

The concept of superspecies applied to Eurasiatic Cervidae¹

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According to E. MAYR (1967) the superspecies can be defined as follows: A superspecies consists of a monophyletic group of totally or essentially allopatric species, differing too much in a morphological respect to be united in one single species. The main character of a superspecies is that geographically it looks essentially like a polytypical species, except that the allopatric populations are so different in morphological or other respects that sexual isolation between these populations can be expected.

If, with this definition in hand, we are looking for superspecies in Cervidae, we will see that the condition of sexual isolation is generally fulfilled as far as populations are concerned, but not concerning individual animals. As a rule the species of Cervidae are interbreeding freely under more or less artificial conditions and in most cases can produce a fertile offspring. That is to say, if they do not differ too much in size, as in that case mating is technically impossible. Different species of Cervidae occurring in the same habitat under natural conditions are, as a rule, of considerable different size. In the case of exceptions to this rule, for instance *Rucervus duvauceli* and *Rusa unicolor* in some parts of India, the species occupy different ecological niches or in some cases a slightly different habitat.

As far as has been investigated now, most Eurasiatic Cervidae show a number of 68 chromosomes (2n). Known exceptions are the Moose (genus *Alces*) and the Reindeer (genus *Rangifer*) with 70 chromosomes and hybrids between these two genera and other deer of the same size are unknown. So sexual isolation between populations of Cervidae in nature is present, but the last part of the definition by MAYR "that the allopatric populations are so different in morphological or other respects that sexual isolation between these populations can be expected" is not really fulfilled. Should we stop looking for superspecies in Cervidae for this reason? No one will consider such different forms as European Red Deer, Fallow Deer, Spotted Deer, Hogdeer, Sika Deer, Sambar or Barasingha as members of one and the same polytypical species, just for the reason that these can interbreed freely, for they keep perfectly well isolated in nature. The same holds true in many other families, such as the Anatidae. In Ruminants the same phenomenon is known not only in Cervidae but also in Cavicornia. Members of such Subgenera as *Bos*, *Bibos*, *Bison* and *Poëphagus* can interbreed freely and the female offspring at least will prove to be fertile. Hybrids with more than two Subgenera of Bovidae in their ancestry are known. In Antwerp hybrids between Bongo ♂ (*Boöcerus eurycerus*) and Sitatunga ♀ (*Tragelaphus spekei*) could be bred. The offspring, only ♀♀, proved to be fertile with a Sitatunga ♂. Now such hybrids are not known from nature, as the species involved are allopatric or inhabit different habitats. But looking for the concept of superspecies in Cervidae we should not lay stress on the sexual isolation as such.

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Let us consider some examples:

1. *Alces*. Moose are living in the northern belt of Conifer forests in Eurasia and North America. One form is living in the Caucasus Mountains. As far as the distribution is not continuous, this is either due to the influence of Man and in the case of the Moose in the Caucasus Mountains to climatic changes during and after the Pleistocene. In literature the European Moose (*Alces alces*) often has been considered a separate species, differing from the American Moose (*Alces americanus*). Bering Street forms the boundary between these two forms. Sexual isolation is not a good criterium in Cervidae, but hybrids between European and American Moose are fully fertile and moreover the morphological and ethological differences are very slight indeed. So there seems no reason to consider the European and American Moose as separate species, which could be united in a superspecies.

