



CLAUDE MARCEL HLADIK, BRUNO SIMMEN, PATRICK PASQUET

PRIMATOLOGICAL AND ANTHROPOLOGICAL ASPECTS OF TASTE PERCEPTION AND THE EVOLUTIONARY INTERPRETATION OF "BASIC TASTES"

ABSTRACT: Taste perception has been studied in non-human primate species and in human populations, in terms of thresholds and supra-threshold responses. Taste thresholds of primate species, including lemurs, monkeys and apes vary in relation to dietary adaptations to beneficent and/or noxious compounds in various environments. Folivorous species such as Propithecus spp. and Gorilla gorilla not only tolerate high concentrations of tannins (corresponding to low taste thresholds), but may also prefer a range of concentrations which are deterrent to other primates. Frugivorous species such as Macaca spp. and Cebus spp. have the highest sensitivity to sugars; however there is a variation of a global trend towards low threshold as the species' body weight increases, according to specialization of feeding strategies. Electrophysiological records in both peripheral and central nervous system (data from Hellekant et al. and Scott et al.) show that primate sensory taste system is basically organized around two major clusters of fibers and their cortical projections. Co-variation between the neural responses to various compounds was observed for sugars, on the one hand, and for tannins and alkaloids on the other hand. Some responses, especially to various salts and acids vary between species, without well-defined relationships to the major clusters. Using co-variation of taste thresholds for the same type of compounds as an analogy in humans (n=412), we found a similar dichotomy of taste responses. In conclusion the human taste perception system is not basically different from that of the other primates, with a dichotomy allowing discrimination of noxious vs beneficent substances as a result of evolutionary interactions, and there is no evidence of a trend towards separate basic tastes.

KEY WORDS: Taste perception – Coevolution – Primate – Angiosperms – PROP status

INTRODUCTION

The anthropology of sensory perception is essential for understanding interactions between man and the environment in an evolutionary perspective (Pasquet, Pagezy 2000). The sensory systems gather information from the environment, in close relation to our emotions and behaviours, especially those which were determinant for survival and reproduction of our ancestors. Conversely, studying sensory perception in the light of evolution is

paramount to highlight the current status of biological and cultural variations of human perception (Holley 1999).

In the perspective of nutritional anthropology, the study of the evolutionary aspects of taste perception is of major importance, although food perception also involves most other senses (Hladik, Simmen 1996, Rolls 1997).

In this paper we present new hypotheses on the shaping of taste perception from a comparative analysis of electrophysiological and psychophysical data in phylogenetically distant non-human primates and man.

From this analysis, the very existence of the so-called "four basic tastes" (sweet, bitter, salty, sour) plus eventually the fifth taste of umami (sodium glutamate) will be questioned as pioneered by authors such as Schiffman and Erickson (1971) or Faurion (1988). Indeed the notion of "four basic tastes" is essentially based on the vocabulary of western languages to describe taste qualities, and one may wonder to what extent this notion fits with our knowledge of sensory physiology in non-human primate taste responses as a result of coevolutionary processes.

MATERIALS AND METHODS

Psychophysical data in humans

Our data concern a sample of 412 individuals of both sexes (131 men, 281 women, aged 18 to 59 years [mean: 36.0, SD: 10.7]) tested during different cross-cultural studies (Gerber, Padilla 1998, Malet *et al.* 1999, Simmen *et al.* 1999, Pasquet *et al.* 2002, Iaconelli 2000) in the European Union, Russia, Tunisia, and Cameroon. The initial purpose of these studies was to investigate variation of taste sensitivity in different populations/environments previously observed by one of us. To minimize the possible effect of aging on taste all subjects over 60 years old have been excluded from our working sample.

After informing the subject on taste categories he or she could be presented with (water, salty, sour, sweet, bitter and astringent), thresholds were determined by presenting, in a semi-randomized order (blind test), various solutions of purified products, starting with the weakest solution in order of increasing concentration (0.3 log steps), until recognition. Solutions were presented in a 2 ml plastic teaspoon and were expectorated by the subject after tasting. Once the subject commented on the taste he rinsed his mouth and one minute elapsed before the next assay. After the subject first recognized the taste of a solution, concentrations above and below preliminary estimated threshold level were presented, again until unambiguous recognition.

