Historical Biogeography of *Temnorhynchus* species
(Insecta: Coleoptera: Scarabaeidae: Dynastinae)

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**Abstract.** The genus *Temnorhynchus* Hope (Insecta: Coleoptera: Scarabaeidae: Dynastinae) is distributed in the Afrotopical and Malagasy regions, Arabia and the East-Mediterranean. The historical development of present distribution areas (range systems) of some taxa of these rhinoceros beetles is discussed, considering autecological and dispersal characteristics of the species and data on fluctuations of climate and vegetation cover. Some phylogenetic branching events of *Temnorhynchus* are correlated with climatic changes of the late Quaternary in Africa, especially with the Last Glacial Maximum (around 18,000 b.p.) and the preceding pluvial (around 28,000 b.p.). The environmental change in the Holocene Altithermal (around 8,000 b.p.) influenced the range systems of extant species. Biogeographical analysis leads to an improvement of the hypothetical phylogenetic system and also to some taxonomic consequences: *T. coronatus* (Fabricius) and *T. baal* Reich & Sauley form the *T. coronatus*-superspecies. *T. burgeoni* Paulian, *T. minor* Paulian, *T. congoanus* Paulian, *T. raffrayi* Fairmaire, and *T. zambezianus* Krell form the *T. raffrayi*-superspecies. *T. retusus* (Fabricius), *T. clypeatus* Klug, and *T. elongatus* Arrow form the *T. retusus*-group.

**Key words.** Africa, Arabia, Madagascar, Systematics, Phylogeny, Historical zoogeography

1. INTRODUCTION

1.1. The genus *Temnorhynchus* Hope

The genus *Temnorhynchus* Hope, 1837, consisting of 31 species, semispecies, and subspecies, is a monophyletic group of rhinoceros beetles (Dynastinae), 9.5–30 mm length, which is easily recognizable by both a flat, bilobed, dorsoventral epicranial plate and the lack of setae at the metatibial apex which are its presumed autapomorphies (KRELL 1993a). Most species are distributed in the Afrotropical realm including Cape and Malagasy subregions, and in the Arabian peninsula. One species lives in northern Africa and the eastern Mediterranean (KRELL 1993a, 1994a).

The habitus of the *Temnorhynchus* species including genital structures is relatively homogenous. Most of the species specific character states differ only slightly which let us presume a possibly recent origin of some species, semispecies and subspecies. Since these recent speciation events may be correlated with the last glacial-interglacial oscillations, the following study was developed after finishing a phylogenetic analysis of the genus (KRELL 1993a, 1995).

1.2. The phylogenetic system – the basis of biogeographical interpretations

Vicariant distribution patterns may help – by reciprocal illumination – to get ideas on sister group relationships of extant species which originated through allopatric speciation (HENNING's (1982: 130) "Vikarianzkriterium"), but a phylogenetic analysis of range systems is not possible because they do not evolve like organisms, because "e.g., they lack competition, and thus other sources of stasis and transformation; and lack radiation [...]; there are no reasons which speak against multiple reversible fusions and separations of areas –
in contrast to organismic taxa” (Schmitt 1989: 188). Hence creation of area cladograms cannot be done by following the same principles as in reconstruction of phylogeny of biological taxa (cf. Gittenberger 1990). Chorological data cannot be reliably used to diagnose relationships of supraspecific taxa because without knowing the fossil record it cannot be settled if migration (Coope 1994: 23) or anagenetic changing of ecological requirements was the strategy employed by the stenspecies reacting to changing environments. Therefore the first step in historical evolutionary research should be a proper phylogenetic analysis (sensu Hennig 1982) based on morphological characters (Brundin 1988; cf. Nagel 1986, 1987). Knowing the sister group relationships is essential when deciding which extant range systems are to be compared. Biogeographical data are useful to explain and corroborate these hypothetical phylogenetic patterns at lower taxonomic levels (Krell 1993a: 245).

I did not use the statistical methods of transformed cladists which are more interested in parsimonious ordering of character states than in reconstructing phylogeny (see, e.g., the criticisms of Schmitt (1989: 188), Crowson (1991) and Wagle (1994)). As Schmitt (1989: 181f) points out, traditional “Phylogenetic systematics [sensu Hennig] is not identical with any sort of current ‘cladism’” and “has not been absorbed by any type of ‘pattern’ or ‘transformed’ cladism”, but is “an independant scientific method, with its own claims and limits” (see also Ridley 1986). The appropriate biogeographical procedure in phylogenetic systematics is, in my opinion, the “Arealsystemanalyse” as described by Nagel (1986, 1987) which is followed here.

In a phylogenetic revision of the genus Temnorchynus Hope (Krell 1993a, 1994b), I gave all known distribution data and sketched some historical interpretations of patterns of extant range systems. In the following study these hypotheses are elaborated to consider more palaeogeographical, palaeoecological and palaeoclimatological findings.

I deal with two levels of biogeographical reconstruction: first the generic level at which plate tectonic events may have caused branchings (chapter 2.1.); second the specific or species group level at which the more recent climatic oscillations are the crucial events for reconstruction of zoogeographical history (chapter 2.2.). For the latter level knowing autecological requirements of the treated species is essential, which is discussed in the following chapter.

Because of the uncertain systematic position of some Temnorchynus species I shall not consider all the range systems of this genus. However, in a few cases dichotomies which could not be recognized by morphological evidence alone will be proposed after biogeographical analysis of possible branching patterns.

A range system (“Arealsystem”) is defined as a partial system of the biosphere referring to a given organism or a group of organisms where their reproduction is possible without continuous migration from outside (i.e. “Fortpflanzungsraum”). According to Nagel (1986: 149), the range system should include areas where no reproduction takes place but which are frequently obligatorily by migrating species. The range system depends on the ecological valence, genetical variability, and phylogeny of the populations as well as of the changing biotic and abiotic mechanisms and is spatially and temporally delimited (Müller 1981: 103; Nagel 1986: 147, 149f). The term range system lays stress on the systemic correlations of the range with the biosphere and its phylogenetic and ecological aspects. As the species is the smallest real entity in phylogenetic/evolutionary research, its equivalent in biogeography is the range system (Müller I.c.).