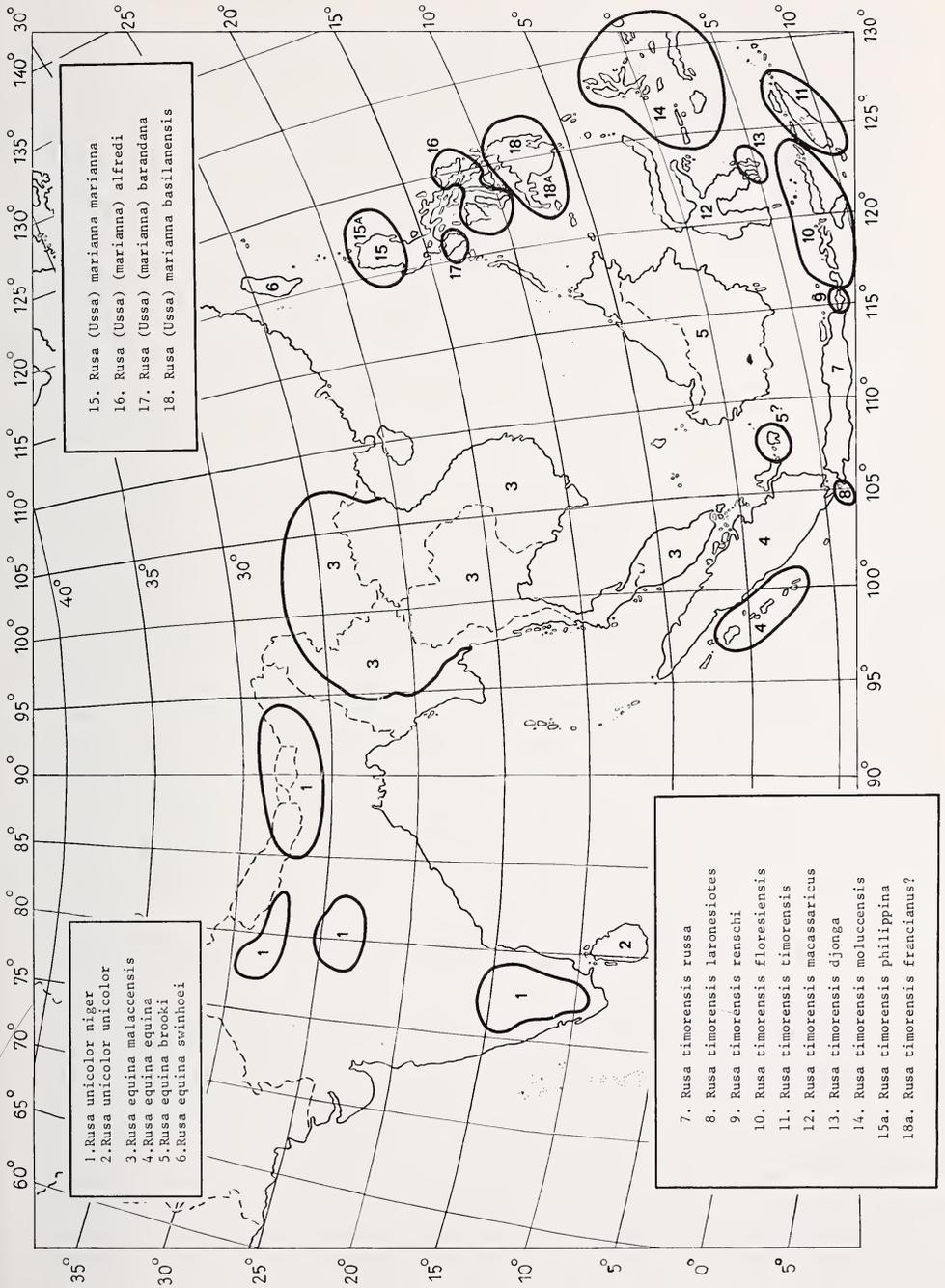
The same holds true for the Reindeer (genus *Rangifer*), living in the arctic belt of tundra. *Rangifer* often is split up in two species and more subspecies have been described than from *Alces*, due to the fact that many of these forms are living on islands in the arctic region. However, there is no good reason to accept more species than only *Rangifer tarandus*.

2. *Cervus elaphus*. Red Deer are living in the belt of deciduous forests from Europe through Asia to North America. A single race is still living in N.W. Africa in the Atlas Mountains. The distribution is discontinuous, not only due to human interference, as certainly is the case in Europe and North America, but also to the change of the climate in Central Asia, which has caused large deserts, uninhabitable for deer. Those forms of Red Deer, such as the Hangul (Kashmir), the Schou (Tibet) the Bochara, Isubra and Yarkand Deer which found a refuge in the mountain forests of Central Asia are nearly all threatened by extinction, due to reckless hunting. Most of these forms originally were considered as good species, but during the last decades only two species are recognized by most authors: the Eurasian *Cervus elaphus* and the North American *Cervus canadensis*. But in this case Bering Street cannot be considered as the boundary between the two species, because some subspecies of Red Deer occurring in North East Asia stand closer to the North American Elk or Wapiti. The boundary between the two species, as given by WHITEHEAD (1972, p. 75) seems rather complicated. There is a difference in ethology between the two groups, notably in the voice of the stags in rut, but I have some doubts as to the validity of the species. In New Zealand, where several forms of Red Deer and American Wapiti have been released in full freedom, the animals are interbreeding in such a way that, even considering the feeble sexual isolation in deer in general, it becomes clear that western and eastern Red Deer cannot be considered as different species at all. Even the difference in size between American Wapiti and European Red Deer does not prevent an interbreeding in New Zealand just as could be expected from two subspecies meeting at the verge of their area.

