

Cenozoic *Papyridea* (Bivalvia, Cardiidae) and the problem of diversification of the epicontinental tropical marine biotas

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Based on studies of the distribution of all known Recent and fossil species of cardiid bivalves *Papyridea* Swainson, 1840 and literature evidence on other representatives of marine and continental biota, the paper presents a review of basic formation stages of presently partitioned marine tropical regions: Indo-Westpacific, East and West Atlantic and East Pacific. The proposed vicariance and dispersal models are assumed non-contradictory and complementary. Due to regional differences in paleotectonic history and the relevant vicariance events, Atlanto-East Pacific, Indo-Mediterranean and Indo-Westpacific regions had separated within the bounds of Paleogene Tethyan Realm, these regions having inherited specific features of Cretaceous biota. Each of those regions possessed own centres of evolutionary radiation. Most effective on subsequent evolution of the Tethyan Realm proved the Mediterranean centre which during Early Cenozoic represented an analogue of present Indo-Polynesian Province of Indo-Westpacific region. Continuous and basically onedirectional Early Cenozoic migrations of biota from Mediterranean to Indo-West Pacific and from Mediterranean to Caribbean are easily explained by a model of climatically determined «diversity pump» [Valentine, 1967] showing good accord with concept by Arambourg [1927] and Ekman [1932, 1934, 1935, 1953]. Paleotectonic events of Miocene proved responsible for spacial isolation of the four present-day tropical marine biogeographical regions.

Key words: tropics, World Ocean, biogeography, Tethyan Realm, Cenozoic, bivalve molluscs.

Кайнозойские *Papyridea* (Bivalvia, Cardiidae) и проблема диверсификации эпиконтинентальных тропических морских биот

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Обзор основных особенностей становления четырех современных тропических биogeографических областей — Индоветпаифической, Восточно- и Западноатлантической и Восточнотихоокеанской. Основан на изучении распространения всех известных современных и ископаемых видов рода *Papyridea* Swainson,

1840, а также анализе литературных данных по распределению других представителей морской и континентальной биоты. Используемые при этом модели дисперсионной и викариантной биогеографии признаются непротиворечивыми и взаимодополняющими. Вследствие региональных палеотектонических различий в пределах Тетисного царства дифференцировались палеогеновые Атлантико-Восточнотихоокеанская, Индо-Средиземноморская и Индоветпаифическая области, унаследовавшие специфические особенности меловой биоты. Каждая из этих палеогеновых областей обладала своим собственным центром эволюционной радиации. Наиболее мощное влияние на последующую диверсификацию биоты тропического Тетиса оказал Средиземноморский центр, который в раннем кайнозое представлял аналог современной Индо-Полинезийской провинции Индоветпаифической области. Повторяющиеся и преимущественно однонаправленные миграции раннекайнозойской биоты из Средиземноморья в Индоветпаифику и из Средиземноморья в Карибский бассейн хорошо объясняются моделью климатически зависимой «помпы разнообразия» [Valentine, 1967] и подтверждают представления К. Арамбура [Arambourg, 1927] и С. Экмана [Ekman, 1932, 1934, 1935, 1953]. Палеотектонические события миоцена обусловили пространственную изоляцию четырех современных тропических биogeографических областей.

Ключевые слова: тропическая зона, Мировой океан, биогеография, Тетисное царство, кайнозой, двусторчатые моллюски.

INTRODUCTION

The origin of the four Recent marine disjunctive tropical biotas - the Indo-West Pacific, Eastern Pacific, Western and Eastern Atlantic [Briggs, 1974, 1995] - is one of the central problems of the historical marine biogeography. It is largely due to the fact, that the origins of the temperate- and coldwater biotas are closely related to tropical ones [Valentine, 1968; Kafanov, 1978], and the latter statement in its turn gains an insight into the Cenozoic history of all over the World Ocean. Quite a rich literature on this topic well correlates with the numerous concepts and opinions, which need to be put into a system¹. I would like to deal into the problem starting from the geologic history of the bivalves of the genus *Papyridea* Swainson, 1840, that might be distinguished easily enough.

The modern representatives of this Cenozoic genus populate mainly tropical waters (intertidal up to 250m) of the Eastern Pacific, the Western and Eastern Atlantic biogeographic regions (Fig. 1). Meanwhile in Paleogene and Neogene they were quite common com-

¹ As it takes place the most prominent of the Briggs's [1995] conclusions do not avoid the debatable points.

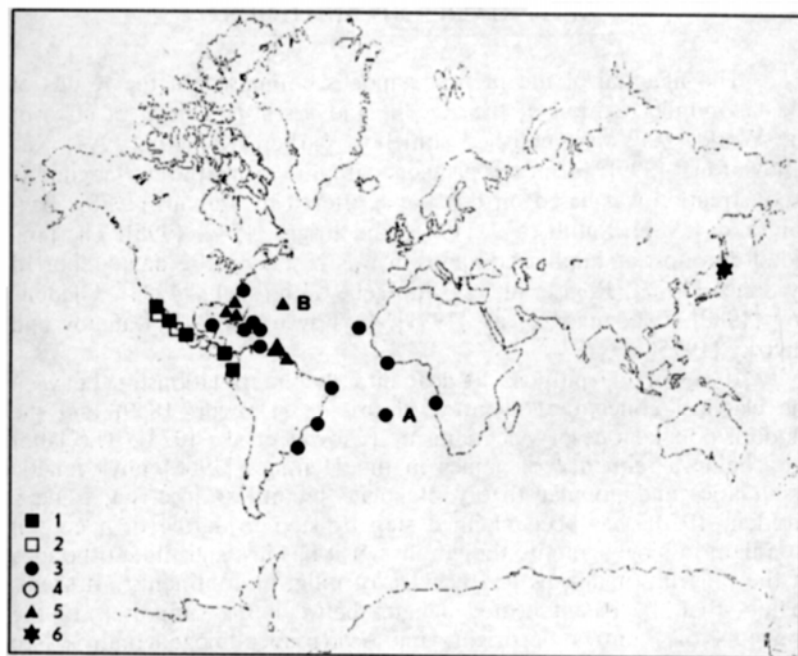


Fig. 1. Distribution of Recent (1-5) and Pleistocene (6) species of *Papyridea*. 1 - *P. aspersa*, 2 - *P. crockeri*, 3 - *P. lata*, 4 - *P. mantaense*, 5 - *P. semisulcata*, 6 - *P. kurodai*. A - Ascension Island, B - Bermuda Islands

Рис. 1. Распространение современных (1-5) и плейстоценового (6) видов *Papyridea*. Виды: 1 - *P. aspersa*, 2 - *P. crockeri*, 3 - *P. lata*, 4 - *P. mantaense*, 5 - *P. semisulcata*, 6 - *P. kurodai*. А - о-в Вознесения, В - Бермудские острова

ponents of a marine biota in the region, corresponding to the modern Russian Far-East and to Japan. To reconstruct the *Papyridea*'s geologic history all the available data on the geographic and geochronologic distribution of all the known species were used. Certainly patterns of biotic invasions must be judged according to the quality of the fossil record in the various parts of the World. However, I fully agree, that «...whether the paleontological record is complete enough or not, we think it is representative enough to reveal the most common aspects. The gaps in the record would have hardly evidenced of the inverse tendencies only» [Meyen, 1987. P. 293].