1.3. Autecology

The autecology of most Temnorchynus species is unknown. A few data from collecting labels and taxonomic descriptions as well as morphological evidence give us some indications for psammophily and nocturnal activity (Krell 1993a). Only the studies of Sweeney (1967) in sugar cane plantations in Swaziland led to fundamental knowledge on the autecological requirements of one species, T. cypeatus Klug, 1855.

Since ecological knowledge is poor, hypotheses about autecology (macroclimatic, vegetation and soil preferences) of the Temnorchynus species are based on their range systems.

The specimens forming the basis of the present study have been collected over the past 200 years. During the course of this period, dramatic man-made changes of habitats as well as climatic oscillations occurred (cf. Krell 1993a: 265). Therefore, the distribution maps (Figs. 2–3, 5–6, 8) do not give the actual distribution of the species but a combination of all the temporal ranges of the last hundred years or an even longer period. However, this is certainly irrelevant for the phylogenetic interpretation of the range systems treated in the present study.

It is evident that this “zoocartographic approach” to autecology can lead only to vague estimations (Dijk 1971) which must be checked empirically by further observations and experiments. Apart from phylogenetic branching patterns, such estimations are, however, the only material that can be used in historical zoogeographical analysis, since palaeoecological knowledge is also poor. More exact autecological data of the ex-
tant species will, however, not automatically lead to more realistic zoogeographic hypotheses, because the palaeoecological knowledge will always be less exact. Thus, in historical biology the hermeneutical spiral ("Hermeneutische Spirale", Stegmüller 1973), or the "principle of reciprocal clarification/illumination" (Hennig 1966: 21, 148, 222; two different translations by Davis & Zancor), is the appropriate way to progress from such vague hypotheses by integrating all the weak facts (for further explanation see Hoffmann & Reif 1988: 202ff).

1.4. The historical development of the present range systems

"Each period of barrier formation during the history of earth initiated a pulse of faunal differentiation and speciation" (Haffer 1990: 55). The crucial event for the origin and development of present range systems is the last period of extensive climatic oscillation, i.e. the Last Glacial Maximum in the Pleistocene about 18,000 b.p. followed by a more humid period than today about 8,000 b.p. (Holocene Altithermal) (Krell, in press). Each previous glacial-interglacial period is more difficult to correlate with phylogenetic branchings because number and systematic positions of extinct taxa are unknown and dispersal rates are high (see chapter 4.2) as is the case with African Dynastinae. Hence, interpretation of range system patterns of extant species should primarily be confined to the last period or the last two periods of climatic oscillation since speciations of extant species may be correlated with these recent events as shown in the next chapter. Nevertheless correlation of phylogenetic branching patterns (as reconstructed by analysis of extant taxa) with former climatic changes can be attempted (for example see Kemp & Crowe (1985) in their study of Afrotropical hornbills) but leads to only weak hypotheses.

1.4.1. Duration of speciation

The age of extant species may be very different. Nagel (1987: 213) in his model monograph on African Ant Nest Beetles (Coleoptera, Carabidae, Paussinae) proposed that the origins of two or three semispecies of Paussus occurred 6,000 years ago. Erwin & Adis (1982: 367f) presumed that in Carabidae species (Coleoptera) with multivoltine or short-term breeding cycles speciation can occur within 10,000–30,000 years. The developing industrial melanism in Biston betularia and other moths during the last 150 years gives an impression of the potential rapidity of phenotypic fluctuation in a changing habitat (Bishop & Cook 1980). Likewise in Vertebrata, especially in birds and fishes, we find subspecific or even specific differentiation within 10,000 years or less (Mayr 1963: 578ff; Moreau 1966: 11; Selander 1971: 106; Rensch 1972: 96f; Futuyma 1986: 245f), although they have longer generations than beetles. Speciations in some cichlid fishes of Lake Nabusabo near Lake Victoria probably occurred in only 4,000 years (Fryer & Iles 1972: 556, 558). In Lake Malawi "distinctive colour forms, and even good species, have evolved within the space of 200 years" (Owen et al. 1990: 544, 547). What is more, in the House Sparrow (Passer domesticus) only 30 to 110 generations are necessary to develop morphological differences between allopatric populations that evoke the taxonomic classification as "good subspecies" (Johnston & Selander 1964).

Morphological constancy over hundreds of thousands or even million years of "species" documented in the fossil record, as indicated e.g. by Elias (1991: 552) and Coope (1994) in Coleoptera of the northern hemisphere, says nothing about the frequency and the duration of speciation processes but indicates only a long term morphological constancy (a low rate of anagenesis) in a successful clade. Branchings, i.e. speciations, are not recognized if one clade remained morphologically constant. Phylogenetic analysis is the basic requirement to determine the age of an extant species by considering fossil record and palaeogeography. In the case of Tenmorhynchus, extant range system patterns suggest that some speciations, sub- and semispeciations occurred during the last climatic changes (Fig. 10). Speciations resulting today in a species group of sympatric, reproductively isolated species, are certainly of earlier origin if allopatric speciation is the regular mode.