In my opinion there is hardly a reason to retain two species, united in one superspecies.

3. *Rusine Deer*. The group of Rusine Deer occurs at present only in tropical Asia. Once they lived also in Europe during the Upper Pliocene as far as we are able to establish from the insufficient data. Teeth, bones and even antlers are not enough to distinguish between most genera in deer. Roughly four groups can be distinguished in recent times:

- a. India, Ceylon. Large, dark coloured deer with dark belly and large, six-tined antlers.
- b. Burma, Thailand, Indo-China, Taiwan, Sumatra, Borneo, islands west of Sumatra, Banka, Billiton. Smaller, dark belly, short but heavy antlers, which differ in structure from a. Both a. and b. are forest dwellers.



Map I

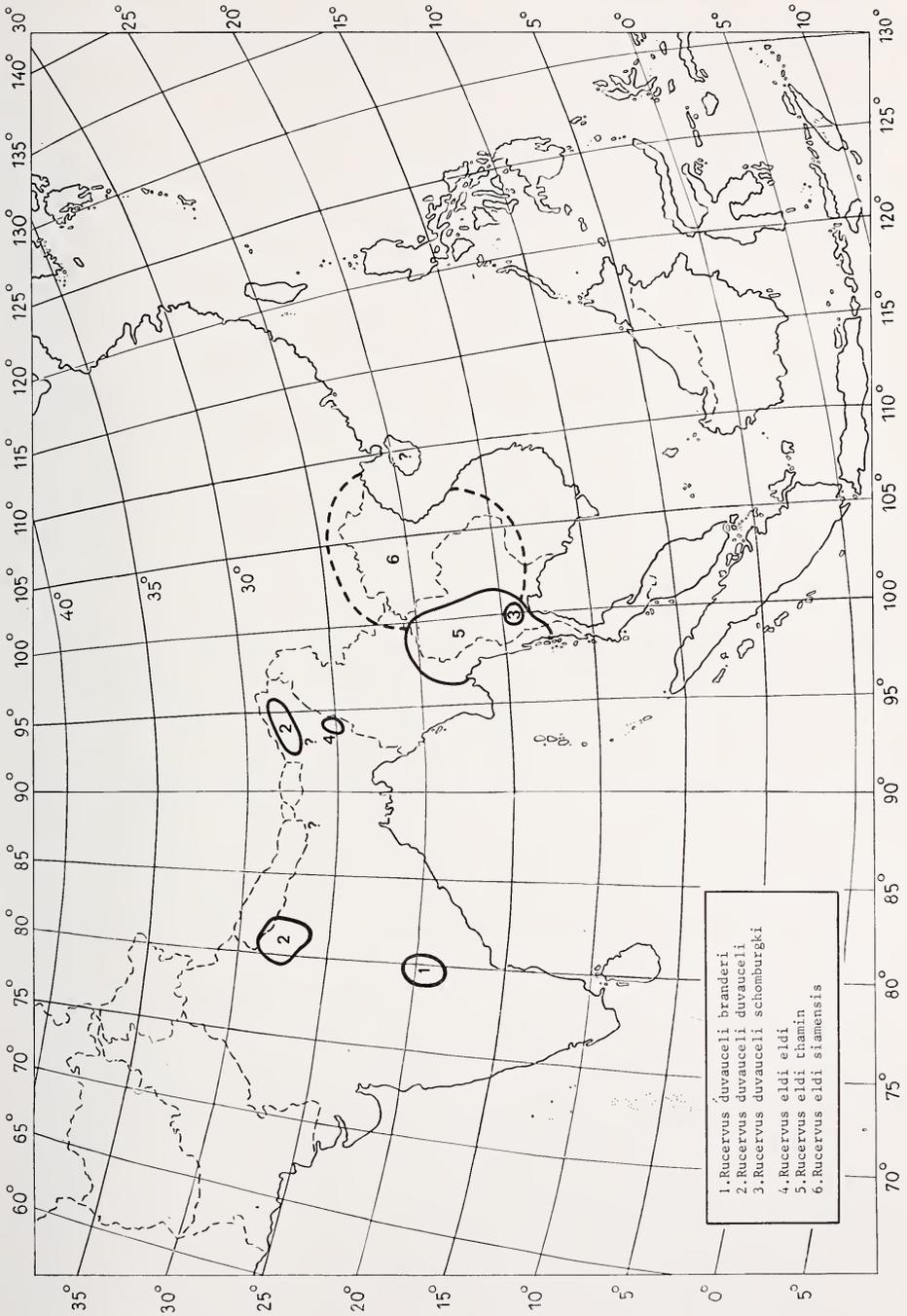
- c. Java, Lesser Sunda Islands, Celebes, Moluccan Islands, Luzon, Basilan (?). Smaller than a. and b. Light coloured belly, slender built, more resembling Red Deer. The antlers are long and slender, in structure somewhat resembling a.
- d. Philippine Islands. Very small as compared with the others. Antlers in structure resembling b. Dark belly in most forms. The subspecific relations between members of group d. are not very clear and one of the four forms which are recognized at present seems to be rather aberrant. The revision given by DOBRORUKA (1971) is not definite in every aspect. This author considers group d. to form a separate subgenus (*Ussa*). In my revision of this group (VAN BEMMEL 1949) the groups b. and c. were treated as separate species. However in this case there seems to be some reason to recognize one superspecies with four (or five?) species.
4. *Rucervus*. Within the subgenus *Rucervus* only two species should be recognized. A third one, *Rucervus schomburgki*, was united with *Rucervus duvauceli* for very good reasons by POHLE (1955). An important paper on this form has been written by ERNA MOHR (1968). *Rucervus duvauceli schomburgki* can be considered as extinct. The present distribution of *Rucervus duvauceli* cum subspec. and *Rucervus eldi* cum subspec. is not continuous due to human influence. *Rucervus schomburgki* has been extinct due to reckless hunting for the antlers, which were considered to have magic powers. The last true Schomburgks Deer was killed in a temple garden 1938 by two drunken men.

