CROIZAT'S BIOGEOGRAPHICAL PRINCIPLES, PANGAEA AND FRESHWATER ZOOGEOGRAPHY

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The main biogeographical principles of L. Croizat (1952, 1958, 1964), most of which were also adopted by the proponents of the „Vicariance Biogeography" are:

1. Species originate through vicariism (geographical isolation), ancestral species splitting, as a result of geographical and climatic changes, in two or more daughter species, each with a smaller range.

The role of geographical isolation in speciation by biparental organisms is now unanimously accepted by students of speciation (see above all Mayr, 1963 and other papers), but most contributions to historical and regional biogeography give little if any attention to this fact. It is significat in this respect that no subdivions of regions, provinces etc. are based on the ranges of pairs or groups of vicariant species or higher taxa.

2. Splitting of wide ancestral ranges into smaller ones being the main phenomenon in the speciation process, the concept of „center of dispersal" (or „of evolution" has to be rejected, being incompatible with alopatric (geographical) speciation.

I cannot accept this viewpoint. The center of dispersal actually is the original range of the ancestral species, that later split in two or more smaller ranges as a consequence of appearance of barriers; the later disapperance of these barriers allows range extension („translation in space" by Croizat) and overlap of formerly vicariant ranges etc. The problem of compatibily between alopatric speciation and the concept of center or origin is dealt with in a paper in press. What can be accepted is that, in many a case it is hardly if at all possible to establish which was the original home of the ancestral species of a lineage (its „center of origin").

3. The present day occurrence of a monophyletic lineage in distant continental areas separated by seas is, at least usually, not the result of long-distance colonisation across the barrier, but the consequence of the presence of the ancestors in a continuous area that later on splitt. This necessarily implies that past geography was different from the present one.

Many older, above all European biogeographers, proponents of th land-bridges theory or of continental drift (v. Ihering, 1927, Jeannel, 1942) expressed similar views, explaining recent disjunct ranges by a different distribution of land in the past.

4. The fact that different and unrelated taxa have similar distribution patterns („tracks") proves that theses patterns are the results of the same geographical past events, Evolution of continents and of biota can hence be deduced from „generalized tracks".

The same views were expressed by various older authors, too: Arldt (1907, 1938) who distinguishes, within each biogeographical realm, several „strata" („Shichten), each of which includes unrelated taxa having similar ages and dispersal histories, or Jeannel (1942) whe recognizes taxa having a general Gondwanian, an Afro-Brazilian, a Palaeantarctic distribution etc.

Croizat did not try to explain most of the numerous distribution tracks he has recognized through Palaeogeography as derived from geological studies; he considers biogeographical arguments to be as decissive as geological ones for assuming former land connections. One must consider that Croizat wrote his major works in a period when most geologists were proponents of continental stability, drift being accepted only by few biogeographers, among which were however some prominent ones, such as Jeannel and Koswig.

Continental drift is now a generally accepted fact and an increasingly greater number of biogeographers explain distributions in the light of continental drift and plate tectonics. Since every one, including the proponents of continental stability, accepts former connections between the northern continents, the problems concerns above all distribution of organisms in southern (Gondwanian) continents.

Many southern distributions can easely be included within the classical scheme, based on continental drift according to Wegener, that was proposed in a clear manner by Jeannel (1942): there are taxa having a general Gondwanian range (i.e. among freshwater ones the crayfish family *Parastacidae,* that is but absent from Africa and India where it is assumed once to have lived, and the amphipod family *Paramelitidae,* distributed în Australia, South Africa and southern South America), others having an „Inabrezian" range in tropical South America, Africa and South Asia (the snail family *Pilidae* and the fish order *Siluriformes,* this having subsequently extended its range northwards), others exclusivively African and South American (the characiform fishes and mutelid mussels) or with an amphinotic distribution in Australia, New Zealand and South America (hyriid mussels, antarctoperlarian stoneflies, stygiocaricid crustaceans).

