботаники. Т. 1. Под ред. Е. М. Лавренко. М.; Л.: Наука, 1965. С. 48–51).

Verboom G. A., Archibald J. K., Bakker F. T., Bellstedt D. U., Conrad F., Dreyer L. L., et al. 2009. Origin and diversification of the Greater Cape flora: Ancient species repository, hot-bed of recent radiation, or both? *Mol. Phyl. Evol*. 51(1): 44–53.

Vtorov P. P., Drozdov N. N. 1978. *Biogeografiya* [*Biogeography*]. Moscow: Prosveshcheniye. 271 pp. [In Russian] (***Второв П. П., Дроздов Н. Н.*** Биогеография. М.: Просвещение, 1978. 271 с.).

Wallace A. R. 1876a. *The geographical distribution of animals. With a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface*. Vol. 1. New York: Harper & Brothers. xxiv + 386 pp.

Wallace A. R. 1876b. *The geographical distribution of animals. With a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface*. Vol. 2. New York: Harper & Brothers. x + 607 pp.

Wiens J. J., Donoghue M. J. 2004. Historical biogeography, ecology and species richness. *Trends Ecol. Evol*. 19(12): 639–644.

Wulff E. V. 1933. *Vvedeniye v istoricheskuyu geografiyu rasteniy* [*Introduction to the historical geography of plants*. 2nd ed. Moscow; Leningrad: Gosizdat. 414 pp. [In Russian] (***Вульф Е. В.*** Введение в историческую географию растений. Изд. 2-е. М.; Л.: Госиздат, 1933. 414 с.).

Wulff E. V. 1944. *Istoricheskaya geografiya rasteniy: istoriya flor Zemnogo shara* [*Historical geography of plants: History of the Earth's floras*]. Moscow; Leningrad: USSR Acad. Sci. Publ. xix + 546 pp. [In Russian] (***Вульф Е. В.*** Историческая география растений: история флор Земного шара. М.; Л.: Изд-во АН СССР, 1944. xix + 546 с.).

Zarenkov N. A. 2017. *Obshchaya biogeografiya: stroeniye Geomeridy – zemnoy versii zhizni* [*General zoogeography: Structure of Geomerida, the Earth version of life*]. Moscow: LIBROKOM. 264 pp. [In Russian] (***Заренков Н. А.*** Общая биогеография: строение Геомериды – земной версии жизни. М.: Книжный дом ЛИБРОКОМ, 2017. 264 с.).

Zavarzin G. A. 2012. Ombrophytes as initial terrestrial inhabitants. In: S. V. Rozhnov (ed.). *Rannyaya kolonizatsiya sushi* [*Early colonization of the land*. Moscow: Palaeontol Inst. RAS. Pp. 4–28. [In Russian] (***Заварзин Г. А.*** Омброфиты как первичные обитатели суши // Ранняя колонизация суши. Под ред. С. В. Рожнова. М.: Палеонтол. ин-т РАН, 2012. С. 4–28).

Zherikhin V. V. 1978. Development and change of the Cretaceous and Cenozoic faunistic assemblages (Tracheata and Chelicerata). *Trans. Paleontol. Inst. Acad. Sci. USSR*. 165: 1–200. [In Russian] (***Жерихин В. В.*** Развитие и смена меловых и кайнозойских фаунистических комплексов (трахейные и хелицеровые) // Тр. Палеонтол. ин-та АН СССР, 1978. Т. 165. С. 1–200).

Zherikhin V. V. 1979. Use of paleontological data in ecological prognostication. In: N. N. Smirnov (ed.). *Ekologicheskoye prognozirovaniye* [*Ecological prognostication*]. Moscow: Nedra. Pp. 113–132. [In Russian] (***Жерихин В. В.*** Использование палеонтологических данных в экологическом прогнозировании // Экологическое прогнозирование. Под ред. Н. Н. Смирнова. М.: Недра, 1979. С. 113–132).

Zherikhin V. V. 1992. Diversity changes in the history of insects. In: B. A. Yurtsev (ed.). *Biologicheskoye raznoobraziye: podkhody k izucheniyu i sokhraneniyu* [*Biological diversity: The approaches to the study and conservation*. St. Petersburg: Zoologicheskiy institut RAN. Pp. 53–65. [In Russian] (***Жерихин В. В.*** Исторические изменения разнообразия насекомых // Биологическое разнообразие: подходы к изучению и сохранению. Под ред. Б. А. Юрцева. СПб.: Зоол. ин-т РАН, 1992. С 53–65).

Zhirkov I. A. 2017. *Biogeography, general and regional: dryland, oceans and continental water bodies*. Moscow: KMK Scientific Press. 568 pp. [In Russian] (***Жирков И. А.*** Биогеография. Общая и частная: суши, моря и континентальных водоемов. М.: Тов-во науч. изд. КМК, 2017. 568 с.).

Zullini A. 2018. Basic problems of biogeography. *Natur. Hist. Sci. Atti Soc. It. Sci. nat. Museo civ. Stor. Nat. Milano*. 5(2): 13–18.

Zunino M., Zullini A. 2010. *Biogeografiya (evolyutsionnyye aspekty)* [*Biogeography (evolutionary aspects)*. Moscow: Italian-Russian Inst. for Ecol. Educ. and Res. 317 pp. [In Russian] (***Дзунино М., Дзуллини А.*** Биогеография (эволюционные аспекты). М.: Итало-российский ин-т экол. исслед. и образования, 2010. 317 с.).