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On endemism and the phenomenon of extremity endemism

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(Coleoptera aquatica)

ABSTRACT
Endemism as a zoogeographical phenomenon is discussed, and types of endemics are defined.

KEY WORDS
Insecta, coleoptera aquatica, zoogeography and endemism.

In 1955 W. Kühnelt discussed the ecological phenomenon of "regional stenoecy" in insects, i.e. living in a restricted range of habitats on the edge of their distribution, far away from the centre of their distribution. Kühnelt observed in many cases that the inhabitants of these border zones sometimes differ in their ecological preferences and behaviour from other specimens of the same species living near the centre of distribution. A water beetle as *Hydroporus morio* Aubé, widely distributed in Scandinavia, can be observed there in different types of water, but the southernmost records of this species in Germany are all from peat pools with strongly acid water. H. Lindberg (1944, 1949) observed that the common *Hydroglyphus pusillus* (Fab.), generally seen in all types of shallow warm pools, prefer brackish water in Scandinavia, frequently occupying coastal rock pools. The cause of this behaviour is the fact that brackish water has a better capacity for thermophilous energy, and *H. pusillus* in its origin is a warmth-loving species. My dear friend Hans Schaeflein would have said: When an Italian builds a house in Italy; he builds it where he finds a place. But when he emigrates to Sweden and wants to build a house there, he builds it on the southern slope of a hill. He represents the warmth-loving species.

A sister phenomenon of Kühnelt's regional stenoecy is a behaviour of insects (observed mainly in water beetles), which I will call extremity endemism. At certain edges of land masses one may observe a significant accumulation of endemic species, much more than in the large area behind, while the usual species are mostly displaced there (Lists 1.1.3; 1.2.3; 2.1; 2.2).
For our purposes an extremity is the end of a way before the obstacle. Not every coast and not every sudden end of a landscape are extremities, but capes of continents especially those encroaching a short way north or south into neighbouring climates (in South Africa, South America, North Australia), eastern or western coasts of continents without the possibility for making way for insects to north or to the south (Eastern Siberia) are true extremities, not islands in the ocean! The same argument is true of high mountains, about that later.

What are the causes of endemism there? In every large area (continent) there is over an epoch a dynamic evolution of species by mutation and recombination. Most descendants are well adapted to life in the place of their origin, but some are not well adapted in some way. The latter can at best migrate to an adjacent area which is a little more tolerable in terms of climate or water chemistry. In the case of the Cape Province of Africa we suppose that descendants of many generations of a species are composed of many well adapted individuals, with only a few predominantly warmth-loving and the same rate of predominantly warmth-avoiding species. The natural dispersion will be as follows: The well adapted species will try to maintain their places; the predominantly thermophilous species will migrate more south, deeper into the moderate climate, but there is the ocean! As a result, they crowd at the southern end of the continent as extremity endemics.

Another reason may be true for some species and genera which have developed anterior to the division of the ancient continent of Gondwana during the Jurassic. Many warmth-avoiding species probably might have developed during the Trias, when Southern Gondwana was still situated between 30°S and 60°S. i.e. in a temperate to cold climate. Today that part constitutes Africa and is situated between 25°S and 35°S, i.e. in a warm to temperate climate. So the adaptations to a colder climate might have effected the necessity for migration of many species southward to the tolerable conditions of the Cape Province.

From the African Cape Province I have noted 44 endemic hydrophilids (List 2.1), that is a rate of 28% of the species known from the South African Republic (Hebauer 1999; 2006). The supposition that the endemism at the Cape is caused by avoidance of warmth is supported by the fact that most of the endemic hydrophilids there are in mountainous waters (Table mountain); many are of a *Crenitis*, a genus well known as being warmth-avoiding and associated with spring water, others are on the shore (*Cercyon aphodioides* d'Orchymont, *gigas* d'Orchymont, *maritimus* Knisch and *pulsatus* d'Orchymont). In the north of Africa the situation is quite different. No extremity endemics can develop because there are several bridges to colder climates (Gibraltar, Sicily, Sinai).

An example of endemism in west-east direction we can observe in Far East Russia, the Primorskij Kraj, the land between Amur River and coast opposite Japan. This coastal strip has a hydrophilid fauna mostly unknown in the whole Eurasian continent, with 22 endemic species = 30% (List 2.2), distinctly influenced by Japan (possibly by ornithophoresis) (Hebauer 1995; Shatrovskiy 1989). The endemism here is supposed to be caused by the step from the severe continental climate of Siberia to the moderate sea climate of the Pacific.