These distributions are consistent with the classical pattern of southern continental evolution as accepted by wegenerians, partially modified according to more recent advances of plate tectonics.

Freshwater Zoogeography furnishes however also examples of distribution which do not correspond to these palaeographical patterns and

even seem to contradict the usual scheme of southern continents evolution. These examples are here mentioned and discussed.

One special distribution pattern, recorded already by Jeannel in terrestrial invertebrates, is the East Gondwanian one: occurrence in the areas corresponding to the eastern part of Gondwanaland (Africa, Australia, New Zeeland, eventually India and/or Madagascar) and absence from South America. Two higher taxa of freshwater peracarid crustaceans have typical Esat-Gondwanian ranges: the isopod suborder *Phreaticoidea* (top of south Africa, India, Australia—Tasmania and New Zealand) and the subfamily *Chiltoniinae* of ceinid amphipods (South Africa, Australia, New Zealand).

This distribution contrasts with the concept of the first splitting of Gondwanaland in Inabrezis and Palaeantarctida, since the two taxa live in Africa and India (parts of Inabresia), but not in tropical South America, and also in Australia and New Zealand (parts of Palaeantarctida) but not in southern South America. If one accepts their former occurrence in Gondwanaland, how could the absence from the western areas of both main fragments of the supercontinent be explained? The answer is given by Croizat's concept that distributions often are very connservative and the ranges of taxa occurring in distant areas correspond to the continuous ranges of their ancestors: the early phreaticoids and chiltoniins probably inhabited the fresch waters of the eastern part of Gondwanaland before its breakup, the descendants surving in the eastern parts of both fragments of the supercontinent, having never extending their ranges westwards, in the areas later to become tropical and southern South America.

Similar but wider ranges have:

A genus of pulmonate snails, *Pettancylus:* Africa, East- and South Asia-western Indonesia, whole Australia—Tasmania, New Zealand (Starobogatov, 1970);

The freshwater amphipod family *Neogammaridae:* southern Australia, India, Japan (probably whole East Asia) (Bousfield, 1977).

Some lineages of prosobranchiates: *Bithyniinae* (tropical and temperate Eurasia, Africa Australia), *Clenchiellinae* (India, the Indochinese peninsula, the Philippines, New Guinea, Tasmania, New Caledonia) and *Pomatiopsidae* (tropical and subtropical South America, South Africa, southern and partially southwestern Australia, South- and East Asia, warm-temperate North America (Starobogatov, 1970; Davis, 1979).

To these can be added the fish genus *Scleropages* of the prevailing Gondwanian *Osteoglossidae,* with one species in South Asia-western Indonesia and two in southern New Guinea-northern Australia.

A more complex distribution is that of the freshwater mussel family *Hyriidae,* the present day range of which includes South and Central America (not the Antilles), Australia—Tasmania—New Guinea and New Zealand (the opinion of Starobogatov, 1970, that the family also includes three African and one Indian genus is not accepted by other

malacologists). This range corresponds to the Palaeantarcc fragment o Gondwanaland. The family includes however also fossil species fro North America that belonged to Laurasia: genera related to South American ones lived in North America during Mesozoic times (P a r o d i z, 1969; S t a r o b o g a t o v, 1970).

Proponents of the continental stability theory may accept that *Pettancylus* and the *Bythiniinae* were initially Afro-Asian, having subsequently reached Australia by crossing sea-arms. In the light of plate tectonics, one may accept on the contrary an older dispersal by continental routes within the southeast of Pangaea before its breakup and retention of this range, just as phreatoicids and chiltoniins retained their east-Gondwanian range. Arguments in favour of this explanation are the occurrence of endemic *Pettancylus* species and of an endemic bythiniin genus *(Hydrococcus)* in southwestern Australia, an area that is hardly if at all accessible to recent South-East Asian intruders and the absence of both lineages from the islands of eastern Indonesia. Were they recent Asian intruders in Australia, their dispersal would necessarily have taken place over East Indonesia.

