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All the new taxa were found in the Oligocene Molasse basin of Switzerland and Savoy. They are used as fossil indices in the biostratigraphical scale of the Lower Freshwater Molasse and their estimated age is from the top of the Lower Oligocene (assemblage zone of Balm) to the Upper Oligocene (assemblage zone of Rickenbach). All the taxa have been determined using the maximum available characters of the masticatory apparatus (maxillary and mandibular fragments and dentary structure) among them the foramina (less dependently of the selection pressures).

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## Introduction

The biozonation of the Lower Freshwater Molasse of Switzerland and Savoy will soon be published. This work is based on the study of a considerable quantity of fossil-remains. Among them the eomyds, cricetids, lagomorphs and theridomyids proved to be the best fossil index. This paper is about the last group of rodents mentioned above, and the purpose here is to describe species that are used as reference fossils in the biozonation.

During the elaboration of our biostratigraphic scale (ENGESSER & MAYO 1987), a special study of the rodent Family Theridomyidae ALSTON 1876 took place. Therefore several papers were published concerning theridomyids (MAYO 1980, 1981, 1982 and

1983), or where the theridomyids were used as biostratigraphic references (MAYO 1984 and 1986 in: ENGESSER et al.) and others will follow. In the case of Issiodoromyinae, a monograph (MAYO 1987) will supply additional information. For this reason, the descriptions in this paper are largely concerned with the systematics. The first part concerning the Subfamily Archaeomyinae has been published (MAYO 1983). Nevertheless, the increase in knowledge has necessitated the elevation in rank of the taxa from subgenera to genera.

The study of this Family (which is for the first time restricted to the successive beds of a single basin) has shown some of the problems of the previously proposed lines of successional species, in which species were found in different basins, and were considered as distributed all over Europe (THALER 1966, and VIANEY-LIAUD 1973, 1976 and 1979); an assumption that I find mistaken. It is well known that parallelisms are very typical in the phylogeny of the rodents, and this that applies especially to the Theridomyidae. The principal problem concerning this Family is that after STEHLIN & SCHAUB (1951), LAVOCAT (1952), DECHASEUX (1963) and THALER (1966), the literature has tended to allocate the different species to only one or two genera, with the purpose of recognizing only one or two lines of evolution within each Subfamily. The genus *Theridomys* JOURDAN 1837 is an example of this. On the basis of a reduced number of characters, it was possible to place species together that were once thought separate.

BOSMA (1974) clearly saw such problems and went back to the previously abandoned point of view of STEHLIN & SCHAUB (1951) and LAVOCAT (1952). For this she had well founded arguments: "VIANEY-LIAUD (1972b) [1973] and HARTENBERGER (1973) considered *Isoptychus* to be synonymous with *Theridomys*, as they believed that the *Theridomys* species evolved from the *Isoptychus* species. In our opinion, supposed phylogenetical relations are no good reason for the allocation to one genus. Most species of *Isoptychus* and *Theridomys* show consistent differences in dental structure and therefore it is preferable to maintain both genera. Species proving to be intermediate in dental structure between *Isoptychus* and *Theridomys* may be referred to one genus or the other in an arbitrary way" (1974, p. 80). This elementary principle that genera are established by generic characters, in the study of theridomyids has been forgotten in recent years. Unfortunately BOSMA, who realized this, could not continue her studies on this group of rodents. Nevertheless, the discovery of fossil remains of *Isoptychus bumbachensis* n. sp. in the Molasse basin of Switzerland – living approximately at the same time as *Theridomys lembronicus* BRAVARD, in GERVAIS, 1848–52, or even younger – has demonstrated that BOSMA's point of view was right. On the other hand, the study of skull fragments, foramina, mandibles and dental structure has allowed the reintroduction of the *Isoptychus* genus, back into Theridomyinae as well as others. *Trechomys* LARTET 1869 has enough generic characters to be maintained separately from *Theridomys* JOURDAN 1837. I believe *Theridomys* arose from *Trechomys*. Until now, we have had a gap between the species that permits us to establish this opinion (*Trechomys major* and *Theridomys lembronicus*). Probably this gap may be filled when the study of the basins in Spain is ready. In spite of this, *Isoptychus* is not a single taxon. At the moment there is evidence that suggests that it will be possible in the near future, to separate it into two subgenera, one with two lines of successional species, with one larger than the other. The same problems of the Theridomyinae occur with two other Subfamilies: Archaeomyinae LAVOCAT 1952 and Issiodoromyinae LAVOCAT 1952. Only one line of successional species

was recognized for each of them. The study of theridomyids in the Molasse basin of Switzerland and Savoy demonstrates that both Subfamilies are very complicated. Some of these problems, concerning Archaeomyinae, can be found in my papers cited above (1981 and 1983), those concerning Issiodoromyinae will be presented in this paper.

### Taxonomic procedure

Under "previous diagnoses" are mentioned some authors who did not offer a real diagnosis although it is possible to find it in their descriptions.

Emended diagnoses are given for most of the taxa, as it seems necessary for the proposition of several new taxa and also for the reintroduction of others which in the relatively recent literature were considered synonyms, or not distinguished at all on the basis of too few numbers of characters. For this purpose a considerable number of generic and subgeneric characters are proposed, and several of the old ones have been reevaluated. The importance of the generic or specific characters must be comprehended by their utilization, and any additional explanation will generally not be offered in this paper.

The generic characters have been based on the complete masticatory apparatus. This is because the maxillary and mandibular fragments are not infrequently represented in the beds, associated with the more frequent dentary structures. The maxillary and mandibular fragments permit us to follow the modifications of the masticatory apparatus, which occur by adaptations to many specific niches in the different sequences of the basin beds. Characters based on the masticatory system are very good, because it is well known that they have been subjected to greater selection pressure. On the contrary, foramina are less involved in such selection pressure. Thus, a reasonable balance between the characters permits us to follow the relationship of a new lineage as distinct from others that have arisen due to parallelisms. The foramina connected with the masticatory apparatus, have also been used as generic characters. Skulls are very rare in stratigraphic localities. For this reason I do not pay much attention to the cranial foramina, in spite of this I do not agree with LANDRY (1957, p. 8) in the taxonomic value of them, but I am closer to the opinion of LAVOCAT (1952 and 1971), PATTERSON & WOOD (1982) and WAHLERT (1974, 1977 and 1978)<sup>2</sup>). Slight modifications in the structure or in the position of these characters have been used to fit the boundaries of interspecific variation. Nevertheless, the modification of the dentary structure has been taken into account, as the results in regard interspecific variation are the most useful. In all cases, the maximum available characters have been used.

In the literature there are some cases where a relatively great difference of position of the incisive foramina has been considered only of interspecific value (see BOSMA 1974, Pl. II, Fig. 4 and 5). In my view such a relatively large modification in the position and the structure of the incisive foramina has a higher taxonomic importance. In the case referred to, it is possible to see the concurrence in the specimens of other important characters above the species level. For instance, the fossette for the *M. masseter superficialis* in *Isoptychus headonensis* BOSMA 1974 and the near absence of it in *Isoptychus pseudosiderolithicus* DE BONIS 1964, which has a more distinctive masseteric ridge and so on (I could

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<sup>2</sup>) Prof. Landry who has read this manuscript in part, told me that he is now in agreement with this opinion.