As indicated above, the occurrence of endemics in the high mountains, especially the Alps, is ambiguous. On the one hand there are living real extremity species, the origin of which is probably the ancient Laurasian continent and which search for the best places, that is the coldest area, because they are cold-adapted (many Carabidae, terrestrial Chrysomelidae etc., but also water beetles, in the southern Himalaya the terrestrial Dytiscidae *Geodessus* spp. etc.). On the other hand we can find boreoalpine species in the Alps. These are northern species from Scandinavia, which have moved to central Europe during the Pleistocene glaciations and then became isolated from their starting. While the climate became warmer and warmer they saved themselves in the sources, brooks and lakes of high mountains. These species are not real endemics but species with a disjunctive distribution.
For the real extremity endemics a way back is available but not usable.

Besides this type of endemism there are other types, in particular island endemism (Lists 1.1.2; 1.2.2). This is a complex phenomenon and shows different forms of paleo-endemism and neo-emdemism, dependant from the origin of the island corresponding, whether it is a former part of an ancient continent, or it is of volcanic origin. The inhabitants can be relicts or migrants. They may have arrived by anemomigration, ornithophoresis, or introduced by man. Insects were frequently driven to islands and have no way forward nor back. By evolution they become more and more genetically isolated and after a long time they evolve there to subspecies and then to distinct species and endemics. A few examples: Canary Is. (*Anacaena haemorrhoa* Wollaston), Cape Verde Is. (*Anacaena conglobata* Wollaston, *A. marchantiae* Wollaston, *Laccobius atricolor* d'Orchymont); Caroline Is. (*Dactylosternum superficiale* Knisch), Corsica (*Anacaena gaetanae* Bameul, *Agabus aubei* Perris), Crete (*Hydraena subinura* d'Orchymont), Galapagos Is. (*Galapagodacnum darwini* (Blair)), Fiji (*Dactylosternum leveri* Balfour-Browne), Hawaii (water beetles little investigated), Madagascar (numerous endemics), New Guinea (171 described Hydrophilidae, 79% of them endemic! - Hebauer 2001), New Caledonia (*Kanala reticulata* Balfour-Browne), New Zealand (numerous endemic genera and species – Hansen 1997), Samoa (*Enochrus tritus* Broun – d'Orchymont), Seychelles (*Bourdonnaisia mahensis* Scott), Tasmania (*Phelea breviceps* Hansen) etc. This tendency is supported by the fact that badly adapted mutants on islands have a better chance of survival than on the mainland, because they have no competition.

A third and somewhat mysterious type of endemism, I call it here central endemism (Lists 1.1.4; 1.2.4) is represented by water beetles as *Cercyon hungaricus* Endroedy-Younga in Hungary, *Enochrus morenae* (Heyden) in Spain, *Arabhydrus gallagheri* Hebauer in Oman, *Spercheus spangleri* Hebauer in Thailand, *Hydroporus zimmermanni* G. Müller in Slovenia, etc. In all these cases we have endemics in a rather homogenous area with the possibility for dispersal in all directions, but these species remain isolated in a small place and we do not know why.

Paleo-endemism (in contrast to Neo-endemism) is a type of isolated occurrence of relicts concerning genera and species arisen anterior to the division of the ancient continents Laurasia and Gondwana. In most case not the species but the genera represent the paleo-endemics, (Lists 1.1.1; 1.2.1) and in most case these paleo-endemic genera are recently distributed in the southern areas of Australian, Afrotropical and Neotropical (the former parts of the ancient continent of Gondwana). (More in a projected paper).

Some mechanisms of life are after all unsolved. For a better understanding of the causes of endemism it would be very useful and informative to evaluate the rate of endemism of every country and to display world maps of endemic species and genera.

List: 1: Endemic monospecific genera

1.1 DYTISCIDAE

1.1.1 Suggested paleo-endemics:

Austrodytes Watts	AU	Australia, NT
Boongurrus Larson	AU	Australia, QLD
Gibbidessus Watts	AU	Australia, NSW
Huxelhydrus Sharp	AU	New Zealand
Typhlodessus Brancucci	AU	New Caledonia

1.1.2 Island endemics:

Senilites Brinck	NT	Tristan da Cuna
Heroceras Guignot	AF	Madagascar
Dimitshydrus Uéno	PA	Japan
Japanolaccophilus Satô	PA	Japan
Laccosternus Brancucci	OR	Sumatra

1.1.3 Extremity endemics:

Tikoloshanes Omer-Cooper	AF	RSA, Cape Prov.
Tyndallhydrus Sharp	AF	RSA, Cape Prov.
Andex Sharp	AF	RSA, Cape Prov.
Coelhydrus Sharp	AF	RSA, Cape Prov.
Darwinhydrus Sharp	AF	RSA, Cape Prov.
Primospes Sharp	AF	RSA, Cape Prov.