D a v i s (1969) explains the distribution of *Pomatiopsidae* accepting a Gondwanian origin, the ancestors of the Asian and North American genera having been carried by the Indian plate, when this drifted from Gondwanaland later to fuse with Asia. Such an explanation is more plausible when accepting the recent viewpoint according to which not only India, but the entire southern Asia and even most of East Asia initially belonged to Gondwanaland.

The dispersal history of hyriid mussels raises more difficulties because of their former occurrence also in North America. Available fossil record suggests, at least for some genera such as *Diplodon,* an older age in North than in South America; P a r o d i z (1969) and S t a r o b o g a t o v (1970) do therefore believe that the family colonized South America from the north; one may suggest similarily that the ancestors of the Australian and New Zealand hyriids came from East Asia. No fossil hyriids are however known from Eurasia. Another, less acceptable theory, would be to assume an exclusively North American origin of the family, its later dispersal to South America and from there to Australasia. Such an explanation is contradicted by the known palaentological data, the earliest Australian fossils having the same, upper Cretaceous, age as the oldest South American ones (S t a r o b o g a t o v, 1970).

A more acceptable explanation is that the family was already distributed along the western and southern margins of Pangaea (later to become the Americas, Australasia and Antarctida) before the supercontinent began to split, having retained its original range (except North America where it became later extinct).

The distribution of several other taxa of freshwater animals ranging in several continental areas, Laurasian and Gondwanian as well, may result from the former occurrence of their ancestors over the entire or extended areas of Pangaea. The *Anostraca* offer two suggestive examples: the family *Branchipodidae,* distributed over most of the eastern he-

misphere *(Parartemia* in Australia, other genera in Africa, Europa, central Asia, India) and *Thamnocephalidae (Branchinella)* has most species in Australia, others in Africa, temperate Eurasia and North America, other genera living in East Asia, North America, tropical and warm-temperate South America). The *Anostraca* inhabit temporary pools and have resistant eggs, being able of passive dispersal. The possibilities of passive dispersal are however reduced, the eggs can be carried only short distances; this is why all genera and species (except *Artemia salina)* have restricted (many even quite restricted) ranges and no family (except again the monotypical *Artemiidae)* is cosmopolitan. The occurrence of the same genus, or of closely related ones *(Branchinella, Parartemia—Branchipodopsis)* in Australia and Africa can not be explained by passive transport of the eggs across the Indian Ocean in the present-day geographical situation, but by the presence of common ancestors in Gondwanaland, within which the area that became Africa was in direct contact with that later to become Australia; it is significant that most Australian *Parartemia* live in the west. i.e. in the area that was closest to Afric.

A Pangaean age and origin can also be accepted for some families or other lineages of *Trichoptera* which have wie ranges over whole or most of the world, most or many of the genera having on the contrary limited distributions: *Hydropsychidae, Philopomatidae, Glossosomatidae* (especially *Agapetinae), Leptocerinae,* eventually *Helicopsychidae* and the genus *Ceraclea* of *Leptoceridae,* within which an African subgenus *(Pseudoleptocerus)* and a species-group have their sisters in North America; these two continents were in contact within Pangaea, after the breakup of which Africa remained a part of Gondwanaland, North America a part of Laurasia. A former wide distribution throughout Pangaea is also probable for the bipolar or anti-tropical families of *Trichoptera: Limenphilidae, Serricostomatidae, Molannidae* and *Brachycentridae.* There are also several gera of *Trichopera* having a wide, almost cosmopolitan distribution, but, at least in some casez, this may be due to more recent range extension.

A Pangaean origin and age is probable also for the two families of *Bathynellacea* widely distributed over most continents but represented by distinct genera and lineages: *Bathynelliade* and *Parabathynellidae* (Schminke, 1975).