Solutions of sucrose (1.5–1600 mM), fructose (2–1000 mM), sodium chloride (4–1000 mM), quinine hydrochloride (0.8–400 mM), citric acid (0.2–25 mM), tannic acid (4–4000 mM) and oak tannin (0.03–8 g/l; OEnofrance; undetermined molecular weight) were presented. Sensitivity to 6-n-propylthiouracyl (PROP) was also investigated after testing the previous substances, using a simplified method with two solutions to determine the taster/non-taster status of a subject. Tasters recognize a bitter taste at 0.1 mM and non-tasters at or above 0.2 mM (Bartoshuk 1979); however, a full range of 13 PROP solutions (0.001–3.8 mM) was used in the Tunisian sample (N=118) to cross-validate, in our data, the two-solution method. Since "water" was among the possible tastes to be named, local drinking water was used to prepare the solutions and for rinsing the mouth between tests. However, the mineral content of drinking water was checked to be

sure it is far below recognition threshold for sodium chloride.

Utilisation of data in non-human primates

In a recent comparative analysis (Hladik *et al.* 2003), we selected, among data obtained in published studies, those concerning compounds used for both non-human primates and in our human studies. Data on non-human primates, were obtained during various electrophysiological experiments by Hellekant and Ninomiya (1994), Hellekant *et al.* (1997a, 1997b, 1998) and by Danilova *et al.* (1998), on anaesthetised marmoset (*Callithrix jacchus*), rhesus monkey (*Macaca mulatta*) and chimpanzee (*Pan troglodytes*). They concern the number of impulses per second recorded from single nerve taste fibres while the animal's tongue was stimulated with solutions at above threshold concentration.

Statistical analysis

To show, for each species, similarities/dissimilarities of responses between the compounds used as stimuli, each set of data was submitted to additive trees clustering (Sappath, Tersky 1977) from Pearson correlation matrix between responses, using SYSTAT (version 9.0) statistical software (SPSS Inc., Chicago). The radial representation (Pasquet, Hladik 2002) of the trees (not provided by SYSTAT) was drawn using the T-Rex Program (freely available at www.fas.umontreal.ca/BIOL/Casgrain/en/labot-trex/index.html).

RESULTS

Additive trees are presented in *Figures 1* and *2*. Stress indices of each tree are low (< 5%), thus indicating good representation of the data concerning 412 human subjects (*Figure 1*), and, for each species of non-human primates (*Figure 2*) about 50 isolated taste fibres. Results obtained from studies of humans and in non-human primates appear remarkably similar with regard to the relationships between taste perception of different compounds, although the methods used for recording taste responses in the different studies were very specific.

The human data (*Figure 1*) show that if an individual has a high sensitivity to sucrose he/she will also show a high sensitivity to fructose. Although co-variation is a clear indication that most receptors involved in sucrose perception are also involved in tasting fructose, the moderate correlation level obtained suggests that various sugars may not elicit exactly the same taste signal. More striking is the correlation between perceptions concerning quinine and the two tannins (tannic acid and oak tannin), shown by relatively short distances in the additive tree. The bitter taste of several alkaloids obviously differs from the astringency of most tannins (whose peculiar taste

(Simmen *et al.* 1999) is not a mere tactile perception due to precipitation of salivary protein). Again, the co-variations found in this alkaloid/tannin cluster might reflect the responses of partially overlapping sets of taste receptors. The weak covariation in individuals' sensitivities to bitter compounds was presented by Delwiche *et al.* (2001) as an evidence supporting multiple receptor/transduction mechanisms with a partly different set of receptors reacting to various "bitter tasting" substances. Furthermore, our data show that sensitivity to sucrose or fructose varies independently of sensitivity to quinine and tannins. Hence, no significant set of taste receptors responds to both sugars and alkaloid/tannin.