MATERIALS AND METHODS

The material of the present paper is composed of the results of the taxonomic revision of the Recent and fossil *Papyridea* of all over the World, that was published somehow earlier [Kafanov, 1997; Kafanov et al., 1999]. From the palaeogeographic terms the biogeographic reconstruction was based on the maps, offered by Hallam [1973], Barron et al. [1981], Smith et al. [1981] and Briggs [1987, 1995]. The provided chronostratigraphic comparison was based on the data, reported by Seneš [1977], Rögl et al. [1978], Ikebe and Tsuchi [1984], Gladenkov [1988], Gladenkov et al. [1991], Ogasawara [1994], Kafanov and Savizky [1995].

It is not my purpose to deal into the interrelationship between the classical concept of «centres of origin» [Darwin, 1859] and the modern popular one of «vicariance» [Croizat et al., 1974]. The latter one, being a sequence of gains in the Hennig's [1966] phylogenetic systematics and popular theory of «plate tectonics» [see, e.g., Dietz, Holden, 1970], has been claimed step by step to a role of a central paradigm in biogeography, though in fact it has just substituted the idea of the pilgrim organisms for the idea of pilgrim continents². It seems to me, that the recent heated debates between the supporters of the concepts of «centres of origin» and «vicariance biogeography» [see Nelson, Rosen, 1981; Nelson, Platnick, 1981], as well as the critique, given to the concept «vicariance biogeography», for its being absolved [Es'kov, 1984; Tatarinov, 1984], were somehow forced. Both concepts do not contradict, but complement each other [see Briggs, 1987, 1995]. For instance, Ghiold, Hoffman [1986. P. 183], summarize the results of the provided cluster analysis of the geographic distribution of 110 extant species of clypeasteroid echinoids the following way: "The resulting biogeographic cladogram contains nevertheless several inconsistencies which can be only explained by secondary dispersal, either by secular migration, or diffusion, or even chance dispersal. We conclude

² «The great richness and diversity of the flora of the southeast Asiatic-Indomalayan-Australasian region... is regarded as in large part due to its composite origin, not primarily to active migration of floras *per se*, but a «rafting» of floras on migrating continents with subsequent limited dispersal» [Schuster, 1972. P. 76]. Hocutt [1987] and Hayami [1989] presented a short, but informative assay on the nature of differences between dispersal and vicariance models in biogeography, as well as the major part of one of the Briggs's [1984] monographs dealt with the topic.

that the biogeographic history of clypeasteroid echinoids is very complex, with both vicariance and secondary dispersal playing a considerable role". The presented biogeographical analysis starts from the similar terms.

RESULTS

RECENT DISTRIBUTION OF POPYRIDEA

Among the Recent fauna we know only five species of *Papyridea* s. s., they populate the nearshore waters of the tropical Atlantic and Eastern Pacific (Fig. 1).

In the Pacific the *Papyridea* (*P.*) *aspersa* (Sowerby in Broderip et Sowerby, 1833) is distributed through the area from the Pariñas Cape (northern Peru) northwards to the Northern Baja California (Mexico), and in the Gulf of California; *P. (P.) crockeri* (Strong et Hertlein, 1937) – from the Mazatlan northwards to the Cedros Island, Baja California, Mexico, and in the Gulf of California; and *P. (P.) mantense* Olsson, 1961 – from the northern Peru northwards to the southern Mexico. *P. (P.) lata* (Born, 1780), that is more known as *P. soleniforme* (Bruguière, 1789) has got an amphi-Atlantic range of distribution: the Hatteras Cape (North Carolina), southwards to the southern Brasil, Bahamas, Cuba, Virgin and Caribbean Islands, Cape Verde Islands, Angola (Western Africa), and Ascension Island (South Atlantic Ocean). The *P. (P.) semisulcata* (Gray, 1825) range involves the Southern Florida, Bermuda and spreads southwards through the West Indies to Trinidad.

These species have not been found among the Paleogene and/or Neogene deposits. Meanwhile the boundaries of the recent range of *P. lata* go rightly along the ones of the Atlantic part of the Atlantic-East Pacific Region of Paleogene Tethyan Realm.

CENOZOIC HISTORY OF POPYRIDEA IN ATLANTIC OCEAN AND IN EAST PACIFIC

The species *P. capsoides* (Bayan, 1873) appears to be the most ancient of the *Papyridea* s. s. and known from the Middle Eocene (Lutetian) deposits of the Paris Basin (Fig. 2). Throughout the deposits

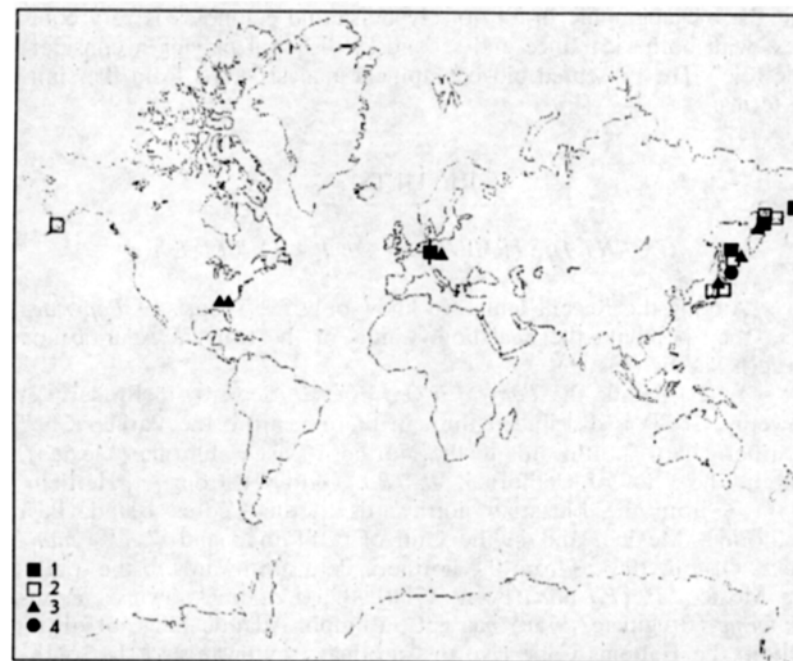


Fig. 2. Distribution of Paleogene and Neogene *Papyridea*. 1 - Eocene, 2 - Oligocene, 3 - Miocene, 4 - Pliocene

Рис. 2. Распространение палеогеновых и неогеновых *Papyridea*. 1 - эоцен, 2 - олигоцен, 3 - миоцен, 4 - плиоцен

of the Mediterranean part of the Tethyan Realm the papyrideas are found up to the early Middle Miocene, e.g. the *P. pontelevisse* (Mayer, 1868) in Langhian of the Loire Basin, France. At the Atlantic coast of the Northern America, in the uppermost Lower Miocene deposits (equivalent to the European Burdigalien fide Vokes, 1965), Chipola Formation of the northwestern Florida, three species of the *Papyridea* s.s were recorded, i.e. *P. bulbosa* (Dall, 1900), *P. miocica* Vokes, 1977, and *P. multicostula* Vokes, 1977. If no Paleogene remains of *Papyridea* were recorded at the Atlantic coast of America in the succeeding years, the ones found in the Chipola Formation should be surely considered the result of migration from the Mediterranean part of the Tethys. As remarks G. J. Vermeij (letter of 22 April 1997), it

seems safe to say that there were no Eocene *Papyridea* in eastern North America, and therefore that a westward migration took place some time before the Early Miocene, as it did in numerous other groups, e.g., molluscs Ocenebrinae, Muricidae [Vermeij, Vokes, 1997].