It is probable that one of the two main groups of primary freshwater fishes has a Pangaeic origin, too: the Osteoglossomorpha which includes not only Gondwanian (*Osteoglossidae, Mormyridae* etc.) or Gondwanian and South Asian families *(Notopteridae),* but also a recent North American *(Hyodontidae)* and several fossil North American and northern Eurasian ones (Greenwood, 1973; Gaudant, 1981). The inner interrelationships within *Osteoglossomorpha* (Greenwood, 1973; Nelson, 1969; Gaudant, 1981) show direct relations between various areas of Pangaea, either Gondwanian or Laurasian:

North America — East Asia — Europe (*Hyodontidae—Lycopteridae—Thaumaturus*);
Africa — India — southeastern Asia (*Notopteridae*);
Africa — tropical South America (*Heterotis — Arapaima*);

tropical South America — Australia/New Guinea — southeastern Asia (*Osteoglossum — Scleropages*).

It would be on the contrary hazardeous to assume a Pangaeic origin for the second higher group of primary freshwater fishes, *Ostariophysi*, that is much younger than *Osteoglossomorpha*. According to Fink and Fink (1981) the *Ostariophysi* consist of a plesiomorphic branch, *Anotophysi*, confined to the inland waters of Africa and an apomorphic, more widely ranging one, *Otophysi* (or *Euostariophysi*); this has one subdivision, distributed mainly in Inabrezian continents (order *Characiformes* — South America and Africa; order *Siluriformes*, more diversified in South America, Africa and southern Asia, also ranging in temperate Eurasia and North America, two euryhaline families having invaded also other areas) and a second subdivision (order *Cypriniformes*), widely distributed throughout Eurasia, North America and Africa but more diversified in South and East Asia. This distribution suggests that the original home was the tropical part of Gondwanaland, the early evolution having taken place after the separation of Laurasia. The splitting of the ancestral *Otophysi* into *Cypriniformes* and *Characiformes+Siluriformes* may have been correlated with the separation of India—Southeastern Asia—East Asia from Africa—tropical South America, the first group being localized from the beginning in the Indo-Asian fragment of the continent; this fragment later came in contact with Laurasia, that was soon colonized by cypriniforms; only much later did this group enter Africa. The dispersal of *Cypriniformes* hence was similar to that of the sublineage of pomatiopsid snails which was drifted by India to East Asia and later to North America (Davis, 1979). The dispersal history of the second branch of *Otophysi* was less complicated: the *Characiformes* remained confined to the African—South American fragment of Inabrezia, the *Siluriformes* extended from India to temperate Eurasia and later to North America.[1]

The distribution of several higher taxa discussed above suggests direct contacts between areas of Pangaea later to become Australia—New Guinea and southeastern Asia (the Indochinese peninsula and the Greater Sundas): *Pettancylus, Scleropages, Neogammaridae, Bythiniinae* and the *Chilobathynella*-group of *Parabathynellidae* (most genera în Australia, New Zealand, southern South America, but *Batubathynella* in Malaya: Schminke, 1975).

Australia—New Guinea, formerly a part of the amphinotic fragment of Gondwanaland and south-east Asia, former a part of Laurasia, lie now

1. The recent finding of archaic *Cypriniformes* in the Cretaceous of tropical South America (Gayet, 1982) suggests however a more complex history of the entire superorder.

close to each other, being separated only by narrow (although deep) sea-arms and by the belt of the eastern Indonesian islands, a recently emerged archipelago. Gondwanaland and Laurasia represent however the two fragments that resulted from the earlier splitting of Pangaea. According to most maps showing the evolution of continents in the light of drift (for example Dietz and Holden, 1970) the two areas were initially distant from each other and came in vecinity only in recent geological times.

Similar problems of dispersal history raise the higher taxa of freshwatter animals ranging in the Inabrezian fragment of Gondwanaland (or in a part of it) and in south-eastern Asia (according to the classical wegenerian opinion a part of Laurasia): the snail family *Pilidae*, the fish order *Siluriformes* the fish family *Notopteridae*, some genera of *Trichoptera* (*Gunungiella, Ostropsyche Paraethaloptera* a.o.).