1.4.2. Rate of dispersal

The dispersal rates of Lamellicornia under natural conditions are not known, but some species became pests soon after introduction. These imported species came into a new suitable environment. The dispersal rate of the invaders is therefore higher than during the adaptation of a species to a newly emerged habitat as happened in the pre-cultural earth history, but it gives an idea of the dispersal ability of a species. The most impressive example for dispersal in the Coleoptera is the Colorado Potato Beetle, Leptinotarsa decemlineata (Say, 1824) (Chrysomelidae), although transported sometimes by human infrastructure. Johnson (1969: 408ff) reported that it dispersed over 2,400 km in only 15 years in the last century in North America. In Europe it needed 35 to 40 years for about 1,900 km, but in the 1950's it advanced 120–350 km/a. Hanski & Cambefort (1991: 295) reported rates of
dispersal of introduced dung beetles (Coprinae) in North America and Australia of 50–129 km/a. BARRERO & LOPEZ-GUERRERO (1992) give dispersal rates of the introduced dung beetle *Digionthophagus gazella* (Fabricius, 1787) from 43 km/a up to 808 km/a in North America. Dynastinae show similar dispersal powers. In the early 1920’s *Heteronychus avator* (Fabricius, 1792) was introduced to Australia from South Africa. Thirty years later it was distributed throughout the 1,500 km coastal area of New South Wales as well as in the regions of Perth and Adelaide (CARNE 1957: 11).

In summary, flying beetles such as *Tennorrhynchus* spp. are able to colonize a newly established habitat (e.g. by climatic change) in a very short time. The rate of dispersal may be reduced by the presence of competitors and predators which may be lacking in the case of imported foreign species. *Tennorrhynchus* is, however, excellently adapted to burrowing in sandy soil, thus having a good chance in any situation where sandy soil is available.

1.4.3. Interpretation of single isolated records

The long-distance displacement of living *Tennorrhynchus* individuals is possible. In 1985 one pair of living *T. retusus* (Fabricius, 1781) was recorded from Albany, Western Australia (ALLSOPP 1987). Founding new populations or new species by single long-distance displacements of single specimens is highly improbable and should not be considered as common explanation of mysterious distribution patterns. Single isolated records near seaports are probably due to man. Moreover, single isolated records far-away from the known distribution area could be due to wrong locality labels.

2. HISTORY OF GEOGRAPHICAL DISTRIBUTION

2.1. The generic level: Plate tectonics and phylogenetic origin of *Tennorrhynchus*

The breakup of Africa and Antarctica-Madagascar-India-Australia began in the Middle Jurassic (RABINOWITZ et al. 1983) and was significant at the Jurassic-Cretaceous boundary (141 m.y. b.p.) (BESSE & COURTILLOT 1988: 11799). Before separation, Madagascar was in contact with the nowadays coastal regions of Tanzania, Kenya, and Somalia. Since the early Cretaceous (121 m.y. b.p./123 m.y. b.p.) Madagascar has been situated in its present position (RABINOWITZ et al. 1983; BESSE & COURTILLOT 1988: 11801). Later the Indian plate separated from Madagascar about 80 m.y. b.p. (late Cretaceous) followed by the opening of the Mascarene basin (BESSE & COURTILLOT 1988: 11805). It is difficult to correlate the tectonic events with separation of biotas. Already in the Lower Jurassic (185 m.y. b.p.) the reconstruction of BESSE & COURTILLOT (1988: 11799) “shows a slight gap between India and Madagascar, in which the continental Seychelles [...] fit rather well”. However, continental contact between Madagascar and India might have been possible till the Upper Cretaceous (cf. OWEN 1983: 93; BESSE & COURTILLOT 1988: 11800, Fig. 5). Faunal exchange between Madagascar and Africa was certainly possible after their geological separation when their distance was short, but it became much less probable from the Upper Jurassic onwards.

According to the phylogenetic analysis based on morphology (KRELL 1993a) the adelphotaxon of *Tennorrhynchus* is the group of the genus *Dipelicus* Hope, 1845, *Lonchothus* Arrow, 1911, and *Anopitis* Decambre & Madge, 1980. *Dipelicus*, distributed from India and Sri Lanka to Australia and the Pacific islands, forms the adelphotaxon of the Malagasy *Lonchothus* and the monotypic *Anopitis* from the Ethiopian highlands (Fig. 1; KRELL 1993a: 246).

The first phylogenetic event within the group of the above-mentioned four genera was the separation of the stem-species of the Afro-Malagasy *Tennorrhynchus* from the stem-species of the more eastern genera *Dipelicus*, *Lonchothus*, and *Anopitis*, but the isolation event cannot be identified unequivocally. If we assume that plate tectonic events may have caused branchings at generic or subgeneric level in insects, based on the phylogenetic analysis (KRELL 1993a) the most reasonable explanations are:

a) that *Tennorrhynchus* originated in the region of Africa and Madagascar. The breakup of Africa and Madagascar caused branching between the subgenera *Tennorrhynchus* s. str. and *Tennorrhynchoidea*. Later the stem species of the *T. (Tennorrhynchoidea) repanus*-group immigrated into East Africa across the Mozambique channel (Fig. 1).

b) that the subgenera *Tennorrhynchus* s.str. and *Tennorrhynchoidea* originated before the breakup of Africa and Madagascar and later the first one became extinct in Madagascar. In this case branching of *Tennorrhynchoidea* s.str. and *T. repanus*-group may be correlated with the breakup of Africa and Madagascar. Both explanations are equally “parsimonious” because we cannot decide whether immigration or extinction is more probable in this case.

Since *Dipelicus* is morphologically isolated among the Australian Dynastinae taxa, CARNE (1957: 25) considered it one of the “recent invaders from the north”. Since its adelphotaxon is distributed in the Malagasy
subregion and Ethiopia, the centre of origin of Dipelicus may be situated between Africa and Australia. Spreading of Dipelicus from Africa through the Arabian/Sindhan area to the Oriental realm, possible since the Burdigalian (Miocene, ca. 19 m.y. b.p.; Rögl & Steininger 1983: 146; Steininger et al. 1985: 562), is not supported by extant relictual populations west of India and is therefore considered to be unlikely. However, the phylogenetic origin of Dipelicus may be correlated with the tectonic separation between Madagascar and India/Sri Lanka in the Upper Cretaceous (Fig. 1). Its centre of origin may hence be situated at the western border of its present range system. The stem species of \{Lonchotus + Ampotis\} remained on Madagascar or Madagascar-Africa. If the ancestor of \{Lonchotus + Ampotis\} had an Afro-Malagasy range, Ampotis alicola is a relic species, separated from its adelphotaon during the Afro-Malagasy separation in the early Cretaceous. The original position of Madagascar at the Somali-Kenyan coast corroborates this hypothesis. If the ancestor species of \{Lonchotus + Ampotis\} was only Malagasy, Ampotis probably originated in a later, secondary importation to the continent because neither Lonchotus nor Dipelicus are found in Africa. No unequivocal correlation between the morphology based phylogenetical system and zoogeographical history was found.