Both species were allopatric, except where the subspecies *Rucervus duvauceli schomburgki* lived within the range of *Rucervus eldi* in Thailand. Both forms had nearly the same size, a feature most uncommon in species of deer occurring in the same region. Originally they were more or less separated ecologically. Schomburgks Deer lived in very wet swamps, Brow-antlered Deer (*R. eldi*) in less wet and somewhat higher areas. This is curious, because the most western form of *Rucervus eldi*, the Manipur Brow-antlered Deer, lives in swamps and even on floating islands of grass. It is hard to say if the situation in Thailand was due to competition between the stronger Schomburgks and the weaker Brow-antlered Deer, the last eventually being driven out of a preferred habitat. Anyway, the extinction of Schomburgks Deer started with the construction of the Siam Railroad. The habitat of Schomburgks Deer got cultivated and large rice-fields came where the deer once roamed. The last remnants of the herds of Schomburgks Deer fled into the habitat of the Brow-antlered Deer and between 1920 and 1930 several Schomburgks stags were seen in the herds of the Brow-antlered Deer. So in a certain way the Schomburgks Deer dissolved in the population of the Brow-antlered Deer.

Could we speak in this case of a superspecies? Not according to the definition by MAYR. But personally I think that, if any, this could be a case of a real super-species.

5. *Hyelaphus*. Three species can be recognized: the Hogdeer (*Hyelaphus porcinus*) of northern India, Burma, Thailand and Indo-China with two subspecies, an isolated form (*Hyelaphus kuhlii*) on the Island Bawean (Java Sea) and another isolated form (*Hyelaphus calamianensis*) in the Calamian group of islands (Philippines). Interbreeding between common Hogdeer and Bawean Deer has been tried without results, but this is no proof because the Bawean doe that was used in the Amsterdam Zoo, a hand-raised animal, most probably was not behaving normally. In this case there could be reasons to consider all forms of *Hyelaphus* as a superspecies in the sense of MAYR. The relationship of some of these forms is proved by the fossil occurrence of a member of the *Hyelaphus* group in Java (*Hyelaphus oppenoorthi*; VAN BEMMEL 1944, 1948b, 1953).