Hence, the aquatic fauna of southeastern Asia (considered a fragment of Laurasia) shows direct and independent (and perhaps also ols) relations to those of areas having belonged to the two main fragments of Gondwanaland: India (part of Inabrezis) and Australia (part of Notogeis). If one adopts the opinion that southeastern Asia initially belonged to Gondwanaland (later to its Inabrezian fragment) no more problems exist concerning the old faunistical relationships between India and southeastern Asia; those of the relationships between South Asia (as a whole) and Australia however remain. These old relations can better be explained by accepting the theory of expanding earth. According to the palaeogeographical maps presented by the proponents of this theory (for ex. Owen, 1976) Australia and southeastern Asia, although separated by a deep but narrow sea, were in close vecinity during the entire Mesozoic and Coenozoic eras.

The freshwater fauna also includes genera and species belonging to prevailing marine taxa, the ancestors of which lived in the sea and colonized inland waters more recently. The distribution of these freshwater animals can be understood only when compared with that of their marine relatives. There are generalized tracks also among marine animals, these differing from the „generalized tracks" of continental (terrestrial and freshwater) ones. Croizat was aware of this fact, when explaining (1958) the distribution of eels *(Anguilla)* in continental waters and in the sea (spawning areas) by the Tethyian origin of the genus. Many other lineages of epigean and hypogean animals are known, living both in fresh and marine waters, the distribution of which is Tethyian; the fish suborder *Cyprinonontoidei* (Rosen, 1964), the genus *Ophisternon* of synbranchifom fishes (Rosen, and Greenwood, 1976; they consider the genus as Gondwanian, i.e. continental; I prefer to consider it Tethyian and peripheral), the snail family *Neritidae*, and several lineages of higher crustaceans (*Lepidomysidae, Stenasellidae, Hadziidae, Cirolanidae*, some groups of atyid shrimps). The Carribbean atyid genus *Typhlatya* also lives in Galapagos and Ascension islands; Croizat deserves mention again for having drawn the attention of biogeographers to the kinships

of the Galapagos fauna with that of the Antilles and not of the geographically closer Ecuador.

Another important category of freshwater animals of marine origin is the circum-Antarctic one, that includes above all four families of salmoniform fishes, the most important one being *Galaxiidae,* Some proponents of Croizat's biogeography, for ex. Rosen (1974) explain the circum-antarctic distribution of *Galaxiidae* by assuming a continental Gondwanian origin. One must however remember that the marine littoral fauna includes an important contingent circum-antarctic lineages. The *Galaxiidae* is one of these. These fishes did not dispersed from some „misterious" center of dispersal; they simply were an euryhaline diadromous group, some of their species gradually becoming resident in freshwater. The ichthyologists who studied the systematics, distribution and biology of galaxiids (in recent years above all Mc Dowall) became aware of the fact that several species, not only *Galaxias attenuatus,* obligatorily spend a part of their life in the sea. It is significant that the strictly freshwater *Galaxias*-species have each a restricted range usually a single river drainage, Mc Dowall, 1970), i.e. are recently differentiated species that had not yet time to extend their ranges by mean of river captures, while the species also occurring in the sea have much wider distributions.

But not all distributions result from the former occurrence of ancestors in the areas inhabited by recent species. Dispersal (range extension) played an important role, too. Croizat does not deny the reality of dispersal (renamed „translation in space"), but he minimizes its role. The same is true for Nelson's, Platnick's „Vicariance Biogeography" which, as pointed out by Croizat (1982; see also Craw, 1982) is far from being identical to „Panbiogeography". Proponents of the Vicariance Biogeography accept the reality of dispersal or range extention, too, however not across barriers but before barriers appear of after their disappearance; they consider that sympatric occurrence of related species is the only evidence that rang extension took place. Actually, the occurrence of the same species, or even of related species, on both sides of geologically old barriers also proves that dispersal took place.

