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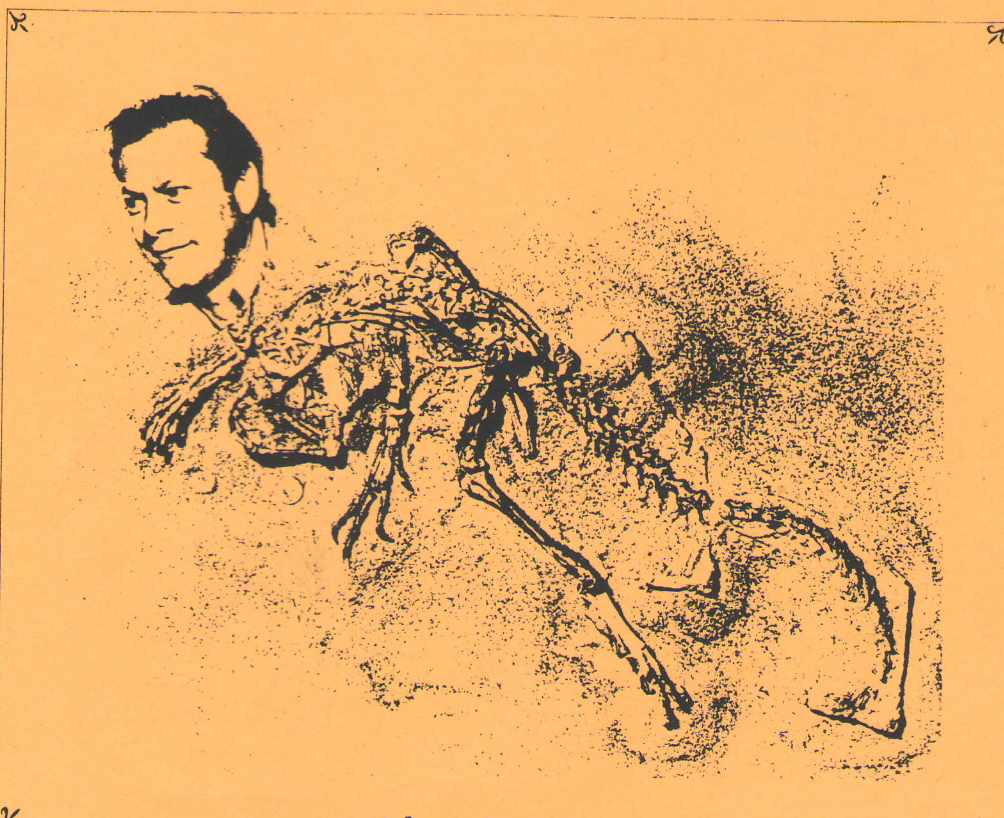

Fossil Fuzz

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A Dire Consequence

With a neck length amounting up to 65 percent of the body length in some individuals (Wild, 1987), the prolacertiform genus *Tanystropheus* has been the cause of many debates in paleontological circles, as to the function and causes of such a neck. This paper aims to summarize the current information on this genus as well as to present the major hypotheses about this unprecedented neck growth.

Tanystropheus is known from partial and complete skeletons in the Upper Anisian Grenzbitumenzone amd the Ladinian of Switzerland and northern Italy, from the Upper Anisian and Ladinian of Germany, Spain, Romania and Israel, and from the Upper Norian or Rhaetian of northern Italy. The best source of *Tanystropheus* material is the 230-million-year-old Middle Triassic sediments from Monte San Giorgio in the Swiss Alps, which was a small, nearly land-locked basin with access to the Tethys Sea (Taylor, 1989).

*Tanystropheus*belongs to the suborder Tanysitrachelia of the order Prolacertiformes (Protorosaurs), together with *Macrocnemus*, *Prolacerta* and *Protorosaurus*, the earliest archosauromorph to appear in the fossil record (Carroll, 1988; Wild, 1973; Wild, 1980). A number of synapomorphies, including an incomplete lower temporal bar, elongated cervical vertebrae, low neural spines on the cervical vertebrae, and a short ischium attest to their monophyly (Benton, 1985; Tschanz, 1988). Apparently, they represent a separate branch of the Permotriassic radiation of the Lacertilia, differing from Eolacertilia mainly by the elongation of the neck and by the increased size (Wild, 1980).

Tanystropheus were marine reptiles, living in the shallow basins of the Tethys Sea. The stomach contents, with hooklets from cephalopods' arms, reveal that the adults were predators, catching fish and cephalopods with their conical, recurved teeth. Peculiarly, the juveniles have tricuspid teeth, and there is a variety of guesses, ranging from aerial insects to seaweed, as to what their diet could have been (Taylor, 1989; Cox, 1975).