The non-human primate taste fibre data (Figure 2) allows a further step in understanding the functioning of the peripheral taste system. In the three species, individual taste fibres highly responsive to sucrose are also responsive to fructose. As for human taste thresholds, distances between these carbohydrates are short in the additive trees. However, correlations vary to some extent among primate species. For instance, in the rhesus monkey, *Macaca mulatta* (Figure 2 B), fructose and sucrose may be partly discriminated at a peripheral level (Hellekant *et al.* 1997b).

In the three non-human primates investigated, there is also a clear relationship between responses to quinine and tannic acid (when tested), and other compounds that taste bitter or astringent to humans, such as caffeine and aristolochic acid. One single taste fibre can be involved in the signaling of these various compounds (and, in some

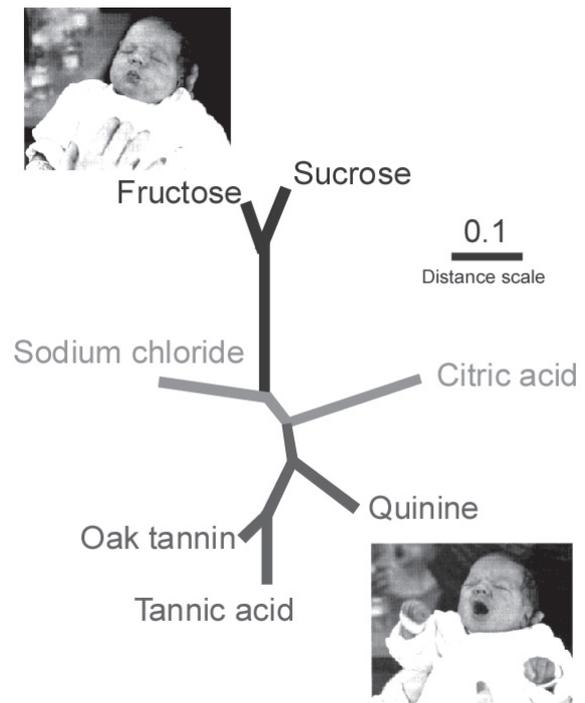
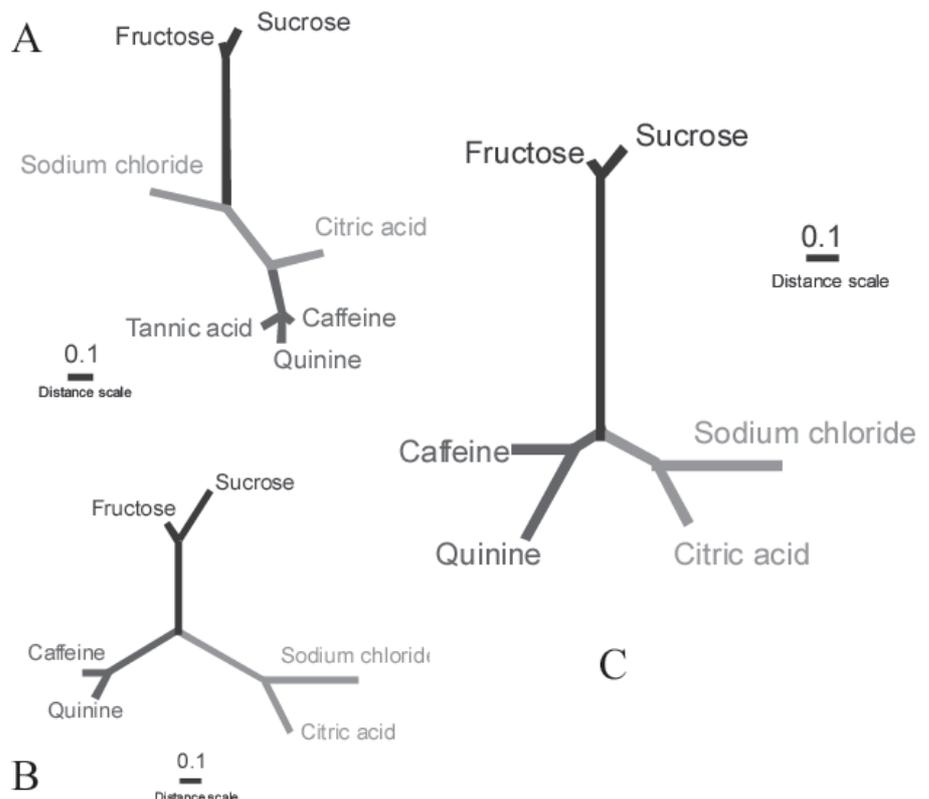