The secondary *Papyridea* s.s. migration into the Eastern Pacific from the Caribbean is beyond questions. Up to the early Middle Miocene (from 16,1 to 15,1 Ma) and up to at least Pliocene (to 3,7-3,1 Ma) the wide-scale and mostly one-way (from Atlantic to Pacific) migrations of the marine biota [see Keigwyn, 1978; Duque-Caro, 1990; Tsuchi, 1996] through the Panamanian Isthmus took place. The Recent Atlantic *P. lata* and Pacific *P. aspersa*, being rather close to each other morphologically, might serve an evidence of the faunas' relationship at somehow recent times, in the Miocene or even in the Pliocene.

CENOZOIC HISTORY OF PAPHYRIDEA IN PACIFIC OCEAN

For the Paleogene and Neogene Pacific the subgenus *Profulvia* Kafanov, 1976 representatives (Tab. 1) are known only, with their ranges lying within the Northwestern Ocean's part (Fig. 2). Within the Cenozoic section of the Northwestern Pacific the *Papyridea* (*Profulvia*) species display themselves as the tropical and subtropical faunistic components. This might be evidenced by their obvious coincidence with deposits of the Paleogene greenhouse-thermohaline climatic regime [Budyko, 1974; Fischer, 1982] and with the zones of thermal maxima of the Neogene glacial-psychrospheric climatic regime (Fig. 3); within the Northwestern Pacific the beginning of the latter one is distinctly marked by the deposits of the Kuluvenian Horizon of Western Kamchatka, Chekhovskian Horizon of South Sakhalin, and Asahi Stage of Hokkaido [Kafanov, Volvenko, 1997]. Besides during all the Neogene period the *Papyridea* (*Profulvia*)'s range of distribution was shifting gradually to the southern part of the region (Tab. 1). In that sight the absence of *Papyridea* among both the Recent and fossil faunas of the Indo-West Pacific looks mysterious.

In the Northern Pacific the *Papyridea* fossils appear first in the similar stratigraphical layer as that in the Mediterranean; so *P. utcholkense* Slodkewitsch, 1938 is known from Snatol'skaya Suite of Western Kamchatka; it is pre-arranged now, that Snatol'skaya Suite dates back to about Middle Eocene (Upper Lutetian) [Gladenkov et al., 1991,

Table 1

Distribution of *Papyridea* (*Profulvia*) species in Cenozoic of the Northwestern Pacific

Species	Age										Area
	Eocene		Oligocene		Miocene			Pliocene		Q	
	M	L	E	L	E	M	L	E	L		
<i>P. utcholkense</i>	+	+	+	+							Kamchatka, Koryak Upland, Chukotka
<i>P. securiforme</i>		+									Kamchatka
<i>P. adacnoides</i>		+									Sakhalin
<i>P. minima</i>		+	+								Sakhalin
<i>P. harrimani</i>			+								Alaska, Koryak Upland, Kamchatka, Sakhalin, Honshu, Hokkaido
<i>Papyridea</i> sp.				+							Sakhalin
<i>P. korfiense</i>					+						Kamchatka
<i>P. angulata</i>						+					Sakhalin
<i>P. kipeense</i>					+	+					Kamchatka
<i>P. noyamiana</i>						+					Sakhalin
<i>P. sakhalinense</i>						+					Sakhalin
<i>P. kurodai</i>						?		+	+	+	Honshu, Hokkaido

Notes. Q - Pleistocene, E - Early, M - Middle, L - Late. *Papyridea* (*Profulvia*) *harrimani* includes herein *P. (P.) harrimani* s. s. (Dall, 1904), *P. (P.) nipponica* Yokoyama, 1924, *P. matschigarica* s. s. (Khomenko, 1938) and *P. matschigarica uspenica* Barinov in Gladenkov et al., 1987 [see Kafanov et al., 1999].

1997]. Meanwhile, with their valves' external sculpture, being secondary reduced, the *Profulvia* leave no doubts of their being originated from the *Papyridea* s.s., i. e. of the *Papyridea*'s secondary dispersal from the Mediterranean to the Northern Pacific via Indo-West Pacific.

In the Late Eocene (Priabonian), besides Kamchatka and Koryak Upland with *P. utcholkense* and *P. securiforme* Slodkewitsch, 1938, the *Papyridea* (*Profulvia*) also reached Sakhalin Island - *P. adacnoides* Kafanov et Savizky, 1982 and *P. minima* (Zhidkova, 1980). In the Upper Eocene and Early Oligocene the *P. harrimani* Dall, 1904, range spreaded almost all over the Northwestern Pacific, from the southwestern Alaska through Chukotka, Koryak Upland, Sakhalin, and

southwards up to Hokkaido and Honshu. The Early Oligocene age of the type-locality of this species, Stepovak Formation, northern coast of Popov Island, southwestern Alaska, is supported by a potassium-argon data of 31.3 ± 0.3 Ma from biotite in a tuff bed [Marincovich, Wiggins, 1990]. In Japan, Honshu and Hokkaido, *P. harrimani* is characteristic for the so-called Asagai-Poronai fauna [Mizuno, 1964; Honda, 1986], which is spread as low as to Eocene [Ibaraki, 1986]. In the Miocene the major *Papyridea* (*Profulvia*) species are timed for the Kakertian stratigraphic horizon in Western Kamchatka and upper part of Ulegorskian horizon in South Sakhalin, as well as for the broad Neogene thermal maximum in the northwestern Pacific [Kafanov, Volvenko, 1997], i.e. *P. kipenense* Slodkewitsch, 1938, *P. angulata* Slodkewitsch, 1938, *P. noyami-ana* Slodkewitsch, 1938 and *P. sakhalinense* Slodkewitsch, 1938. After the Miocene the *Papyridea* (*Profulvia*) range was limited to the Japanese Islands only – Pliocene Suginoia

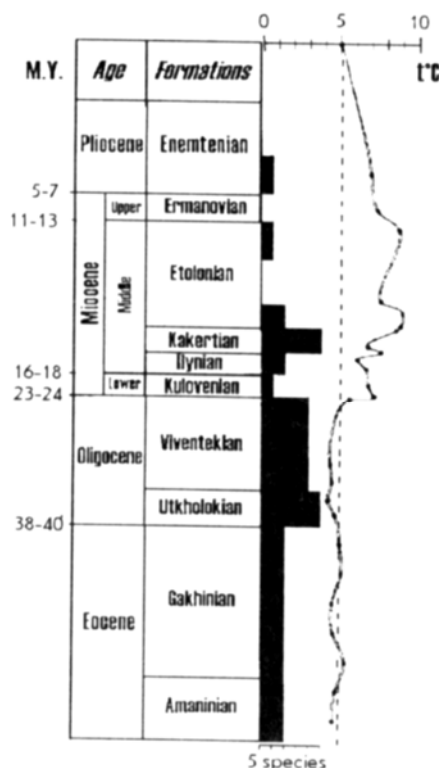


Fig. 3. Geochronologic distribution of *Papyridea* in the Cenozoic section of Northwestern Pacific. Paleotemperature curve (mean annual for sea surface) for Western Kamchatka redrawn from Kafanov and Volvenko [1997]; vertical dashed line denotes the level corresponding to the present-day temperature