A good example of dispersal in a not too remote past, is given by the present distribution of the snail family *Viviparidae* in the south western Pacific area. Here live representatives of the subfamily *Bellamyinae,* the range or which encompasses tropical Africa, South- and East Asia, the islands of western and eastern Indonesia, the Philippines, New Guinea and the eastern half of Australia (without reaching the southeastern extremity of the continent); it is absent from southwestern Australia, Tasmania and New Zealand (Starobogatov, 1970). The numerous species from eastern Indonesia, the Philippines and New Guinea belong to the widely ranging African and South Asian (but not East Asian) *Bellamya;* those from eastern Australia to the endemic *Larina* and *Notopala.* Were the subfamily a remnant from Pangaea and Gondwanaland in Australia, like *Pettancylus* etc., the species from New Guinea (an island of the Australian shelf) would have been closer to the Austra-

lian than to the south Asian ones, bellamyin snails would have been widely distributed throughout the continent, including the southwest and Tasmania and would have been, on the contrary, absent or but scarcely represented in the eastern Indonesian islands, which are rather recently emerged and belong net her to the south Asian, nor to the Australian shelf. It is therefore accepted here that the bellamyins were initially restricted to Africa, South- and East Asia, having extended their range to New Guinea—Australia in recent, Neogene, times.

One must accept range extension also for the two largest lineages of ostariophysan fishes: *Siluriformes* (from the Inabrezian fragment of Gondwanaland to Siberia—Europe and to North, America) and *Cypriniformes* (from South and Easth and East Asia to Siberia—Europe and North America on one hand, to Africa on the other).

Accepting C r o i z a t' s main assumption that the occurrence of many lineages in distant continents is a consequence of the presence of their ancestors in the same areas in periods where these continents were intimely connected, does by far not mean that all data included in C r o i z a t' s main works (1958, 1964) were rightly explained and must be accepted as such, neither that his entire philosophy is here accepted.

One example of wrong interpretation by C r o i z a t concers the freshwater fishes of Africa, above all the *Cyprinidae,* a prevailing South- and East Asian family, that also ranges in Africa, being, comparatively to other fish family, better represented in the east. C r o i z a t believes that eastern Africa has its own, and presumably old relationships with Asia, just because of the abundance of cyprinids and other prevailing Asian lineages. Actually the *Cyprinidae* are quite numerous also in western Africa (here live for example *Garra*-species closely related to western Asian ones and many endemic genera); only in comparison with other families, all of which are richely represented in western and poorely in eastern Africa, does the western African fauna of *Cyprinidae* seem to be poor (the family representing a smaller percentage of the entire fish fauna). All African cyprinids, eastern and western as well, are close to South Asian ones; the family is here considered a recent intruder in the inland waters of Africa.

Another example concerns the crayfishes. These crustaceans belong to three families (H o b b s, 1974): two closely related ones have a northern distribution (*Astacidae:* Europe-parts of western Asia and western North America; *Cambaridae:* eastern North America—Mexico and northert East Asia), the third *Parastacidae,* that is more distantly related to the above named ones, has a disjunct southern (Gondwanian) range in Madagascar, Australia—New Guinea, New Zealand and temperate South America. Treating the crayfishes as a whole and without considering the generical interrelationships, C r o i z a t (1958, 2 a: 906—915) gives an unrealistical sui-generis interpretation of the biogeography of these animals, speaking about a „node of dispersal" or a „northern and southern track" by New Guinea, connecting northern East Asia to Australia and also suggests relationships between southern Mexico and northern Chile, between Madagascar and the Mediterranean area or the Aralo-Caspian

area and south Mexico. Actually the crayfishes of New Guinea have their closest relatives on the Australian mainland, those of Madagascar and of Chile in southeastern Australia—Tasmania, the Mexican ones in eastern United States, the Mediterranean and the Aralo-Caspian ones in central Europe, etc. (Riek, 1972; Hobbs, 1974).