2.2. The specific level: Exemplary cases for the historical development of extant range systems

2.2.1. The subgenus Temnorhynchus

Prell, 1934 (Fig. 2)

The five Malagasy Temnorhynchus species form the monophyletic group Temnorhynchus s.str. (Fig. 1) the internal phylogenetic relationships of which are still unsettled (Krell 1993a: 262, 267). The Temnorhynchus s.str. species are not distinctly allopatric (Fig. 2). Since overlapping range systems have not resulted in hybridization, their speciation probably occurred a long time ago. Only the chorologically insufficiently known T. perrieri Fairmaire, 1899 shows al-

Fig. 2. Malagasy endemics of Temnorhynchus, maps of records.
lopatry with most of the other *Temnorhynchodes* range systems. This species, although rather small, is similar to *T. descarpentriesi* Paulian, 1946 and *T. acutemarginatus* Dechambre, 1976. *T. perrieri* could have originated during Quaternary climatic oscillations (Hervieu 1975: 138ff) through allopatric speciation with one of these species.

However, the vast man-made degradation of the Malagasy vegetation (Battistini & Hoerner 1986: 63ff; Green & SuSSman 1990) must have strongly influenced the range systems of these species during the recording time. Today their original correlations are no longer detectable. Furthermore the knowledge of the palaeoecological history of Madagascar is poor and controversial. The old and established hypothesis that the Malagasy dry deciduous forest which has been nowadays reduced to a few small relictual patches once covered the whole western part of the island in the pre-settlement Holocene time (Battistini & Hoerner 1986: 66) has recently been contradicted by Burney (1987; see Matsumoto & Burney 1994).

Burney found, through palynological and microfossil study, that Holocene open vegetation existed before the human settlers had come to the island.

Since knowledge of the Malagasy Holocene phytogeography is such poor and equivocal, historical zoogeography concerning Madagascar can only be considered speculation.

In the years of 1981, 1985, and 1986 some specimens of previously unrecorded *T. truncatus* (Klug, 1833) were found on Mauritius. Since Jean Vinson (1906–1966) who had carefully studied the beetle fauna of the Mascarenes did not include this species in his faunal lists it is certain that *T. truncatus* was only recently introduced to Mauritius, perhaps in the 1970’s (Fig. 2 (right arrow); Krell 1993a: 269).

2.2.2. The *Temnorhynchus (Temnorhynchodes)* repandus-group (Figs. 3–4), the continental taxon of *Temnorhynchodes*

This species group is well supported by unequivocal synapomorphies (Krell 1993a: 270f). It is the adelphotaxon of the remaining *Temnorhynchodes* species (= *Temnorhynchodes* s.str.) (Figs. 1, 4; Krell 1993a: 262). If the branching between the subgenera *Temnorhynchus* and *Temnorhynchodes* is correlated with the breakup of Africa and Madagascar (chapter 2.1, a), later allopatric speciation between the Malagasy *Temnorhynchodes* s.str. and the continental *T. repandus*-group was possible – from the parsimonious point of view – only by dispersal of the stem species of the *T. repandus*-group from Madagascar to Africa.

The *T. repandus*-group consists of two species. *T. scutiger* Kolbe, 1905 is found only in the tropical rain forest biome (Krell 1993a: 273). Its present range system coincides with the Pleistocene Cameroon-Gabon refuge (Kingdon 1971: 65; called the West Central refuge by other authors) (Fig. 3). Since its current distribution does not fall outside of this refuge, it is probable that this species withdrew or even originated in this region during the Last Glacial Maximum in the Pleistocene.

The guineo or, if we consider the doubtful single records east of Lagos (Krell 1993a: 271), the guineo-east African range system of *Temnorhynchus repandus* Burmeister, 1847 includes areas of mangrove (Conakry) and of mosaic of lowland rain forest and secondary grassland (Sierra Leone, Dahomey gap, Lamto) (Fig. 3). Thus this species does not depend on closed rain forest and therefore its range was not necessarily reduced during the Pleistocene lowland forest fragmentation.

![Fig. 3. *Temnorhynchus repandus*-group, biogeography. – Full symbols: examined records (Krell 1993a, 1994b); empty symbols: literature records; big empty circles: records of *T. repandus* with inexact collecting locality.](image-url)
Parapatric speciation may have happened between a stenotropic lowland rain forest population living in the Gabon-Congo region during an interpluvial (becoming *T. scutiger*) and a more generalistic one (becoming *T. repandus*) which could survive in the savannas around the Gabon-Congo forests. The latter may even have preferred this habitat. Extensive environmental change as occurred during the Last Glacial Maximum could have induced this speciation (cf. Haffer 1990: 55) (Fig. 10).

### 2.2.3. The *Tennorrhynchus coronatus*-superspecies

Krell (1992: 340f) called *Tennorrhynchus coronatus* (Fabricius, 1781) sensu Endrödi (1976: 272) "*Tennorrhynchus coronatus* (F.)-?Gruppe", because it comprises some morphologically distinct forms which are, however, not yet phenogeographically studied. According to Haffer (1986:175f) the category "species group" is defined as closely related species with exten-
sively overlapping ranges having reached ecological compatibility. It should not be used for species or subspecies with unclear phylogenetic relationships (contrary to the widespread practice in taxonomy). The appropriate category for the taxon *T. coronatus* is the superspecies, in which a group of paratypes, semispecies, and subspecies is comprised.