Рис. 3. Геохронологическое распространение *Papyridea* в кайнозойском разрезе северо-западной Пацифики. Палеотемпературная кривая (среднегодовые температуры поверхности воды) для западной Камчатки даны по Кафанову и Волвенко [Кафанов, Волвенко, 1997]; вертикальные прерывистые линии соответствуют современным значениям температур

and Shigarami Formations in Honshu; Lower Pleistocene Nakanokawa, Shimonoporo, Zaimokuzawa and Umaoi Formations in Hokkaido, Sawane, Haizume and Kota Formations in Honshu [Akamatsu, Suzuki, 1992; Amano, Tanaka, 1992], and it was represented by a single species *P. kurodai* Sawada, 1962. The uppermost stratigraphical level of the *Profulvia* distribution might be marked by the records of the *P. kurodai* in the Lower Pleistocene (1.5 to 0.7 Ma) Shimonoporo, Zaimokuzawa and Umaoi Formations of Ishikari Lowland, Hokkaido [Akamatsu, Suzuki, 1992]. This event might correspond the time of appearance of warm-water benthic molluscs in the Sea of Japan area (about 1.1 Ma) since its basin's spreading and since opening the Tsushima-Korean Straits [Hayami, 1989; Chinzei, 1991; Kobayashi et al., 1996].

DISCUSSION

RELATIVE HOMOGENEITY AND PROVINCIALISM OF PALEOGENE TETHYAN REALM

Contemporary hypothesis of plate tectonics [see Briggs, 1987] allows for dismembering of a Mesozoic megacontinental land mass, Pangaea, into two supercontinents, Laurasia and Gondwana. Encompassing the current position of the Indo-West Pacific Oceans, the Tethys Ocean was circumglobal from the Jurassic to the Miocene and separated those two supercontinents. Fragmentation of Gondwana allowed for the northward track of India across the Tethys to collide with Asia, closing the Indo-Mediterranean-Atlantic seaway by Early Miocene in conjunction with the suturing of Africa and Europe.

At present there is no question concerning the origin of four Recent interrupted marine biotas from the unique tropical biota of the Paleogene/Early Neogene Tethys, circumglobal tropical ocean/sea stretching between Central America and Australasia³ across South and Southeast Europe, Southwest and Middle Asia [Stevens, 1980a, b; Ahmad, 1982; McKenzie, 1982, 1986]. The land boundaries of this belt are distinctly outlined by the range of occurrence of fossil palm trees [see Kremp, 1964] and mangroves [McCoy, Heck, 1976].

³ At Middle Oligocene the northern margin of Australia (New Guinea) was close enough the Indonesian region and was warm enough to permit the larger foraminifera to invade the Australian, New Zealand and the Solomon-Fiji Islands chain [Chaproniere, 1980].

Absence of any important biogeographical barriers and relatively homogeneous climatic conditions of tropical zone proved favourable for relative biogeographical homogeneity of the whole of Paleogene/Early Neogene Tethyan Realm and extensive migrations of the marine [Keen, 1950; Brinkman, 1966; DuShane, 1969; Gertman, 1969; Hottinger, 1971; Newell, 1971; Sanfilippo et al., 1973; Samanta, 1974; McCoy, Heck, 1976; Nolf, Capetta, 1976; Chahida, Papp, 1977; Piccoli, Massari Degasper, 1977; Strougo, 1977; Franco et al., 1978; Grecchi, 1978; Enay, 1980; Saperson, Janal, 1980; Steurbaut, Jonet, 1981; Voicu, 1981; Cabdulqadir, Carush, 1982; Franco, 1982; Ali, 1983a, b; Piccoli, Savazzi, 1983; Sorbini, 1983; Bonaduce et al., 1984; Buckeridge, 1984; Piccoli, 1984; Zacchello, 1984; Poignant, Lorenz, 1985; Goncharova, 1986a, b; Kotaka, 1986; Piccoli et al., 1984, 1986a, b; Robba, 1986; Hayami, 1989; Masuda, 1991; Ogasawara, Noda, 1996; and many others] and terrestrial [Haseldonck, 1972; Koch et al., 1972; Palamarev, 1973; Flerov et al., 1974; and many others] biotas within the bounds of this region.

Thus, the Eocene fauna of echinoids exhibits 52,3% of the genera common for Indo-West Pacific and Mediterranean, and the Oligocene and Early Miocene faunas 50% and 29,4% respectively [Ali, 1983a]. Zacchello [1984] and Piccoli et al. [1986a] are also reporting of a large number of species of molluscs common for Indo-West Pacific and Mediterranean. For instance, Hayami [1989] indicated that common pectinid (Bivalvia) species between Southern Asia and Mediterranean region (including Eastern Africa) are known in the Oligocene and Early Miocene.

In the opinion of Knobloch [1986], close similarity between and even identity of species of terrestrial plants occurring in Central Europe and North America may be explained only by alterations in configuration of continents and seas during Cretaceous and Early Cenozoic. In my opinion, invoking of vicariance model in this case seems unreasonable. Traces of similarity between present-day biota of certain areas and the Paleogene/Early Neogene biota of even geographically separated portions of Tethyan Realm [e.g. Hong, 1983; Little, 1983; White, 1983; Wu, 1983; Vermeij, Collins, 1988] may be reasonably motivated by relative homogeneity of this latter realm and historical succession of regional biogeographical features, this succession observed since Early Paleogene until Recently.

At the same time, excessive extent of Tethys as well as regional differences of its paleotectonic history and the relevant vicariance events [see: Dietz, Holden, 1970; Ridd, 1971; Knox, 1980; Whitmore,

1982; Kay, 1984; Nishimura, Suparka, 1990; Michaux, 1991] have specified a clearly pronounced provincialism of Paleogene/Early Neogene Tethyan Realm. Particularly noticeable from the studies of marine Bivalvia, this provincialism is already distinct in Cretaceous [Coates, 1973; Kauffman, 1973, 1979] and persists in Early Tertiary [Hayami, 1989]. Basing on the occurrence of hermatypic corals, Coudray and Montaggioni [1982] believe that the isolation of Indo-West Pacific due to plate collision was responsible for the development of a well-defined biogeographical province. With respect to Kauffman's Indo-Mediterranean Region, Popov [1994, 1995a, b; 1996] has recently clearly demonstrated the presence of regional zoogeographical differences (on the level of subregions and provinces) in the fauna of marine Bivalvia in Late Eocene, Early and Late Oligocene and Early Miocene. Thus, within the range of Western, Central and Eastern portions of Paleogene/Early Neogene Tethyan Realm, well-defined Atlanto-East Pacific, Indo-Mediterranean and Indo-West Pacific regions may be distinguished. Since the latter region is closely connected with the formation and development of North Pacific («boreal») region (see below), the distribution of fossil and Recent Papyridea well fits in this scheme (Fig. 4).