Concerning such interpretations, I fully agree with Mc Dowall (1978, a paper that is mainly a critique of the „generalized-tracks concept"). Who insists on the necessity to thoroughly analyze the inner relationships of large taxa, before giving an interpretation of their distribution.

An important problem raises: in which measure do, or do not, phylogenetic relationships play a role in the biogeography of Croizat. A few authors (Ball, 1976; Mc Dowall, 1978) claim that Croizat does not consider phylogenetical relationships when tracing „tracks" or interpreting distribution. Craw (1979, 1982), who is presently the most vehement supporter of Croizat's orthodox viewpoints, gives on the contrary arguments that Croizat's biogeography is based on strict phylogeny, by quoting several sentences from the main works of this author, in which the importance of phylogeny is emphasized. Actually, these sentences represent only a theoretical viewpoint; when discussing the distribution of various lineages, Croizat is far from paying attention to the interrelationships of genera and species, at least in most cases. The example of crayfishes, mentioned above, is typical in this respect.

Many of the viewpoints of Croizat's biogeographical philosophy can not be accepted. Three of these were already mentioned: the rejection of the center-of-origin concept (what else is however „node of form-making" or „gate of Angiospermy" of not centers of origin with other words?), the minimization of the role or dispersal and the little use of phylogenetical analyses in biogeographical considerations. Concerning the last point, it is regretable that Croizat (1982) rejects the coupling of his panbiogeographical method with the strict phylogenetic (cladistic or Hennigian) analysis, as done by the proponents of the Vicariance Biogeography.

There is another important viewpoint of Croizat no accepted here: the opinion that the range of the ancestral species can be estimated by adding the ranges of descendant species. This may be true only in the case of two or a few recently differentiated species, which result from the splitting of a common ancestor and had not yet the possibility to extend their ranges. In the casses of lineages which underwent a long evolution, above all those including numerous species, range extension obligatorily did occur, the common range (or „track") of the lineage is much wider that that of the initial ancestor, representing the entire area over which the lineage evolved.

It could also be objected that Croizat did not make use of paleogeographical reconstructions as derived from geological studies. This is true above all for the period when Croizat wrote his major works and when most geologists were proponents of the stability of continents. In his more recent papers, Croizat mentions the results of plate tec-

tonics. A special remark deserves in this respect a recent paper of Croizat's most active supporter, Craw (1982) who asserts that New Zealand is far from representing a geological unitary area, having resulted from the fusion of several „microplates", each having its own history; it would also be a mistake to consider that New Zealand represents, biogeographically, a „single area of endemism". This explains also the complex nature of the freshwater fauna of this small country (actually a „micro-continent"), that consists above all of species belonging to anphinotic lineages and having their sisters in Australia (parastacid crayfishes, hyriid mussels, various stoneflies etc.), but also of marine derivatives with either southern (galaxiids and other salmoniform fishes etc.) or tropical affinities (the torrentfish *Cheimarichthys* and a peculiar group of snails, *Melanopsidae,* with Tethyian affinities) and a number of genera or suprageneric lineages of *Trichoptera* which are absent from Australia—Tasmania, being on the contrary present, or having their sisters, in areas such as southeastern Asia, the eastern Indonesian or the Melanesian archipelago etc.: *Zelomyia* (Psychomyidae), *Hydropsyche,* seven genera of *Serricostomatidae* etc.

The main contribution of L. Croizat to Biogeography is to have demonstrated, by using thousands of examples, that the recent distribution of most lineages corresponds to old, above all late Mesozoic geography, when the outlines of continents and oceans were different from the present-day ones.

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PRINCIPIILE BIOGEOGRAFICE ALE LUI CROIZAT, PANGEA ŞI ZOOGEOGRAFIA DULCICOLĂ

(Rezumat)

L. Croizat (1958, 1964) explică răspîndirea disjunctă a taxonilor, reprezentaţi prin genuri şi specii diferite în continente sau insule separate de mări, prin prezenţa strămoşilor lor în întreaga zonă ocupată de speciile actuale, în perioadele în care continentele şi insulele respective erau reunite. Reactualizarea teoriei translaţiei continentelor, sub numele de tectonică globală, oferă o bază paleogeografică solidă acestei concepţii.