Applying the concept of the superspecies to the different cases mentioned here is not easy. And this brings us to the question what the reason of the difficulty



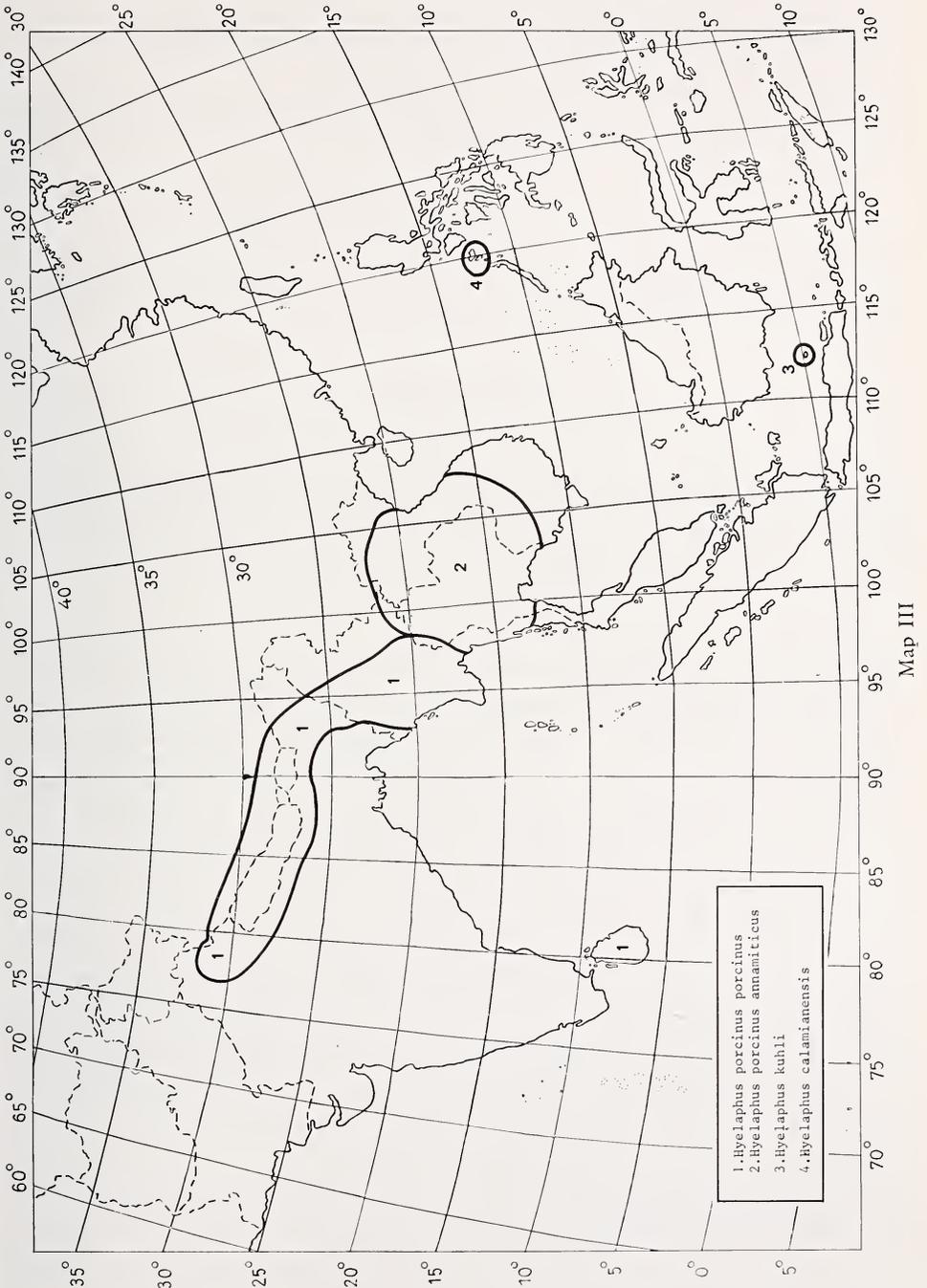
really is. RENSCH developed the concept of the *Rassenkreis* (= MAYR's polytypic species) and *Artenkreis* (= MARY's superspecies) already 1929. These concepts have been most useful and they are still the foundations of modern systematics. The only weak point in this system is, that in many cases it seems impossible to find where the polytypic species becomes a superspecies. This supposes a break in the evolution of a dynamic complex of populations and lower taxa and ignores the fact that the development of taxa is a very gradual process.