### 2.2.3.1. Temnorhynchus coronatus (Fig. 5)

The most commonly recorded taxon of the *T. coronatus*-superspecies comprises some taxa not yet properly diagnosed which show together a sudano-zambezian distribution pattern and are all traditionally subsumed under the name *T. coronatus*. It is widespread in the Afro-tropical realm but is absent in the equatorial rain forest zonobiome (Fig. 5; Krell 1993a: 280f). If this siliphoby is caused by autecological requirements, and not by recent intraspecific competition, then the continuity of the intraspecific gene flow of *T. coronatus* was not affected by the fragmentation of the tropical forests into refugia (Maley 1987; Hamilton & Taylor 1991: 69ff; Servant et al. 1993: 34f) during the Last Glacial Maximum. Thus, even further extension of the range was possible at that time. Since an undivided extensive range system has existed for a long period, clinal variations and local forms could evolve. After the spreading of tropical rain forests during the present interglacial since about 12–13,000 b.p. (Maley 1990: 384; Thomas & Thorp 1992: 219; Elengea et al. 1994) morphologically definable subspecies or semispecies evolved from these clines. These are still waiting for proper taxonomic treatment. Two of the geographic forms have been studied and discussed below.

### 2.2.3.2. Temnorhynchus coronatus autochth (Faimaire, 1868)

The Malagasy populations resemble those of the East African coastal area with which they may be con-subspecific. However, the Malagasy populations show a reduced phenotypic variability (Krell 1992: 338) which could indicate that they originated from a small founder population, introduced from the East African mainland. This could have occurred in the Quaternary (a few thousand years ago) when the forest which covered the whole island in the Tertiary (Hervieu 1975: 137), became reduced, because specimens of both *T. coronatus autochth* and the continental populations of *T. coronatus* are only rarely recorded from rain forest localities (Fig. 5).

### 2.2.3.3. Temnorhynchus coronatus, Arabian subspecies

The individuals of the Arabian Peninsula, although smaller and relatively uniform, are otherwise similar to those from northeastern Africa. The Arabian specimens show the most extreme reduction of the apical emargination of the epicranial plate in a south and west to northeast morpholine approximating the habit of *T. baal*. I shall describe them as subspecies of *T. coronatus* as the first step to clear up the taxonomy of the *T. coronatus*-superspecies in the northeastern part of its range.

The Red Sea began to open in the Miocene about 19 m.y. b.p. (Rögl & Steininger 1983: 146). The Red Sea joined the Indian Ocean in the Middle Pleistocene (3.5–3 m.y. b.p.) (Rögl & Steininger 1983: 153). Because of the morphological resemblance of the Arabian to the African populations it is improbable that the Arabian ones are a relic from the Miocene. There was either gene flow till the Pleistocene (across the Djibouti-Yemen land bridge), or the Arabian *T. coronatus* populations developed from Neogene founders as discussed below. The Bab el Mandeb between Yemen and Djibouti where the minimum distance between the Arabian Peninsula and the African continent is only 20 km is an ineffective barrier to migration of flying insects, especially during southwest monsoons in summer (Arabia to Africa) and northeast monsoons in winter (Africa to Arabia). An immigration from Eritrea or Djibouti to Yemen is likely, especially during interglacials when the southwest monsoons were stronger (Duplessy 1982; Prell & Van Campo 1986; Emeis et al. 1995) and the climate of the coastal area was wetter (Sanlaville 1992).

Anton (1984: 295) gives a clear table of correlation of climatic phases, geomorphological evolution, and vegetation of Saudi Arabia since the Oligocene. The present arid phase on the Arabian Peninsula began about 6,000 b.p. (Anton, I.:; Gärden 1988: 92; Sanlavel 1992: 10). At present, the range system of Arabian *T. coronatus* comprises the two main regions with more than 100 mm/y precipitation which are separated by a hyperarid corridor (cf. map in Sanlaville 1992: 6). Since this corridor developed during the present arid period, the disjunct distribution of the Arabian *T. coronatus* probably originates from an undivided range system during the last pluvial more than 6,000 years ago. The isolation between the continental and the Arabic populations of *T. coronatus* was hence probably established during the Last Glacial Maximum (18,000 b.p.) (Fig. 10) when *Temnorhynchus* disappeared in the hyperarid corridor (cf. Fig. 5: presumed isolation barrier) from Sudan to Djibouti.

### 2.2.3.4. The origin of Temnorhynchus baal Reiche & Saury, 1856 (Fig. 5)

The northermmost populations of *T. coronatus* from the Sahara and Arabia show a more shallow emargination of the apex of the apical plate than the southern ones, similar to that of *T. baal* which occurs in northeastern Africa, Arabia and the Levant. There is no character displacement in the
overlapping areas of their range systems. The Arabian
*T. coronatus* looks especially similar to *T. baal*. Hence
speciation of *T. baal* (or the stem species of (*T. baal* +
*T. sjoestedti*), if these species are adelphotaxa (see
Krell 1993a: 282)) and the northeastern populations
of *T. coronatus* happened in northeastern Africa (Fig.
5) as described in the following. Since no relictual
populations from Jordan or Iraq are known where the
ecological conditions are favourable for *Temnorhyn-
chus*, speciation in the northern part of the Arabian
Peninsula is rather unlikely.

The first Tertiary land connection between Eurasia and
Africa and the opening of the Red Sea occurred in the
Lower Miocene about 19 m.y. b.p. and has been pre-
sent since the Upper Miocene (Rögl & Steininger
1983: 145f, 150). Colonization of the Levant from
northeastern Africa is possible since that time. Later an
isolation barrier formed, e.g., an hyperarid corridor in
southern Nubia/Sudan (as far as Djibouti; Fontès et al.
1973) including the Nile valley during the last glacial,
I.e., 21,000–12,500/11,000 b.p. (Adamson et al. 1980;
Degens & Spitz y 1983: 9; Paulissen & Vermeersch
1989; Pachur & Hoelzmann 1991) (Fig. 5), replaced in
Ethiopia by the cold Ethiopian highlands (see map 3 in
Littmann 1988: 110). During the glacial/interpluvial
periods, refugia for *Temnorhynchus* existed in the
Bar-Yosef 1990: 60) and in the Nile delta region
which was certainly not dessicated (cf. Degens &
Spitz y 1983: 8f).