1.1.4 Central endemics:

Andonectes Guéorguev	NT	Ecuador
Hydrotrupes Sharp	NA	California
Anisomeria Brinck	NT	Chile
Hoperius Fall	NA	USA, Arkansas
Melanodytes Seidlitz	PA	Italy (Toscana)
Comaldessus Spangler & Barr	NA	USA, Texas
Crinodessus K.B. Miller	NA	USA, Texas
Kintingka Watts	AU	Australia, WA
Microdessus Young	NT	Brazil
Sinodytes Spangler	PA	China, Guangxi
Tepuidessus Spangler	NT	Venezuela
Trogloguignotus Sanfilippo	NT	Venezuela
Haideoporus Young & Longley	NT	Texas
Iberoporus Castro & Delgado	PA	Spain
Secaliporus Watts	AU	Australia, NA
Stygoporus Larson & LaBonte	NA	USA, Oregon
Vatellus Aubé	NT	French Guyana
Napodytes Steiner	NT	Ecuador

1.2 HYDROPHILIDAE

1.2.1 Suggested paleo-endemics:

Cylomissus BROUN	AU	New Zealand
Phelea HANSEN	AU	Tasmania
Tritonus MULSANT	AF	Madagascar
Scoliopsis D'ORCHYMONT	OR	Sri Lanka
Acidocerus KLUG	AF	Africa, Mozambique
Peltochares RÉGIMBART	AF	Africa, Gabon
Hybogralius (RÉGIMBART)	AU	Australia, SWA
Limnocyclus BALFOUR-BROWNE	AU	New Caledonia
Pseudorygmodus MORONI	NT	Chile
Eurygmus HANSEN	AU	Australia, QLD
Rygmostralia D'ORCHYMONT	AU	Australia, NSW
Exydrus (BROUN)	AU	New Zealand
Andotypus SPANGLER	NT	Chile
Petasopsis HANSEN	AU	Australia, QLD
Hemikruia HANSEN & HEBAUER	AF	Madagascar
Colerus HANSEN	AF	Madagascar

1.2.2 Island endemics:

Elocomosta HANSEN	OR	Sarawak
Rhachiostethus HANSEN	OR	Sarawak
Dactylostethus D'ORCHYMONT	OR	Sumatra
Galapagodacnum (BLAIR)	NT	Galapagos
Tylomicrus SCHÖDL	OR	W.Malaysia
Nannomicrus BAMEUL	OR	Sri Lanka
Litrosurus D'ORCHYMONT	OR	Sarawak
Stanmalcolmia BAMEUL	OR	Sulawesi
Kahanga HANSEN	NT	Panama
Emmidolium D'ORCHYMONT	NT	Taiwan

1.2.3 Extremity endemics

Kruia SPANGLER & PERKINS	AF	Liberia
Agnaeformia SHATROVSKIY	PA	Far East, Primorje
Moraphilus D'ORCHYMONT	AF	Guinea
Delimetrium HANSEN	AF	RSA

1.2.4 Central endemics

Arabhydrus HEBAUER	OR	Oman
Gentilina HEBAUER	AU	Australia, NA
Ophthalmocyclus KOMAREK	OR	India
Troglochares SPANGLER	NT	Ecuador
Gemelus GARCÍA	NT	Venezuela
Dieroxenus SPANGLER	NT	Ecuador
Hydroglobus BRUCH	NT	Argentina
Coeloctenus BALFOUR-BROWNE	AF	Tanzania
Mucetum D'ORCHYMONT	OR	Singapore
Heteryon SHARP	NT	Mexico
Lala HANSEN	NT	Brazil
Morastus D'ORCHYMONT	OR	India
Acaryon HEBAUER	AF	Madagascar
Gillisius D'ORCHYMONT	OR	India
Pseucyon D'ORCHYMONT	AF	Ethiopia
Nitidulodes SHARP	NT	Panama
Sacosternum HANSEN	NT	Panama
Motonerus HANSEN	NT	Costa Rica, Mexico
Quadristernum BALFOUR-BROWNE	AF	Rwanda
Anchorosternum JIA, WU & PU	PA	China (Guangxi)
Oreocyon HEBAUER	OR	Nepal
Cyrtonion HANSEN	AF	Ghana
Pyretes BALFOUR-BROWNE	AF	DR Congo