Răspîndirea a numeroase grupe de animale dulcicole corespunde fie cu vechea Gondwană în întregime, fie cu fragmentul sau paleantarctic (Australia, Noua Zeelandă, sudul Americii de Sud), cu cel inabrezian (America de sud tropicală, Africa, Madagascar, India) sau exclusiv cu cel africano-brazilian. Strămoşii acestor grupe s-au răspîndit în vechile continente respective care ulterior s-au fragmentat, ceea ce a determinat şi întreruperea arealelor. Există însă şi grupe dulcicole ale căror areale nu corespund fragmentelor succesive ale Pangeei sau Goodwanei: de exemplu unele sînt răspîndite în jumătatea estică atît a Paleantarctidei (Australia, Noua Zeelandă) cît şi a Inabreziei (Africa, eventual India sau Madagascarul) lipsind în jumătăţile vestice (partea sudică şi cea tropicală a Americii de Sud): de ex. subordinul *Phreaticoidea* de izopode, subfamilia *Chiltoniinae* de amfipode. Alte grupe (familia *Neogammaridae* de amfipode, genul *Pettancylus* de gasteropode pulmonate, subfamiliile *Bythininae* şi *Clenchielinae* de prosobranchiate sînt răspîndite în zone continentale corespunzătoare părţii estice atît a Gondwanei cît şi a continentului nordic Laurasia, iar familia de lamelibranchiate *Hyriidae* în fostul fragment paleantarctic al Gondwanei, avînd însă reprezentanţi fosili şi în America de Nord. Se explică răspîndirea acestor grupe admiţînd că strămoşii lor au trăit nu în întreaga Pangee sau Gondwană, ci numai în părţile acestor supracontinente care corespund arealelor speciilor actuale sau fosile. Origine în Pangea are şi un important grup de peşti primar dulcicoli, *Osteoglossomorpha;* majoritatea familiilor actuale ale acestui grup trăiesc în continentele sudice (foste părţi ale Gondwanei), dar una trăieşte în America de Nord iar mai multe familii fosile sînt cunoscute din întreaga emisferă nordică.

Părerea unor paleogeografi, după care sud-estul Asiei şi parţial chiar estul au aparţinut Gondwanei iar nu Laurasiei explică bine răspîndirea unor grupe de animale dulcicole. Separarea Indiei (sau a întregii Asii sudice) de Gondwana şi ataşarea la continentul asiatic a permis unor grupe de origine gondwaniană sau inabreziană să se răspîndească şi pe emisfera nordică (familia de prosobranchiate *Pomatiopsidae,* ordinul de peşti *Cypriniformes*). Teoria expansiunii pămîntului implică vecinătatea Australiei şi Noii Guinee de Asia sudică în tot cursul erelor secundară şi terţiară, ceea ce explică bine unele afinităţi faunistice.

Punînd în relief partea pozitivă a concepţiilor biogeografice a lui Croizat, autorul nu este de acord cu o serie de păreri sau puncte de vedere ale acestuia: negarea realităţii centrelor de răspîndire, minimalizarea rolului răspîndirii grupelor (extinderea arealelor), o prea mică atenţie acordată interrelaţiilor filetice în cadrul grupelor analizate, afirmaţia că arealul general al unui taxon ar corespunde arealului speciei ancestrale.

Se pune în relief extinderea relativ recentă a arealului familiei de prosobranchiate *Viviparidae* (subfamilia *Bellamyinae*) din sudul Asiei în Noua Guinee şi Australia; de asemenea ordinele de peşti Cypriniforme şi Siluriforme şi-au extins mult arealul. Interpretarea răspîndirii unor grupe de animale dulcicole (îndeosebi racii din familiile *Astacidae, Cambaridae* şi *Parastacidae*) de către Croizat este eronată.