TETHYAN CENTRES OF RADIATION

Within the limits of the three regions of Paleogene Tethyan Realm there evidently existed areas of top biodiversity which should be considered centres of evolutionary radiation. In the contemporary tropical zone, the richest, most diverse marine and terrestrial biota is confined to the triangle formed by the Philippines, the Malay Peninsula, and New Guinea. Excessively high level of biodiversity of this area, already indicated by Wallace [1892], had evidently hypnotised most later researchers treating Indo-West Pacific, particularly the above mentioned area, a most important centre of Cenozoic evolutionary radiation for both terrestrial and marine biota [Ekman, 1935, 1953; Bailey, 1949; Darlington, 1957; Takhtajan, 1969; Talbot, 1970; Briggs, 1974, 1984, 1987, 1995; Aubréville, 1976; McCoy, Heck, 1976; Bande, Prakash, 1986; and many others]⁴. In this case Caribbean [Kruckow,

⁴ The whole Tethyan fauna is often even named the «Indo-West Pacific» [Cabdulqadir, Carush, 1982], and Ekman [1935, 1953] points to «Indo-West Pacific character

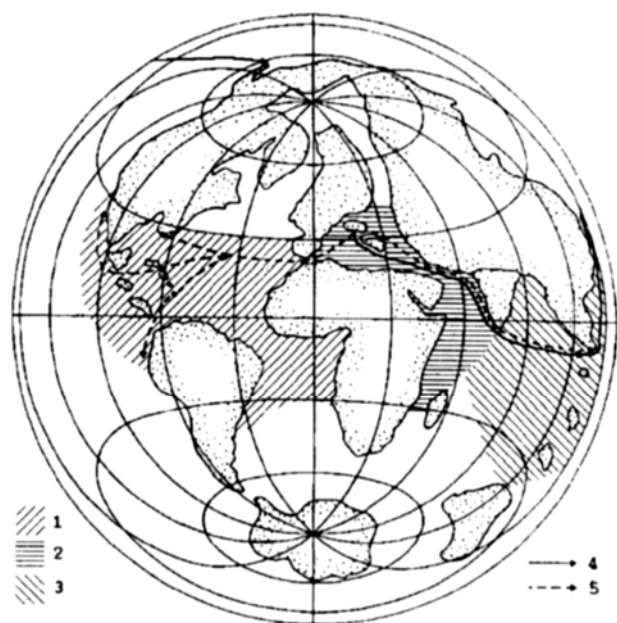


Fig. 4. Hypothetical dispersal of *Papyridea* and related groups. 1 - Atlantic-Mediterranean Region, 2 - Indo-Mediterranean Region, 3 - Indo-West Pacific Region, 4 - Eocene migration, 5 - Oligocene and Miocene migrations. Eocene paleogeographic map redrawn from Briggs [1987]

Рис. 4. Гипотетическая схема расселения *Papyridea* и сходных групп. 1 - Атлантико-Средиземноморский регион, 2 - Индо-Средиземноморский регион, 3 - Индо-Вестпацифический регион, 4 - эоценовые миграции, 5 - олигоценовые и миоценовые миграции. Основа эоценовой палеогеографической карты дана по Бриттсу [Briggs, 1987]

1982] and Atlanto-Mediterranean [McCoy, Heck, 1976] areas are treated as secondary centres of radiation. Another independent Australian centre [Fell, 1954] is being distinguished in Eocene, where, with the existence of broad connections with Malayo-Pacific, there was a strong influence of palaeoaustral groups [Fleming, 1957; Stevens, 1980b].

of the Lower Tertiary Atlantic fauna». This has much in common with well-known conclusions of Günther [1886] on the similarity between contemporary ichthyofaunas of Japan and Mediterranean.

Exclusive species richness of Indomalayan-Australasian area is mostly explained recently by paleotectonic reasons [see Ridd, 1971; Mironov, 1977; Knox, 1980; Springer, 1982; Whitmore, 1982; Kay, 1984; Nishimura, Suparka, 1990; Michaux, 1991], particularly by antiquity of Pacific Ocean [Briggs, 1974] or juxtaposition of composing elements of two rich biotas – the Laurasia-derived and Gondwana-derived [Schuster, 1972]⁵. At the same time a concept formulated by Arambourg [1927] and detailed by Ekman [1932, 1934, 1935, 1953] retains its validity [see e.g. Taylor, 1971; Masuda, 1991]. This concept considers the highest diversity in the Indo-West Pacific area to be the result of species retracting their ranges into «accumulation area» as a consequence of deteriorating environmental conditions. If this is true, it is natural to admit the secondary nature of Indo-West Pacific centre of radiation and the existence of a primary, evolutionary more meaningful centre. Secondary nature of Indo-West Pacific centre of radiation proves to be true in particular by that the average evolutionary age of taxa is increased on direction from Indo-West Pacific to peripheries, that is shown on a series of animal groups [see Stehli, Wells, 1971; Briggs, 1984; Kafanov, 1987].

Popov et al. [1993] believes that a most important centre of origination of mollusc faunas in Middle Eocene was Anglo-Paris basin, though a strong Southern French centre in Western Mediterranean is already traced in Cretaceous [Kauffman, 1973]. At that time Mediterranean part of the Indo-Mediterranean Region constituted a complete analogue of the present Indo-West Pacific. Europe represented a set of numerous islands encompassed by three blocks of continents: North American, Siberian-Asian and South American-African. Extremely rich continental and marine biota existed under stabilised climatic conditions close to contemporary conditions of tropical climate [Curry et al, 1969; Durand, 1969; Chateaufneuf, 1980; Ollivier-Pierre and Esteoule-Choux, 1980; Privy-Gill, 1984; Peres, 1985; Pantić, 1986; Zubakov, 1990]. Paleogene Mediterranean centre was responsible for the formation and development of *Papyridea* as well as numerous other supraspecies taxa of marine and terrestrial biota.

⁵ Of course, numerous different explanations are also available. Thus, Vermeij [1989, 1991] believes that the degree of habitat specialization and enemy-related adaptation (evidently due to a large amount of species) among shallow-water tropical marine species was greatest in the Indo-West Pacific. Unfortunately, in this and similar cases, researchers are involuntarily forced into a logical mistake *petitio principii* by making reference to that particular characteristic which should rather be explained.