The isolation barrier between *T. baal* and *T. coronatus*
could also have been a dense rain forest strip during a
pluvial period. In the last pluvial the Sahelian vegeta-
tion zones were shifted 500–600 km northwards (Neu-
106 for northern Sudan). If this shift included the more
southern forest zones, then dense forest would have
covered the southern quarter of Sudan between 11,000
and 7,000 b.p. as proposed by Wickens (1975: 56; cf.
Barakat 1995: 106 and the maps in Crowe 1978: 53
and Nagel 1987: 151, 211).

The phylogenetic origin of *T. baal* was, however, not
carried by this climatic change because a relictual pop-
ulation in the Hoggar indicates that speciation had
already finished (see next chapter). The isolation
barrier must have existed during the Last Glacial Max-
imum (interpluvial) or the preceding pluvial which
took place in the Pleistocene between 30,000 and
21,000 b.p. (Pachur & Hoelzmann 1991) (Fig. 10).

If *T. baal* and the East African *T. sjoestedti* Kolbe,
1910 are adelphotaxa which separated during the Last
Glacial Maximum, then the phylogenetic origin of
their stem species was no later than in the Pleistocene
pluvial. In Fig. 10 the most probable phylogenetic
history of these taxa is proposed.

### 2.2.3.5. Historical development of the range system
of *Temnorhynchus baal*.

- **Northeastern Africa and the Hoggar**

Most specimens of *T. baal* have been recorded from
Lower Egypt and the Levant (Krell 1993a: 282). This
concentration north of its presumed origin, as indi-
cated by the presumed isolation barrier in Fig. 5, is
certainly a result of the development of the present
hyper-arid conditions in northeastern Africa since
5,000 b.p. (dating after Wendt et al. 1977). The few
recorded *T. baal* populations of Sudan, Ethiopia, Stir-
tea, and Somalia are probably relics from a wetter pe-
riod or are due to dispersal events. Since the entomo-
fauna of these regions is insufficiently known, further
collectings are necessary to define the southern border
of the present range system of *T. baal*.

The isolated record of *T. baal* from the Hoggar moun-
tains (Fig. 5) indicates that a relictual population exists
in the Hoggar because dispersal by man through the
Sahel in east-west direction from Egypt to the Hoggar
is highly improbable. The hyperarid Sahara forms an
isolation barrier for this species (Fig. 5), but in the past
the southern border of the Sahara was shifted north-
wards or its southern part was interspersed with more
humid areas: Schulz (1987, 1991) and Neumann &
Schulz (1987) found a northward shift of the savanna
border of 400 km up to ca. 19°22′N in northern Mali,
Niger and southwestern Libya during Middle Holoc-
cene (8,000–6,000 b.p.). In its reconstruction of the
Middle Holocene vegetation of the central Sahara,
Schulz (1991: 198) shows the Hoggar reached by
*Commiphora-Acacia-Bauhinia* savanna from the
south. The plant cover developed its present character
from about 5,700 b.p./4,000 b.p. onward (Schulz
having studied the eastern Sahara, demonstrated that
the Sahelian vegetation zones shifted about 500–600
km northwards at 7,000 b.p. and 300–400 km at 5,700
(1989), Lézine (1989) and Lézine et al. (1990) came
to similar conclusions. However, Littmann (1987, 1988)
doubts continuous shifting of savanna vegetation as it
could only exist in ecologically favourable areas. A
mosaic pattern of savanna patches in an arid region ex-
isted in the southern part of the Sahara. This view is
supported by the results of Peters (1988) and Bal-

In summary, the Hoggar was connected floristically to
the Nile valley by continuous or patchy savanna vege-
tation in the Middle Holocene, from at least 8,000 b.p.
to 6,000 b.p., and probably in the Pleistocene as well.
From 6,500 b.p. to 4,500 b.p. a corridor of increased
precipitation may have existed from the Hoggar to the
Mediterranean coast as far as the Nile delta (Nichol-
sen 1978: 20). Both periods of time were sufficient for
2,000 generations of Temnorhynchus (see Sweeney 1967: 77), and enough for T. baal to increase its range system from its assumed origin (Egypt/Sudan) to the Hoggar mountains (cf. dispersal rates discussed above). During the upper Holocene southward shift of the Sudan savanna and desertification of the central Sahara, the Hoggar became an island habitat bearing now a relictual population of T. baal. Temnorhynchus coronatus s.str. is also recorded from the Hoggar (Fig. 5) being part of the northernmost population of this taxon. It may be a relic from the last humid period, too. Transitional forms to T. baal are not known.

• Greece, Cyprus, and the Levant

T. baal is found in northeastern Africa, Arabia, the Levant, Cyprus and Greece (Fig. 5). Northeastern Africa, Arabia and the Levant form an continuous range. Isolated records from Cyprus, Crete, Naxos, and Doiran/Macedonia have been published (Krell 1993a: 282f).

The Taurus range forms a division between the Anatolian and the Levant fauna (Kosswig 1955). Indeed the range system of T. baal is interrupted at the Taurus (Fig. 5). Trihas & Legakis (1987: 127) say that the fauna of the Aegean islands "now represents a combination of tertiary relics [sic] and Near East as well as European colonizers, from which many endemic species have evolved." Until the Upper Miocene and later during the Messinian Mediterranean salinity crisis (5 m.y. b.p.) a continuing landmass from the Aegean islands to Anatolia and the Levant, including the Cypriot region, existed (Rögl & Steininger 1983: pl. 13; Steininger et al. 1985: 566). No subsequent connection of Cyprus to the mainland has existed (Swiny 1988: 1; Schüle 1993: 400). As we can see e.g. in T. cribratus Bates, 1884 (see Krell 1993b: 261ff), T. zambezianus Krell, 1992 (see Krell 1992: 356), T. coronatus, T. tridentatus Lansberge, 1886 (see Krell 1992: 340f; 1993a: 279f; unpublished results), the Temnorhynchus species tend to form geographical races or clines. Greek and Cypriot T. baal populations are rather founded by Holocene invaders than caused by relic populations from the Tertiary (5 m.y. b.p.) because of their eidoonomic similarity to the individuals of the Levant and Egypt, and because the present northeastern range system border lies at the Taurus range. Hence chorology cannot falsify the hypothesis that T. baal and T. coronatus branched in the Pleistocene. How could these invasions have happened?