TOXOPEUS (1930) has discussed this question in some length and proposed three systematic concepts which seem to me to be preferable to the terms used by RENSCH and MAYR (VAN BEMMEL 1948 a). In short, TOXOPEUS united the *Rassenkreis* (= polytypic species) and the *Artenkreis* (= superspecies) in one other concept, which he called *species-complex*. The *species-complex* is: "the temporary compound of the local developments of a type of life that constitutes a syngameontic unit of a definite area". "The species-complex, mostly called species, consists of a number of local forms, called subspecies. The subspecies should be defined as a complex of individuals, acting as the local representatives of the species-complex." "If we proceed to compose the subspecies to species-complexes, we will find that always a number of subspecies are more similar inter se, than they are with one or more other subspecies. These similar subspecies are inhabiting always a connected area or ring of islands. This assembly of subspecies, smaller than the species-complex, but composed of the same elements as the species-complex, is called a *grex*. Some subspecies represent the only subspecies of a *grex* with no immediate relatives. Within the species-complex they have the same rank as a *grex* of (what TOXOPEUS called) *subtile forms*. Such subspecies are called *gregal form*".

"If two different subspecies of the same species-complex occur together in the same area without interbreeding they should be treated as different species. These two subspecies are not two complexes. But which of the two should be considered then as a different complex, and to which complex all other forms, which up till now were treated as one complex, should be reckoned? The answer is that, though living in the fauna of one area as two different species, both belong to one and the same species-complex. The subspecies is (per def.) the local representative of the species-complex in a certain area and this is true for both of the two subspecies." This phenomenon is called *species-duplex* by TOXOPEUS. Now according to RENSCH, subspecies of the same species should not only represent each other, but also exclude each other geographically. This still holds true, as TOXOPEUS pointed out, but only for subspecies of the same *grex*. The nomenclatural difficulties arising from this concept can be overcome rather easily, but this would bring us too far and is not important in this context.

If we now return to the examples of the Cervidae mentioned here, another solution can be given easily and no real difficulties will remain.

Alces alces can be considered as a species-complex with only one *grex*. There is no good reason to consider the Eurasian and American Moose as separate greges. The same holds true for *Rangifer tarandus*. *Cervus elaphus* can be considered as one species-complex, with several greges and possibly some gregal forms, which will not further be discussed here. All Russian deer recently living in Asia could be considered as belonging to one and the same species-complex, divided in four greges, with the possibility that one of the subspecies in the Philippines (*Rusa alfredi*) should be considered as a gregal form. The subgenus *Ussa*, as proposed by DOBRORUKA, in my opinion should be considered as a *grex*. According to DOBRORUKA this species complex shows duplicity in some of the Philippine islands, where subspecies belonging to the *grex* *R. marianna* are living side by side with subspecies belonging to the *grex* *R. timorensis*. *Rucervus duvauceli* and *Rucervus eldi*, which have been considered as



good species up till now, should be united in one single species-complex and merely be considered as separate greges, showing duplicity in western Thailand. As for *Hyelaphus* we can consider *Hyelaphus porcinus* cum subspecies as a grex of a species-complex and the deer from Bawean and the Calamian islands as two gregal forms of that same species-complex.

Of course these concepts are all theoretical and their value is only relative. But in my opinion the concepts of TOXOPEUS represent the dynamic nature of the species as a function of place and time in the best way.

Summary

The concept of the superspecies sensu E. MAYR is applied to several taxa of Eurasiatic deer and compared with the taxonomic concepts as proposed by L. J. TOXOPEUS. Questions which are difficult to answer if the concept of superspecies is applied can be solved better by using the more dynamic concepts of TOXOPEUS.

Zusammenfassung

Der Begriff Superspecies angewandt auf eurasische Hirsche

Der Begriff Superspecies sensu E. MAYR wird an Beispielen eurasischer Hirsche besprochen und mit taxonomischen Begriffen, welche von L. J. TOXOPEUS 1930 vorgeschlagen wurden, verglichen. Daraus wird klar, daß viele Probleme, welche sich bei Anwendung des Begriffes Superspecies auftun, besser und deutlicher gelöst werden können, wenn man sich dem dynamischen Artbegriff TOXOPEUS' zuwendet.

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