*SCOPE AND TREND OF EARLY CENOZOIC
TRANS-TETHYAN MIGRATIONS*

The primary nature of Mediterranean centre of radiation is completely supported by the fact that most marine taxa which inhabit Indo-West Pacific at present or inhabited it in the recent past (Papyridea), find their fossil predecessors in Paleogene and Early Neogene deposits of the Indo-Mediterranean Region (Tab. 2,3)⁶. This refers to supraspecies taxa as well as species: according to Piccoli et al. [1986a], of 361 species of Bivalvia, Scaphopoda and Gastropoda reported in Mediterranean Neogene, 16,6% is presently occurring in Indo-West Pacific. Similar features of geochronological distribution are also demonstrated by numerous fresh-water-related invertebrates [Starobogatov, 1970; Lutz, 1985; Papazian, 1985]. Numerous paleobotanical data on terrestrial angiosperm plants also give evidence of the same effect [Takhtajan, 1969; Boulter, 1970; Krutzsch, 1970; Mai, 1970a, b, 1971a, b; Palamarev, Usunova, 1970; Pétrescu et al., 1970; Fataliev, 1971; Kvaček, 1972; Petrov, Drazheva-Stamatova, 1972; Lobreau-Calén, Caratini, 1973; Czeczott, Juchniewicz, 1975; Holý, 1975; Gruas-Cavagnetto, Bui, 1976; Pétrescu, 1976; Rüffle, 1976; Rüffle, Jänichen, 1976; Hans-Joachim, 1977; Crepet et al., 1980; Pétrescu, Givulescu, 1986; and many others]. The present marine and continental biota of Caribbean also demonstrates a similar relation pattern with Paleogene (and even Cretaceous) biota of South Europe and Mediterranean [Greenfield, 1968; Kay, 1968; DuShane, 1969; Gertman, 1969; Mai, 1971a, b; Newell, 1971; Kauffman, 1973, 1979; Lobreau-Calén, Caratini, 1973; McCoy, Heck, 1976; Popov, 1983; Mironov, 1983; Noda, 1986; Hayami, 1989; and many others], though the presence of Atlanto-East Pacific and Indo-West Pacific Regions and the relevant independent centres of radiation have predetermined possible migrations from Caribbean and/or Indo-West Pacific into Mediterranean or availability of common elements of biota [Keen, 1950; Via Boada, Cals, 1979; Bernasconi, Robba, 1982; Kotaka, 1986; and others].

Careful analysis of the above data suggests the following three characteristic features:

⁶ For taxonomically well-understood subfamilies and families, this holds practically always, e. g. Pectinidae, Carditidae, Tapetinae, Cardiidae [Popov, 1983; Goncharova, 1986a,b; Masuda, 1986; Keen, 1980].

Table 2

Geological and geographical distribution of some marine molluscan taxa
in the Paleogene/Neogene Indo-Mediterranean Region and in Australasia

Age	Region	
	Mediterranean and Eastern Atlantic	Australasia, including Japan
Recent	8, 10, 12, 13, 14, 16, 18, 19, 21, 22, 25, 26, 29, 34, 35, 37, 52	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 50, 51, 52
Pliocene	3, 6, 8, 14, 19, 22, 23, 24, 25, 26, 30, 31, 732, 34, 40, 41, 47	1, 2, 3, 4, 6, 8, 10, 11, 13, 15, 18, 22, 23, 25, 29, 32, 34, 37, 38, 44, 47, 48, 50, 51
Late Miocene	6, 7, 8, 11, 14, 16, 19, 22, 23, 24, 25, 26, 29, 30, 31, 32, 33, 34, 35, 38, 40, 41, 42, 45, 50	1, 2, 3, 4, 6, 8, 10, 11, 13, 15, 18, 22, 23, 29, 37, 38, 44, 47, 48, 49, 50, 51
Middle Miocene	2, 4, 6, 7, 8, 11, 14, 16, 19, 23, 24, 25, 26, 29, 30, 32, 33, 34, 35, 37, 38, 39, 40, 41, 42, 44, 47, 48, 49, 50, 53	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 13, 14, 15, 17, 18, 19, 20, 23, 29, 33, 48, 49, 50, 51
Early Miocene	1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 14, 16, 17, 18, 19, 23, 24, 25, 28, 29, 32, 33, 34, 35, 37, 38, 41, 42, 44, 47, 49, 50, 51	1, 2, 4, 6, 11, 13, 14, 15, 17, 18, 19, 20, 23, 33, 48, 49, 50, 51
Oligocene	1, 2, 4, 5, 6, 7, 8, 11, 14, 15, 16, 17, 18, 19, 23, 24, 28, 29, 33, 34, 35, 44, 45, 47, 49, 51	1, 4, 15, 20, 21, 33
Eocene	1, 2, 5, 7, 9, 10, 11, 12, 13, 14, 15, 16, 17, 20, 21, 22, 23, 27, 28, 29, 33, 35, 36, 37, 43, 44, 46, 48, 51, 52	12
Paleocene	5, 28, 33, 36	

Notes. Taxonomic group (Arab figures), source and comments: 1 - *Hawaiarca* (Bivalvia, Arcidae) [Noda, 1986]; Eocene *Arca* (*Acar*) *boschi* from Biarritzense Formation, Spain, questionably assigned to this genus; 2 - *Trisidos* (Bivalvia, Arcidae) [Masuda, 1991]; 3 - *Amusium* (Bivalvia, Pectinidae) [Masuda, 1991]; 4 - *Amusiopecten* (Bivalvia, Pectinidae) [Masuda, 1991]; 5 - *Fimbria* (Bivalvia, Fimbriidae) [Masuda, 1991]; 6 - *Megacardita* (Bivalvia, Carditidae) [Popov, 1983; Masuda, 1991]; 7 - *Discors* (Bivalvia, Carditidae) [Masuda, 1991]; 8 - *Lutraria* (Bivalvia, Mactridae) [Masuda, 1991]; 9 - *Tellinella* (Bivalvia, Tellinidae) [Masuda, 1991]; 10 - *Solecurtus* (Bivalvia, Solecurtidae)