Similarity between regions of extensive medieval sugar cane cultivation and isolated records of Temnorhynchus in the last two centuries are evident (compare Fig. 1 in Galloway 1977 and Fig. 93 in Krell 1993a. – In the 7th century Saccharum officinarum L. spread to the Levant, Egypt, Cyprus, in the 9th century to Crete (Blume 1985: 23f). The sugar production declined in Egypt and the Levant in the 14th century and increased simultaneously in Cyprus, Crete, and the western Mediterranean where it continued till the end of the 16th century (Galloway 1977: 181; Blume 1985: 28). One hundred years ago, in the south of Cyprus, a few cane cultivations still existed (Suck 1900: 144). The northern expansion of sugar cane cultivation in Greece (Peloponnesus) is not known (Ritter 1841: 400). Today, eastern Mediterranean cane cultivation is restricted to northeastern Africa, especially Upper Egypt (Blume 1967). It is not known if sugar cane has ever been cultivated on Naxos, but according to Carpaneto (1985) the faunas of the Cyclades and Crete are not completely different (Jaccard index for Carabidae: 15.82; for coprophagous Scarabaeoidea: 28.95); hence migration between both regions is probable, with or without sugar cane,).

Although mentioned in Box's (1953: 14) list of sugar-cane insects we have no specific pest records of T. baal from cane fields (Willcocks 1925: 207; Ezzat & Atries 1969). Only Hafez & Bishara (1961: 155) mentioned it within a group of Dynastinae species claimed to be "more or less injurious to [Egyptian] agriculture" (without any further data), damaging sugar cane among others. Considering the aetiology of congeneric species (Sweeney 1967) it is, however, probable that T. baal feeds on sugar cane if it is cultivated on sandy soil. In Egypt, sugar cane "was grown mainly on al-Baq and al-Bars soils, being of a loamy texture" (Blume 1985: 26). This might have protected the plantations from severe damage by Temnorhynchus.

Temnorhynchus could be spread by cane cuttings, stalks or rooted plant transport and survived in the sugar cane plantations at their destinations. Before legislation designed to restrict introduction of foreign insects was enacted, spreading of sugar cane pests occurred commonly (Pemberton & Williams 1969: 5f).

• Arabia

Only two individuals of T. baal have been recorded from the Arabian Peninsula (Krell 1994b: 147). Both were found in the Yemens and bear a character considered plesiomorphic for Temnorhynchus and for the T. coronatus-superspecies: one or more ocular canthus bristles never found in African or Levantine specimens. This may be caused by hybridization with Arabian T. coronatus which displays this character state constantly. Alternatively (and in my opinion more likely) a relic population of T. baal could have survived in the Yemens, introduced or staying here since
the speciation time of *T. baal* and Arabian *T. coronatus* between 30,000 b.p. and 18,000 b.p.. During the summer monsoon months, adults of *T. baal* were collected in Sudan and Somalia (Krell 1994b: 146). An immigration from there to Yemen is likely, especially during interglacials when the southwest monsoons were stronger and the climate of the coastal area was wetter (see above).

### 2.2.4. The *Temnorhynchus raffrayi*-superpecies (Figs. 6–7)


Since only three females of *T. kasanganus*, which is sympatric with *T. raffrayi*, are known (Krell 1993b), it is not discussed here. All the other species are allo- or parapatric (Fig. 6; Krell 1993a). We can observe a continuous transformation series from the big *T. tridentatus* to the smaller *T. burgeoni*, and further on to the small *T. congoanus* and the other small species: Small individuals of *T. tridentatus* look like *T. bur-
geoni, small *T. burgeoni* look like *T. congoanus*. However, *T. zambezianus occidentalis* shows a pleiomorphic character state (ocular canthus bristles) which is present in *T. tridentatus* and the other more basally branched species, but lacking in the remaining species of the *T. raffrayi*-superspecies (cf. phylogenetic argumentation scheme in Krell 1993a: 264; and Fig. 10).

It is not possible to localize the region of the morphologically reconstructed branching event between the *T. tridentatus* ancestor and the stem species of the *T. raffrayi*-superspecies because the extant range system of the former is too vast (map in Krell 1993a: 317) and the event happened too long ago.

The next branching pattern cannot be reconstructed from morphological evidence alone (Krell 1993a: 264, 288ff); it might have happened a) between *T. zambezianus* and the stem species of (*T. burgeoni* + *T. congoanus* + *T. raffrayi* + *T. minor*), if the sizes of body and male cranial plate were reduced convergently in *T. zambezianus* and (*T. congoanus* + *T. raffrayi* + *T. minor*); or b) between the common stem species of *T. zambezianus* + (*T. congoanus* + *T. raffrayi* + *T. minor*) and *T. burgeoni*; in this case the reduction of the ocular canthus bristles happened three times convergently (in *T. burgeoni*, *T. zambezianus* s.str., and in (*T. congoanus* + *T. raffrayi* + *T. minor*)).

Both homoplasies are probable, but the hypothesis b is difficult to correlate with palaeogeography because the range system of *T. burgeoni* is almost completely surrounded by the range systems of its adelphotaxon comprising species of diverse autecological requirements. In this case, the hypothetical isolation barrier between *T. burgeoni* and its adelphotaxon cannot be fixed geographically, whereas in hypothesis a a correlation with palaeogeography is simple as discussed below. That is why I prefer this one.