LIST 2: EXTREMITY ENDEMISM

2.1 Endemic species (extremity endemics) of South Africa

HYDROPHILIDAE (44 species)
Afrotormus metallescens HANSEN, 1999
Afrotormus minutus HANSEN, 1999
Allocotocerus mistus (D'ORCHYMONT, 1939)
Allocotocerus nitidus (GUÉRIN-MENEVILLE, 1834)
Anacaena capensis HEBAUER, 1999
Anacaena glabriventris KOMAREK, 2004
Anacaena reducta KOMAREK, 2004
Anacaena tenella HEBAUER, 1999
Berosus continentalis KNISCH, 1922
Berosus crassipes SCHÖDL, 1995
Berosus maximiliani SCHÖDL, 1994
Berosus obesus SCHÖDL, 1995
Berosus pudens BALFOUR-BROWNE, 1954
Cercyon capensis (D'ORCHYMONT, 1937)
Cercyon gigas D'ORCHYMONT, 1925
Cercyon pulsatus D'ORCHYMONT, 1937
Crenitis calva HEBAUER, 1994
Crenitis capensis D'ORCHYMONT, 1942
Crenitis cinnamomea HEBAUER, 1994
Crenitis danielssoni HEBAUER, 1994
Crenitis excusa HEBAUER, 1994
Crenitis glabricollis HEBAUER, 1994
Crenitis lineata HEBAUER, 2005
Crenitis zimmermanni KNISCH, 1924
Cylorgymus repentinus HEBAUER, 2002
Delimetrium sericeum D'ORCHYMONT, 1937
Enochrus hartmanni HEBAUER, 1998
Enochrus rocchii HEBAUER, 2002
Grodum endroedyi HANSEN, 1999
Grodum striatum HANSEN, 1999
Helochares parallelus HEBAUER, 1999
Helochares serpentinus HEBAUER, 1998
Helochares uhligi HEBAUER, 1999
Laccobius recurvipennis GENTILI, 1989
Laccobius tarsis GENTILI, 1988
Limnoxenus sjöstedti KNISCH, 1924
Parastromus turneri BALFOUR-BROWNE, 1948
Regimbartia condicta D'ORCHYMONT, 1941

HYDROCHIDAE (6 species)
Hydrochus amrishi (MAKHAN, 1998)
Hydrochus capensis PÉRINGUEY, 1892
Hydrochus fabiani (MAKHAN, 2002)
Hydrochus irmae (MAKHAN, 2001)
Hydrochus lachmoni MAKHAN, 1996
Hydrochus lucidus BALFOUR-BROWNE, 1954

2.2 Endemic species (extremity endemics) of Far East Siberia (Primorskij Kraj) HEBAUER (1995) lists 103 species of Hydrophiloidea:

	Total	endemic	%
HELOPHORIDAE	26	2	0.8
HYDROCHIDAE	2	1	50
SPERCHEIDAE	1	0	0
HYDROPHILIDAE	74	22	30

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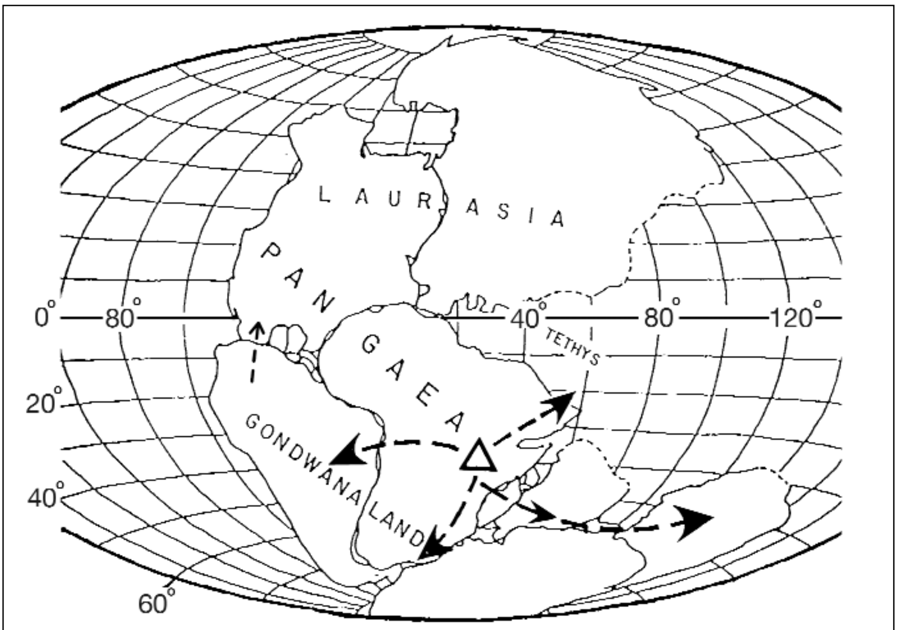