[Masuda, 1991]; 11 - *Clementia* (Bivalvia, Veneridae) [Masuda, 1991]; 12 - *Pinna* s. s. (Bivalvia, Pinnidae) [Popov, 1994 and oth.]; 13 - *Lima* s. s. (Bivalvia, Limariidae) [Popov, 1994 and oth.]; 14 - *Cardita* s. s. (Bivalvia, Carditidae) [Popov, 1983]; 15 - *Trachicardium* (Bivalvia, Carditidae) [Kafanov, unpubl. data]; 16 - *Cardites* (Bivalvia, Carditidae) [Popov, 1983]; 17 - *Vepricardium* (Bivalvia, Carditidae) [Kafanov, unpubl. data]; 18 - *Chama* (Bivalvia, Chamidae) [Popov, 1996]; 19 - *Glans* (Bivalvia, Carditidae) [Popov, 1983 and oth.]; 20 - *Venericardia* (Bivalvia, Carditidae) [Popov, 1983 and oth.]; 21 - *Tapes* s. s. (Bivalvia, Veneridae) [Goncharova, 1986a], *T. comptoni* from Middle Eocene of England questionably assigned to this genus; 22 - *Ruditapes* (Bivalvia, Veneridae) [Goncharova, 1986a]; 23 - *Paphia* (*Callistotapes*) (Bivalvia, Veneridae) [Goncharova, 1986a]; 24 - *Venerupis* s. s. (Bivalvia, Veneridae) [Goncharova, 1986a], 25 - *Venerupis* (*Polistitapes*) (Bivalvia, Veneridae) [Goncharova, 1986a], one undescribed species from Lower Eocene of New Zealand possibly belongs to this subgenus; 26 - *Irus* s. s. (Bivalvia, Veneridae) [Goncharova, 1986a]; 27 - *Clavagella* s. s. (Bivalvia, Clavagellidae) [Smith, 1962]; 28 - *Pycnodonte* (Bivalvia, Ostreidae) [Hayami, Kase, 1992]; 29 - *Anadara* s. l. (Mollusca, Arcidae) [Noda, 1991; Nevesskaya et al., 1993]; 30 - *Spondylus fauroti* (Bivalvia, Spondylidae) [Grecchi, 1978]; 31 - *Megaxinus lamyi* (Bivalvia, Lucinidae) [Grecchi, 1978]; 32 - *Crassostrea* (Bivalvia, Ostreidae) [Nevesskaya et al., 1993; Kafanov, unpubl. data], Recent findings in Northeastern Atlantic was caused by anthropogene introduction; 33 - *Nemocardium* s. s. (Bivalvia, Carditidae) [Keen, 1950]; 34 - Tiaracanthiinae (Gastropoda, Cerithiidae) [Lozouet, 1986]; 35 - *Triforis* (Gastropoda, Cerithiopsoidae) [Bouchet, Fechter, 1980]; 36 - *Agathodonta* (Gastropoda, Trochidae) [McLean, 1984]; 37 - Juliidae (Gastropoda, Sacoglossa) [Kay, 1968]; 38 - *Taurasia* (Gastropoda, Muricidae) [Beets, 1984]; 39 - *Sansonia* (Gastropoda, Vitrinellidae) [Taviani, Sabelli, 1982]; 40 - *Monetaria annulus* (Gastropoda, Cypraeidae) [Grecchi, 1978]; 41 - *Ficus ficus* (Gastropoda, Fidae) [Grecchi, 1978]; 42 - *Metula clathrata* (Gastropoda, Buccinidae) [Grecchi, 1978]; 43 - *Patelloida profunda* group (Gastropoda, Acmacidae) [Lindberg, Vermeij, 1985]; 44 - *Babilonia* (Gastropoda, Buccinidae) [Altena, Gittenberger, 1981]; 45 - *Bathybembix* (Gastropoda, Trochidae) [Janssen, 1994]; 46 - *Golumya* (Gastropoda, Cerithiidae) [Houbrick, 1981]; 47 - *Clio* (Gastropoda, Cavolinidae) [Bernasconi, Robba, 1982; Shibata, 1986]; 48 - *Creseis* (Gastropoda, Cavolinidae) [Bernasconi, Robba, 1982; Shibata, 1986]; 49 - *Vaginella* (Gastropoda, Cavolinidae) [Bernasconi, Robba, 1982; Shibata, 1986]; 50 - *Cavolinia* (Gastropoda, Cavolinidae) [Bernasconi, Robba, 1982; Shibata, 1986]; 51 - *Xenophora* (Gastropoda, Xenophoridae) [Masuda, 1991]; 52 - *Lepidochitona* (Polyplacophora, Lepidochitonidae) [Eernisse, 1986]; 53 - *Cryptoplax* (Polyplacophora, Cryptoplacidae) [Baluk, Radwanski, 1977].

1. Though it is assumed [Berggren, Hollister, 1977; Kennett, 1982; Kuzjminskaya, Jasamanov, 1985] that the currents in Paleogene and Early Neogene Tethys were basically directed from east to west, the exchange of marine biota between Mediterranean and Indo-West Pacific was basically effected in the reverse direction, i.e. from west to east. This contradiction may probably result from the fact that the dependence between directivity of migrations and of paleocurrents is rather overestimated on geological time scale. Thus, in the discussion of Neogene trans-Arctic migrations of molluscs from North Pacific toward North Atlantic, the present author [Kafanov, 1979] had already

Table 3

Geological and geographical distribution of some marine animal groups in the Paleogene / Neogene Indo-Mediterranean Region and in Australasia

Age	Region	
	Mediterranean and Eastern Atlantic	Australasia, including Japan
Recent		1, 3, 4, 5, 6, 7, 8, 9
Pliocene	1, 3, 4, 5	2, 3, 5
Late Miocene	1, 3, 4, 5, 9	2, 5
Middle Miocene	1, 3, 5, 7, 9	2, 5
Early Miocene	1, 3, 5, 6, 9	2, 5
Oligocene	2, 3, 5, 9	2, 5
Eocene	2, 4, 5, 8	

Notes. Taxonomic group (Arab figures), source and comments: 1 - *Virgulinitella* (Foraminiferida) [Grindell, Collen, 1976]; 2 - *Tubulogenerina* (Foraminiferida) [Gibson, 1987]; 3 - *Yajimaina* (Crustacea, Ostracoda) [Malz, 1981]; 4 - *Retroplumidae* (Crustacea, Brachyura) [Via Boada, Cals, 1979]; 5 - *Clypeaster* (Echinodermata, Echinoidea) [Ali, 1983a, b; Ghiold, Hoffman, 1986]; 6 - *Alepes* (Pisces, Teleostei) [Bannikov, 1985]; 7 - *Platycephalus* (Pisces, Teleostei) [Radwanska, 1984]; 8 - *Trachycaranx* (Pisces, Teleostei) [Bannikov, Fedotov, 1984]; 9 - *Myripristis* (Pisces, Teleostei) [Greenfield, 1968].

pointed to the fact that gastropod *Neptunea* characterised by direct development and bivalve *Serripes* distributing with the aid of pelagic larva, show a practically simultaneous appearance in Pliocene deposits of North Atlantic. However, as generally believed by Bernasconi and Robba [1982], the Tethyan seaway seems to have had a rather low efficiency on the migration of pteropods from Atlantic-Mediterranean toward Indo-Pacific and *vice versa*⁷.

2. A predominant west-to-east migration trend between Mediterranean and Australasia was typical for representatives of both marine and continental biotas.

3. During the Paleogene and Neogene common taxa are found in Mediterranean and Australasia at various geological levels (Tab. 2, 3). Franco [1982] believes that this phenomenon is better explained by temporary, repeated, marine connections than by the survival of the

⁷ However, evidence presented by these authors together with data cited by Shibata [1986], completely supports the predominant trend of migrations as one from Mediterranean to Indo-West Pacific.

same taxa in the two basins after their separation. However, I think, that this phenomenon is explained by two indicated reasons.

It follows from the paleomagnetic evidence [Barron, 1983; Hickey et al., 1983] that from the Late Paleocene (Thanetian) and Early Eocene (Ypresian), the configuration of continents as well as land-sea area ratio were approximately the same as to-day. Accounting for the second of the above features, it may be assumed that a predominantly one-sided (from Mediterranean toward Indo-West Pacific) trend of trans-Tethyan migrations and their continuity were basically caused by paleoclimatic reasons.