The *Tanystropheus* specimens range in size from the 50cm-long juveniles to the 6m-long adults of *Tanystropheus longobardicus*. They were able to walk on land, but the webbbed and enlarged hind limbs were mainly used for propulsion in the water, though the animals were poorly streamlined and were likely not very efficient swimmers. The tail might have provided extra power for swimming, but cannot have been essential, since specimens with tails shed by autotomy have been found. This was very likely an adaptation to distract predators, as seen in the modern lizards to which *Tanystropheus* is related (Taylor, 1989).

The most distinctive characteristic of the genus is the extremely elongated neck. Even though a relatively long neck is a characteristic of the prolacertiforms, in *Tanystropheus* this has been taken to the extreme, the neck getting longer and longer with each additional species. In the most advanced species, *T. longobardicus*, the neck makes up more than 60 percent of body length (Tschanz, 1988). This increase in the absolute neck length took place by a lengthening of each individual neck vertebrae compared with a given mid-dorsal vertebra and by an increase in the number of neck vertebrae, from 8 in *Prolacerta*, to 9 in *Macrocnemus*, and finally to 12 in *T. longobardicus*, this change taking place in 5-6 million years. The missing dorsal vertebrae and the relatively low position of the shoulder girdle indicate that dorsal vertebrae were included into the neck (Wild, 1987). The neck vertebrae have thin, elongated ribs which ran below and to each side of the vertebral column, each overlapping several other vertebrae (Taylor, 1989; Tschanz, 1988). The neck vertebrae have foramen or foramina all the way to the head, possible indicating an adaptation for blood circulation to the head, which would be problematic with such a long neck.

Most of the controversy surrounding *Tanystropheus* involves the adaptive significance, if any of the long neck. Wild (1974), argues that the anterior neck vertebrae with the skull and the posterior neck vertebrae could move in the lateral and dorsoventral direction, and the middle-neck vertebrae could be bent in the dorso-ventral direction, with the relatively elastic neck ribs stabilizing an S-shaped neck that was adapted to catching rapidly moving prey. He proposes that the adults probably caught cuttle-fishes and fishes from the shore, darting them in heron fashion, while the terrestrial juveniles fed on flying insects, which would also explain their tricuspid teeth, and their absence in completely marine sediments. According to Wild (1987), this adaptation towards rapid acquisiton of high energy food would have provided the selection pressure towards an increase in neck length.

Tschanz (1988), however, indicates that not only the stiff, bundled ribs of the neck vertebrae make the neck too stiff for any bending, but also that they reduce the insertional areas of cervical musculature significantly. He argues that such a neck would be impossible to even hold up, let aside to be employed for catching fast-moving prey in heron fashion. He also indicates that any *Tanystropheus* with a shed tail would be unable to balance itself on the ground due to the extreme length of its neck. Such a neck not only would make an almost fully (except egg-laying) obligate aquatic mode of life necessary (the buoyancy of water supporting most of the weight of the neck), but it would also be advantageous in water, with the stiffness of the cervical ribs helping *Tanystropheus* to swim without interference from bending of the neck and the resulting yawing (Taylor, 1989; Tschanz, 1988). This would also solve the problems with head circulation indicated by Wild. Tschanz' conclusion is corroborated by a comparison of the skeleton of *Macrocnemus* with that of *Tanystropheus*,indicating that many terrestrial adaptations in the former genus are absent in *Tanystropheus* (Rieppel, 1989).

Tschanz' hypothesis is that, the neck *per se* had no adaptive value, but was a consequence of a strong, constant, positive allometry with the body size, the neck length being linearly related to the body size with a slope greater than one. He points out that the positive allometry was decelerated compared to the closely-related *Macrocnemus*. He sees this decreased morphological development in the ontogony of a hypothetical ancestor as a proof of neoteny in *Tanystropheus*. This indicates that the elongated neck of *Tanystropheus* had reached an adaptive limit, the neck length of *T. longobardicus* probably representing the longest viable neck length. Thus, the neck length was probably an indirect consequence of selection for large size, maybe for defence or sexual competition (Taylor, 1989), making it necessary for *Tanystropheus* to become aquatic, rather than the long neck being adaptive for predation, as argued by Wild. Evidence for high juvenile mortality (Wild, 1987), may mean that the long neck was in fact a hinderance for foraging, with only the low-metabolism adults surviving through long periods without food, or specializing on large, slow prey which the juveniles could not utilize. The uncontrolable positive allometry, coupled with a relatively small population size (Wild, 1987), very likely spelled the end of*Tanystropheus*.

Tanystropheus is a very good example of what the indirect consequences of selection can cause through allometry. Just like *Megaceros*, whose end was speeded up by its giant horns that were also allometrically related to its body size, *Tanystropheus* succumbed to the unexpected results of hyperpomorphy, or growth to a new size range (Tschanz, 1988). This is a good lesson for not seeking evolutionarily adaptive explanations for every phenotype before employing a thorough morphological analysis.

