

Taxonomic procedure

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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)²). 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

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

not examine the specimens). The same occurs with the two specimens of *Isoptychus* figured by VIANEY-LIAUD (1973, p. 306, Fig. 5). In both cases, similar different characters concerning the fossa for the superficial masseteric muscle are represented. In addition, the presence of a fully developed mesoloph in *I. headonensis* and the incomplete development of the mesoloph in *I. pseudosiderolithicus* may be an important character distinguishing the taxa at a higher level. VIANEY-LIAUD (1979, p. 148) identified the species *I. headonensis* BOSMA 1974 as belonging to the genus *Thalerimys* TOBIEN 1972. This opinion is followed also by HOOKER (1986, p. 422). But at least in the maxillary fragment assigned to *I. headonensis*, there are represented several diagnostic characters of *Isoptychus*, which cannot be found in the species *pseudosiderolithicus*. On the other hand, I have the same opinion as HOOKER (1986) about the value of the wrinkled enamel in isolation from other characters. I believe that it is the same applies to teeth with many protuberances and no other related characters.

Something similar occurs with the structure of the infraorbital canal ventral to the infraorbital foramen. Concerning Theridomyidae, I stand by my previous point of view about the value of this character, as I have found it to be very useful (1982, p. 699–701, Fig. 1). That is, when there are several maxillary fragments of the same taxon available in a layer, its range of variation is very small and above all, a similar structure is maintained in all of the specimens. A deep infraorbital canal should be considered as a “primitive” generic character. In the transition towards loss of it, a single specimen can have a part of the maxilla without the canal and an other one with a very shallow canal, for instance, like the Holotype of *Protechimys* (*Protechimys*) *gervaisi* (THALER 1966). But loss and acquisition of a deep infraorbital canal with high variation of its external ridge – as considered by VIANEY-LIAUD (1973) for the “*Theridomys*” and “*Blainvillimys*” lines – does not occur in the same genus. In Theridomyids it seems to be that the tendency is for the gradual loss of the deep infraorbital canal in Theridomyinae, to maintain it with slight modifications in Issiodoromyinae and to lose it completely in Archaeomyinae.

Applying the Student t-test, the 5 per cent level of significance – as is usual – has been chosen. For the Pearson’s coefficient of variation SIMPSON et al. (1960) has been followed. But FREUDENTHAL & CUENCA’s coefficient of variation has also been taken into account (FREUDENTHAL & CUENCA BESCOS 1984). Concerning the Theridomyidae populations of stratigraphic localities, most of the Pearson’s coefficient of variation for length of $M^{1/2}$ or $M_{1/2}$ is between 4 and 6 (as example see p. 1079, Tab. 54). Rarely it was found to be $c8$ and when it is really higher than 8 – with N good enough –, generally there was clear evidence of other closely related species represented in the sample. Typical examples of this are the samples with Theridomyidae of the carstic fissure filling of Pech Desse and Pech du Fraysse (see VIANEY-LIAUD 1976 and 1979), where it is possible to apply the SIMPSON’s rule: “Much higher values [than 10] usually indicate that the sample was not pure, for instance, that it included animals of decidedly different ages”. I am also following GINGERICH (1974 and 1976) in the interpretation of the values of V for the Pearson’s coefficient of variation. Values of V higher than 8 for the length of $M^{1/2}$ and $M_{1/2}$ – contrary to the opinion of VIANEY-LIAUD (1976 and 1979) and VIANEY-LIAUD & LEGENDRE (1986) – are considered as representative of more than one species. It should be assumed that where N is too small for V to be significant, that despite this, V will be shown. This because it is useful for comparisons with other stratigraphic samples with few or only a

single specimen, and this can be compared by using the logarithmic method of plotting. As an exception, where V is very high because there are too few specimens, it will be considered useless to mention it.

Terminology

The terminology for the teeth of STEHLIN & SCHAUB (1951) has been followed. I am also using some terms described in previous papers (1981, p. 1011 and 1983, p. 832, 833 and 898, Fig. 54) although this is with reference to other genera (Fig. 1).

Pseudograben is the union in the upper teeth between the sinus and some syncline, or in the lower ones between the sinusid and some synclinid. This union is variable. Its deepness changes with the genera and species. Generally, all the Oligocene generic taxa of Theridomyidae – with the exception of *Isoptychus* – follow this evolutionary tendency. Although in mosaic: with different rhythm and on different teeth. The pseudograben is an intermediary step. Its union occurs during the evolutionary process from a shallow to a relatively deep depth. Its presence in some teeth (for instance in M^1 – M^2) or absence in others (e.g. P^4 or M^3) shows the differences among or within different lines of evolution. The pseudograben always permits us to see, at least at some point in its stage of wear, the union of the sinus with some syncline, or the sinusid with some synclinid. At some posterior stage of wear, the sinus or the sinusid will be separated from the syncline or synclinid. The sinus could be joined in a pseudograben in the upper teeth with the following syncline: in *Toeniodus* – although only shallowly – with I or II syncline; in *Protechimys*, *Archaeomys*, *Monarchaeomys*, *Rhombarchaeomys*, *Issiodoromys*, *Nesokerodon* and *Oensingenomys* with the II syncline. The sinusid is joined in the lower teeth with the following synclinids: *Toeniodus* with IV synclinid (see explanation p. 1070–71). *Theridomys*, *Trechomys* and *Blainvillimys* also with the IV synclinid but only shallow in depth. *Protechimys*, *Issiodoromys*, *Nesokerodon* and *Oensingenomys* with the III synclinid. The pseudograben stage in the lower teeth of *Archaeomys*, *Monarchaeomys* and *Rhombarchaeomys* is as yet unknown (Fig. 1).

Graben is a posterior evolutionary stage. The union between sinus or sinusid respectively with a syncline or synclinid is fully developed. The pseudograben is now transformed into a graben, and the separation of the sinus or sinusid with the syncline or synclinid does not occur any more in any stage of wear (Fig. 1).

Semigraben is sinus-like or sinusid-like, but very much longer. It appears when the labial aperture of the graben in the upper teeth, or the lingual in the lowers, is closed by abrasion. The extrasinus or extrasinusid distance (see below, p. 1005) is generally very small. The presence of graben and pseudograben and sinus or sinusid and semigraben is shown in some species, with a distinct boundary or grade of evolution in the same population. In such rare cases it will be designated in an arbitrary way as “semigraben” or “sinus” and “sinusid”, depending of the predominant evolutionary stage in the population (see below, p. 1005 and Fig. 1).

Tubular syncline or synclinid is a relatively “primitive” stage of evolution in Theridomyidae (see MAYO 1980, p. 1014, Fig. 2 and 1983, p. 898, Fig. 54). In unworn teeth it is generally very broad. In the worn stage it is a more or less broad island of enamel on the occlusal surfaces. It is typical for Theridomyinae, Issiodoromyinae and some synclines of Archaeomyinae.