Fig. 1. Pangaea anterior to the division of the ancient continent of Gondwana (after Martens, 2000; modified): △ = Suggested site of origin of Hydrophiloidea; ----- = Suggested way of primary distribution.

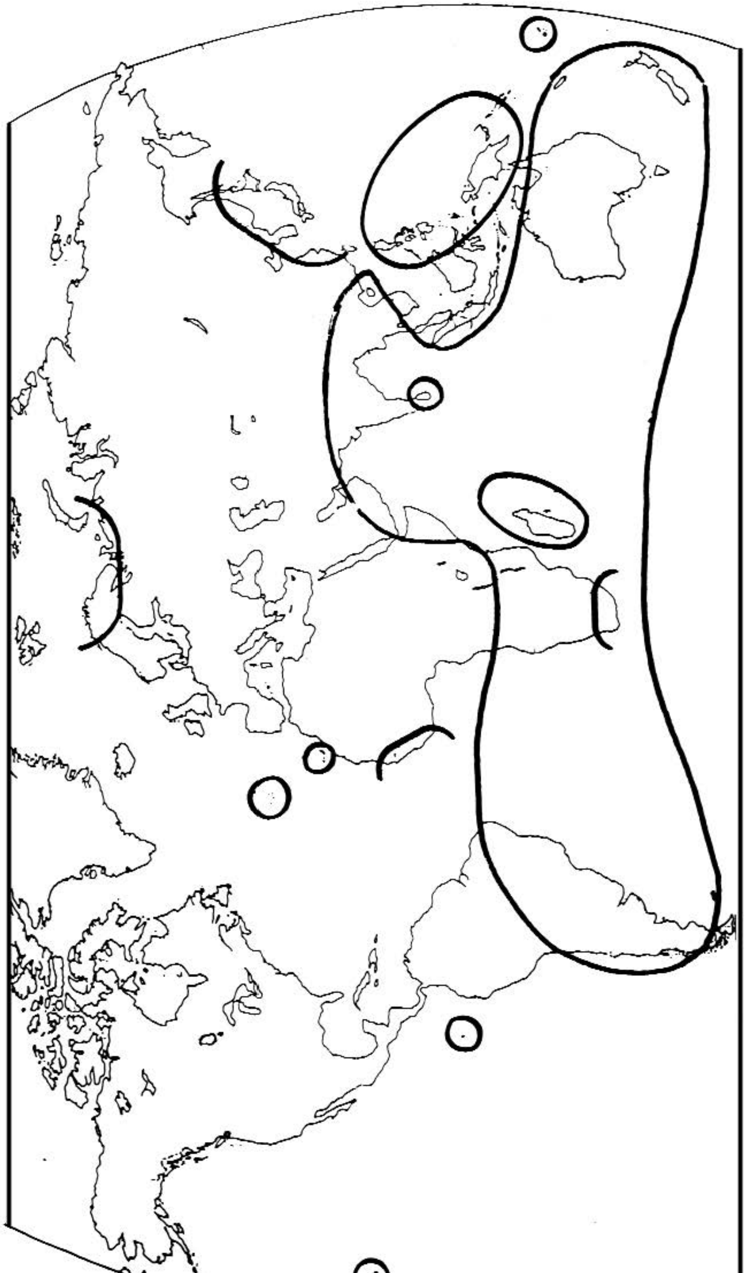

Fig. 2. Preferred sites of endemism:
Large closed curve = Preferably Paleo-endemism; Open arcs = Extremity endemism; O = Isle endemism with endemic genera.