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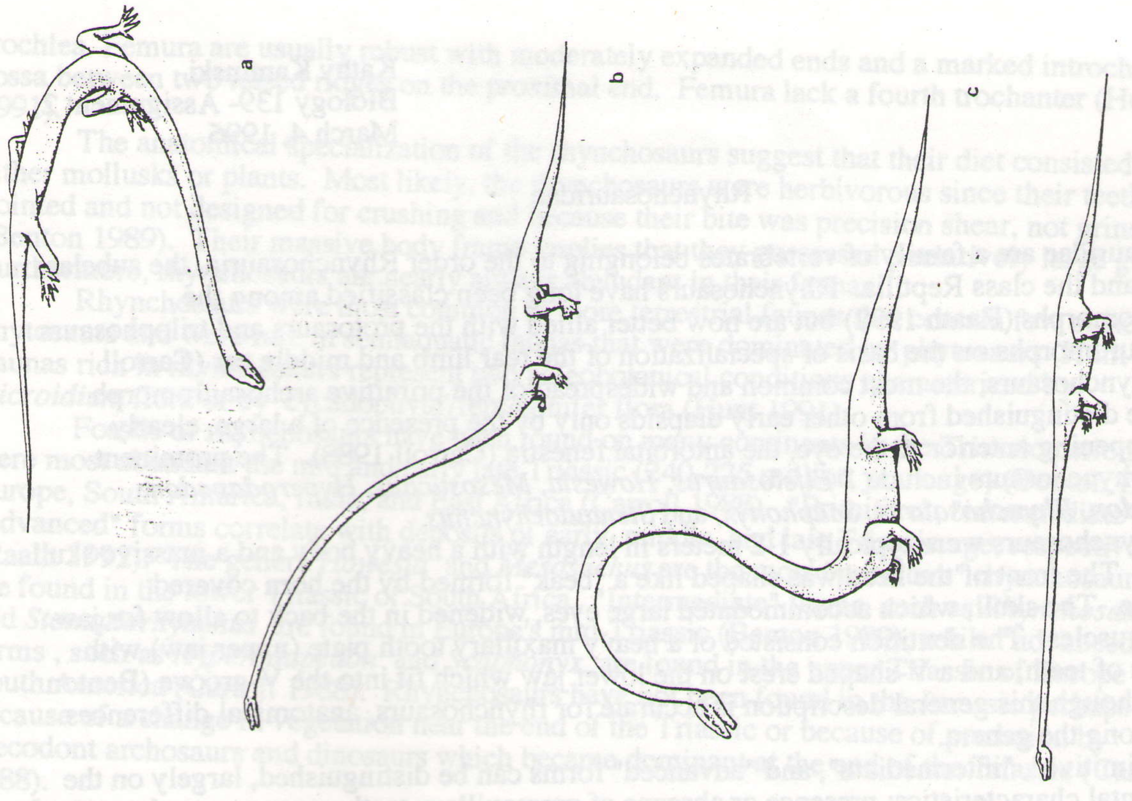

TEXT-FIG. 1. Different reconstructions of *Tanystropheus longobardicus*. *a*, as a mainly terrestrial reptile (redrawn after Peyer 1931). *b*, as a terrestrial reptile, with its neck in a 'normal', elevated position (redrawn after Wild 1973). *c*, with the neck in a swan-like position, if the head is positioned more forward the animal is supposed to tilt (redrawn after Kummer 1975). *d*, with the neck in horizontal position. This represents the most advantageous position for terrestrial and aquatic life (Tschanz 1985, 1986).

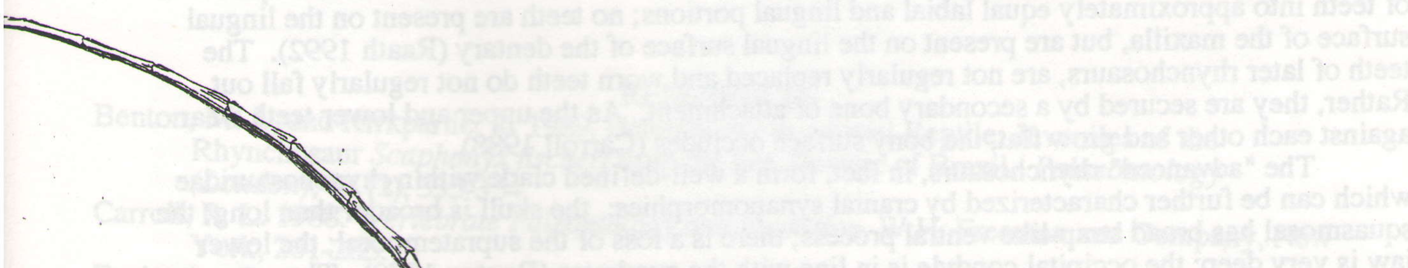

FIG. 1. — *Tanystropheus longobardicus* (BASSANI), reconstruction of the skeleton (after Wild, 1974).
FIG. 1. — Tanystropheus longobardicus (BASSANI), *reconstruction du squelette (d'après Wild, 1974).*