The hypothetical isolation barrier between *T. zambezianus* and the ancestor of its adelphotaxon existed between central Africa around 10°S and the central part of southern Africa (cf. Fig. 6). Alternatively the northern forest/forest mosaic/woodland ancestor of *T. burgeoni*-*congoanus*/*raffrayi*-*minor* differentiated from the southern grassland/woodland *T. zambezianus* for ecological reasons. Both causes are conceivable during an interpluvial when equatorial forests withdrew northwards from the presumed range of *T. zambezianus* ancestor in the western Limpopo-Zambezi region. In any case *T. zambezianus* probably spread later eastwards along the big streams of Limpopo and Zambezi, lost their ocular canthus bristles to become the subspecies *T. zambezianus zambezianus*. The western form lost some of the preapical bristles at hind tibia and is called *T. zambezianus occidentalis*. Both are very similar and a transitional form is known (Krell 1992: 367) thus indicating that the subspeciation happened recently (during the Last Glacial Maximum ?; cf. Fig. 10, or during the Holocene Altithermal), or that the gene flow between the two subspecies is strong.

During a pluvial period between ca. 30,000 b.p. and 20,000 b.p. (Perrott & Street-Perrott 1982; van Zinderen Bakker & Coetzee 1988: 169, Fig. 4; Hamilton & Taylor 1991: 73; cf. Servant et al. 1993: 29; Elenga et al. 1994), the tropical lowland (or montane ?) forest may have occupied the entire Congo basin and extended southwards (Fig. 6; cf. map in Crowe 1978: 53) causing ecological/geographical differentiation: In the southern forest/woodland mosaic region, *T. burgeoni* became established. In the (lowland) forest a silviculous species developed: the stem species of *T. raffrayi*, *T. congoanus*, and *T. minor*.

Some East African pollen records contradict a pluvial period around 28,000 b.p. (Bonnefille et al. 1992; Aucour et al. 1994: 232). If in central Africa this era was not humid enough to allow spreading of rain forest, the described speciation pattern might happen in the preceding pluvial prior to 70,000 b.p. (Hamilton & Taylor 1991: 66) or in the Njilien (40,000–30,000 b.p.) which was humid according to Schwartz et al. (1985), Maley (1990: 384, 387), and Aucour et al. (1994: 232), e.g.

During fragmentation of the lowland forest in the Last Glacial Maximum (18,000 b.p.; see above), the west-central African strictly silviculous *T. congoanus* was separated from the eastern *T. raffrayi*, which currently occurs in the Zanzibar-Inhambane coastal mosaic (climax vegetation was mostly forest) and in the wetter Zambezi miombo woodland (White 1983) (not in savannas as claimed by Krell (1993a: 287)). Only one specimen of *T. minor* is known with the vague locality “Dahomey” thus preventing further interpretation (Fig. 10).

Zoogeographical considerations lead to an improvement of a part of the hypothetical phylogenetic system (Fig. 7) which was not reconstructable from morphological evidence.

### 2.2.5. The *Tenuorhynchus retusus*-group (Figs. 8–9)

This species group (“Sammelgruppe” 4.3.4.2.3. in Krell 1993a: 294) consists of *T. retusus* (Fabricius) and its adelphotaxon, (*T. clypeatus* + *T. elongatus*). Since the systematic position of *T. cribatus* is still unresolved (Krell 1993a), it is not included in this group for the present. If *T. cribatus* does really turn out to belong to this part of the genus, the biogeographical hypothesis may need profound revision.
The range system of *T. retusus* is situated in the coastal area of South Africa and Namibia as well as along the Orange River (Orange) (Fig. 8; KRELL 1993a: 297f). Most records are from the “Cape regional centre of endemism” (WHITE 1983) and adjacent northwestern regions. Single old and inexact records from Sudan, Eritrea, and Tanzania could be due to wrong labels or single importations (KRELL 1993a: 298; KRELL 1994b: 153f). The centre of the range system of *T. clypeatus* lies in Tanzania and Mozambique northeasterwards of the range system of *T. retusus*. In the Cape region the range systems of *T. clypeatus* and *T. retusus* overlap. *T. elongatus* Arrow was found only in a restricted area in the Transkei region (Kaffraria, Pondoland) in South Africa (Fig. 8; KRELL 1993a: 297). Such a group of closely related species with overlapping ranges is termed a species group (HAPPER 1986: 175).

Considering present range systems speciation between *T. retusus* and the ancestor of (*T. clypeatus* + *T. elongatus*) happened presumably near the southern or southeastern coast of South Africa. If *T. elongatus* is a relic population from this ancestor having undergone only little or no dispersal, then the isolation barrier between *T. retusus* and the ancestor of *T. clypeatus* + *T. elongatus* was situated south of the Transkeian territory, i.e. south of the present range system of *T. elongatus*. Speciation of *T. elongatus* and *T. clypeatus* could have taken place northeast of Pondoland (cf. Figs. 8, 9). If *T. elongatus* is a recent split off population, the geographical region of the branching event between *T. retusus* and its adelphotaxon is not reconstructable.

If a reduction of 50-60% of the present precipitation occurred, an arid corridor of Karoo might have developed in the region southeast of the Transkeian territo-
3. EPILOGUE

Some recent morphology based phylogenetical branchings can be correlated with Late Quaternary palaeoecological changes caused by climatic oscillations (Fig. 10). Furthermore, by reciprocal illumination, biogeographical analysis can improve the phylogenetic reconstruction when morphological evidence is not sufficient for reliable reconstructing of dichotomies between extant adelphotaux (Krēll, in press). Because of scarce and sometimes equivocal data on Quaternary palaeoecology, palaeogeography and palaeoclimatology of Africa, the conclusions of the present study are not always based on unequivocal evidence. However, the given scenarios are consistent and hence of explanatory and heuristic value awaiting further corroboration by reciprocal illumination between ecology, biogeography and Quaternary sciences.
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