Towards a causal history of present range patterns in the rhinoceros beetle genus Temnorhynchus Hope (Insecta: Coleoptera: Scarabaeidae)

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Abstract. The way to a causal history of present range patterns consists of three steps: 1. alphataxonomical examination; 2. phylogenetic analysis sensu Hennig; 3. biogeographical analysis, considering present vicariance patterns and correlations between phylogenetic branching patterns and palaeoclimatological and palaeogeographical history of the range of the group studied. This procedure is shown by the author's recent study of the afrotropical beetle genus Temnorhynchus Hope (Coleoptera: Scarabaeidae: Dynastinae).

Key Words. Biogeography, Afrotropis, Coleoptera, Scarabaeidae, Temnorhynchus.

The rhinoceros beetle genus Temnorhynchus Hope (Scarabaeidae: Dynastinae) is a monophyletic group consisting of 31 species and subspecies. Its range extends from the eastern Mediterranean and the Arab Peninsula to Mauritania, Southern Africa, and Madagascar (Krell 1993 a).

The crucial point for any further evolutionary study in zoology is a careful alphataxonomical examination because diagnosis of species is always the first step in systematics and its foundation. If a taxonomical revision exists, it is frequently more or less typological, as in the present case (Endrödi 1976). Hence, the herein defined species-group taxa should not be used uncritically as units for phylogenetic and biogeographical analysis. In Temnorhynchus the typological classification of character states of a morphcline resulted, for example, in completely different positions of two "species" (T. freyi Endrödi, T. cribratus Bates) in the proposed "system" (i.e. the given determination key). These two taxa could be treated as subspecies of T. cribratus (cf. Krell 1993 b). Moreover, many sloppy synonymizations and subspecifications in the literature and the discovery of three new species in repeatedly revised material (Krell 1992, 1993 a and b, 1995), indicated the necessity to reconsider the existing alpha-taxonomy.

The second step is the phylogenetic analysis sensu Hennig based on morphology (Krell 1993 a). However, the available morphological data are not sufficient for a sound and completely dichotomous phylogenetic reconstruction (cf. Figure 1). As in most tropical taxa molecular data are not available and not obtainable for most species in justifiable time. Chronological data are available. However, they are less reliable than morphology to find out phylogenetic relationships of taxa above species level, because a) by lack of a fossil record we do not know whether migration or anagenetic changing autecological requirements was the strategy of the stemspecies reacting to changing environment, and b) the number and the systematic positions of extinct species and their vicariance patterns remain unknown.

However, chorology can be fruitful, by reciprocal illumination ("wechselseitige Erhellung"), to diagnose sister group relationships of extant species if they are caused by allopatric speciation. Furthermore it helps to explain some of the reconstructed branching patterns. In the present study (Krell 1996) the reconstructed hypothetical phylogenetic branching events are compared and correlated with palaeoecological changes in the Late Quaternary considering the present range systems of extant species (Figures 2–3).

Crucial times for the development of present range systems are the humid period at about 8.000 YBP, the last glacial maximum at 18.000 YBP, and the preceding pluvial at 28.000 YBP or earlier. In glacial maxima the lowland rain forest was reduced to small fragments (refuges) whereas during pluvial periods the forest zone increased. Both changes may induce splitting or uniting of range systems leading to speciation or character displacement (cf. Krell 1996).

Since the end of the seventies the amount of palynological, palaeoecological and palaeoclimatological literature has grown enormously. Some results are contradictory, particularly if climatological interpretations developed from studies of single localities are applied inductively to the whole region. One of these problems affecting the present study is the different climatological interpretation of the time before the last glacial maximum in the central African forest region. Some authors claimed the period between 30.000 YBP and 20.000 YBP to be humid (e.g. Hamilton & Taylor 1991: 73), some suggested it to be dry (e.g. Bonnefille et al. 1992). Maley (1990: 384) dated the pluvial before the last glacial maximum at 40.000 YBP to 30.000 YBP, a period assumed to be colder and drier by Hamilton & Taylor (1991: 73).

Despite these inconsistencies which are difficult to evaluate by a zoosystematist, correlations between phylogenetic branching events within the genus *Temnorhynchus* (Figure 1, e.g.) and pluvial or glacial maxima are inferable in nine cases (Krell 1996). Some of them are shown in Figure 3. The comprehensive study has been published elsewhere (Krell 1996).
Figure 1: *Temnorhynchus raffrayi* superspecies; phylogenetic scheme of argumentation based on morphological characters (from Krell 1993a: 264, modified; because of its unsettled systematic position (Krell l.c.: 294), *T. kazangaicus* Krell is omitted).

Figure 2: do.; hypothetical phylogenetic tree, after biogeographical analysis.

Figure 3: do.; correlation between phylogenetic branching events and palaeoclimatological changes.
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References


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