Repeated migrations of biota from Mediterranean to Indo-West Pacific and from Mediterranean to Caribbean during Early Cenozoic may be easily explained by «diversity pump» model [Valentine, 1967] and show good accord with the concept of Arambourg [1927] and Ekman [1932, 1934, 1935, 1953]. The overall directed climate cooling which started since late Middle Eocene, 44-43 Ma ago [Keller, 1983], caused direct effect on the Paleogene-Mediterranean centre of diversity, which may be distinctly traced by alterations in Paleogene-Early Miocene associations of Bivalvia [Popov, 1994, 1995a, b, 1996] and fish [Arambourg, 1965] in basins of West Eurasia. Marine (including *Papyridea*, Fig. 4) and continental biotic elements were gradually and continuously forced out of the Mediterranean area into climatically better stabilised tropical regions of Indo-West Pacific and Caribbean where at least part of these elements have survived till now⁸. In the eastern portion of Tethys, this diversity pumping had proceeded until the end of Early Miocene: the closure of the Tethyan seaway took place about 18 Ma ago, during the Burdigalian, due to junction of Africa and Eurasia, so that the connection with Indo-West Pacific ceased to be operative [Berggren, Hollister, 1977; Kennett, 1982; Briggs, 1987, 1995]. The peak of Malayo-Pacific and Australian migrations in South-Western Pacific [Stevens, 1980b] falls on Early Miocene. Since Middle Miocene the marine faunas of Mediterranean and Australasia are showing marked differences [Piccoli et al, 1986a, b; Hayami, 1989; Masuda, 1991] and the assumed periodic connections between Mediterranean and Indo-West Pacific via Red Sea and Suex Bay [Ali, 1983a] in Middle Miocene may rather be explained by the availability of pre-Middle Miocene relicts of common origin. Con-

sidering the time of separation of marine biota of Western Atlantic and Eastern Pacific [Keigwyn, 1978; Duque-Caro, 1990; Tsuchi, 1996], one should agree with the opinion of Newell [1971] concerning Miocene origin of the Recent tropical marine regions. Lindberg [1972] indicates that close relationship between the Recent ichthyofaunas of coasts of England and Indo-Malayan archipelago may easily be explained by large-scale fluctuations in the level of Global Ocean during the Quaternary epoch. True, the latter author in his own way (in Popper's standpoint) falsifies his assumption: «A convincing argument against our interpretation could be the discovery in Miocene or Early Pliocene deposits of the Indo-Malayan Archipelago of fossilized ichthyofauna similar to the fossilized fauna of the Mediterranean». In the light of the above discussion, Lindberg's concept seems groundless.

After the isolation of Mediterranean from Indo-Pacific about 18 Ma ago, part of Mediterranean paleorelicts of Tethys had survived in the Mediterranean itself as well as in the Eastern Atlantic. In the Messinian, 6.5-5 Ma ago, the connection between the Atlantic and Mediterranean was evidently broken, and the latter was subjected to drying out [Hsü et al., 1973; Maldonado, 1985; Péres, 1985]. After the Messinian events, the connection with the Atlantic was reestablished and recolonization of Mediterranean proceeded very swiftly, basically due to Atlantic settlers⁹, though partly due to immigrants from the Red Sea [Grecchi, 1978].

INFLUENCE OF INDO-WEST PACIFIC REGION ON BIOTA OF NORTHERN PACIFIC

Wide spreading of *Papyridea* (*Profulvia*) in Early Cenozoic deposits of North Pacific (Fig. 2) and an obviously heat loving nature of the fauna of these deposits (Fig. 3), causes to focus our attention on the nature of North Pacific biogeographic region which, in contrast to tropical Tethyan Realm, is treated as «boreal» by most researchers. This latter consideration is in contradiction to the occurrence, along with *Papyridea*, of numerous typically tropical/subtropical genera of molluscs – *Eocypraea*, *Cymatium*, *Conus*, *Miltha*, *Plicatula*, *Pteria* in the

⁸ For simplicity this phenomenon may be designated as "Tethyan biospreading".

⁹ Within the composition of invertebrate macrobenthos fauna of Mediterranean, 62% accounts for the species common with the Atlantic fauna [Ben-Tuvia, 1983].

Paleogene of the northernmost areas of the Region as far as east and West Kamchatka [Pronina, 1969; Gladenkov et al., 1991] and South-East Alaska where the occurrence of *Papyridea* (*Profulvia*) *harrimani* has been reported.

Based on quantitative comparison between the Recent and Cenozoic faunas of Bivalvia of Northwestern Kamchatka, Kafanov and Volvenko [1997] proved that Paleogene faunas of this area existed at average annual temperatures of about 5°C with minimal annual temperature fluctuations¹⁰. These conditions corresponded to greenhouse-thermohaline climatic regime; therefore, with all the vagueness of the terms "boreal" and "subtropical" with reference to Paleogene paleoclimates, North Pacific Region of that epoch should be better treated as "paratropical" [see Kafanov, Volvenko, 1997].

The dual nature of North Pacific Region was further intensified by the fact that at the northern margin of Indo-West Pacific, in the region of the present-day North Japan and Sakhalin, there formed a local centre of radiation of biota which in Neogene had acquired typically cold-water features (among molluscs – *Portlandia*, *Megayoldia*, *Cyclocardia*, *Clinocardiinae*, *Conchocele*, *Liocyma*, *Neptunea*, *Buccinum*, *Margaritae* and some others) [Kafanov, 1978, 1984; Honda, 1994]. Here too was a centre of splitting of genera and species of temperate deciduous hardwoods – Arcto-Tertiary flora [see Little, 1983].

In all probability, migrations of Tethyan elements from Indo-West into North Pacific Region had passed via Taiwan-South Japan province which in Paleogene was a component part of Indo-Westpacific [Honda, 1991, 1994]. Migrations of Indo-Westpacific taxa in Central Pacific showed an obvious decrease in the eastern direction, limiting themselves to the so-called «East Pacific Barrier» [Horikoshi, 1973]. It is believed [Ekman, 1935; Briggs, 1974. P. 102] that «the East Pacific Barrier is a formidable stretch of deep water that lies between Polynesia and America». Considering that most bottom invertebrates, especially those in tropics, are possessing pelagic planktotrophic larvae [Thorson, 1936] feeding on phytoplankton, it should be assumed that the vertical distribution of these larvae is basically limited to the boundaries of euphotic zone. Therefore major depths do not present a

¹⁰ It is worth noting that for the whole area of the present-day Sea of Japan the longterm average annual surface water temperature account for about 12,3° C; however, the annual temperature amplitude reaches 16,5° C (as reported by Head Department of Navigation and Oceanography of the Defence Ministry of the USSR, 1989).

biogeographical barrier for most tropical shelf bottom invertebrates. Most likely, East Pacific Barrier serves a western boundary of the East Pacific Region formed in Miocene; the local population of this area prevents from penetration of alien biogeographical elements of biota [see Vermeij, 1991].

Wide distribution of *Papyridea*, tropical by origin, in temperate latitudes of North Pacific serves good example of so-called "extraequatorial persistence" [Meyen, 1986] known from the early Carboniferous and indicating long-term survival of tropical taxa in extra-tropical areas. Hypothetic mechanism of extra-equatorial persistence is evidently that of previously mentioned "diversity pump" [Valentine, 1968; Stebbins, 1974; Kafanov, 1978]. At the temperature rises, heat-loving species migrate into areas previously occupied by cold-loving species, and at subsequent cooling off they stay in warmer sections of those areas and gradually adapt themselves to a cooler environment. Marginal marine basins may be a key for this adaptation [Nishimura, 1981; Ogasawara, 1996]. As a rule, no penetration is occurring from higher latitudes toward the tropics: instead, the boundary of extra-equatorial taxa shifts southward. The latter phenomenon may also be observed in *Papyridea*. The distribution range of their last north pacific representatives (*P. kurodai*) is limited by Honshu and Hokkaido but penetration of *Papyridea* into contemporary fauna of Indowest Pacific excessively rich in species due to Tethyan biospreading and high rate of local speciation, proved impossible because of powerful competitive pressure from local population.

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