FIGURE 1. Additive tree showing the degree of similarity of taste thresholds for various purified compounds in a sample of 412 human adults (data from Hladik *et al.* 2003). The dichotomy between beneficial substances (sugars) opposed to potentially noxious substances (alkaloids and tannins) also corresponds to the gusto-facial reflexes of the human baby, as shown by the views recorded in video sequences by Matty Chiva.

FIGURE 2. Additive trees showing the degree of similarity of the response profile of isolated fibers of the taste nerve of non-human primates (data from Hellekant and Danilova, in Hladik *et al.* 2003), respectively for the marmoset, *Callithrix jacchus* (A), the rhesus monkey, *Macaca mulatta* (B), and the chimpanzee, *Pan troglodytes* (C).



instances, of citric acid; Hellekant, Ninomiya 1994, Hellekant *et al.* 1997 a,b, Danilova *et al.* 1998). Furthermore, a high response to soluble sugars in an individual taste fiber involves a low response (or no reaction) to quinine, tannins, or to various other compounds including salts and acids. These data point out a clear dichotomy, in non-human primates, between compounds likely to be toxic (perceived as bitter or astringent in humans) and compounds likely to be beneficial (perceived as sweet in humans).

DISCUSSION

The results show a great similarity in taste responses, suggesting that taste perception in human does not fundamentally differ in the Primate Order. Consideration of the evolutionary history may explain most of the present taste adaptations to beneficent *vs* potentially noxious compounds in the environmental context of our ancestors (Hladik *et al.* 2002a).

Coevolution of primates and angiosperms

Angiosperms (the plants with flowers that can bear fleshy fruits) coevolved with primates and other vertebrates mostly during the 65 millions year of Cenozoic. As shown by Van der Pijl (1969), among other authors, there is evidence that animals, by dispersing seeds in their feces, contribute to selecting plants with the most nutritious fruits, allowing simultaneously for an increased fitness of the fruit eaters.

Primate sensory perception partly results of this coevolutionary processes. In this respect, Regan *et al.* (2001) suggested that color vision was shaped in relation to the color of ripening fruits.

As far as taste perception is concerned, the ability to discriminate sugars can be considered as a consequence of selective pressure towards efficient acquisition of high-energy foods. In the extent primate species, for instance, the largest the body mass, the highest the sensitivity towards soluble sugars (Simmen, Hladik 1998). This global adaptive trend allows the large primates to include a wide range of fruit species with various concentration in sugar (but all tasted, thanks to a high sensitivity), thus, in the total, a large amount of energy necessary to meet energy requirement.

The taste of soluble sugars is attractive for all primate species, with an initial gusto-facial reflex observed in newborns of all species including humans (Steiner *et al.* 2001). The dichotomy that we illustrated in this paper (*Figure 1*), between perception of sugars opposed to that of potentially noxious compounds (such as alkaloids and tannins), also appears as a basic organization of taste perception, although the Primate Order evolved in separate branches on the continental plates that were drifting apart during the Cenozoic. The angiosperms providing fruits with sugar also developed in parallel in the separated continental plates.

Some aspects of coevolution of plant composition in relation to primate tasting ability are relevant to this parallel evolution of primates and angiosperms. The "false sugars" occurring in the fruit pulp of some African plant species correspond to biochemical mimicry (Hladik 1993), favoring seed dispersal of some plants without sugar in the fruit. The perception of such substances is restricted to the Old World primates, where the plants evolved. For all American primates (and for most lemurs of Madagascar, that also evolved separately), the solutions of "false sugars" are tasteless and not discriminated from plain water, whereas they appear as extremely sweet for humans and all primates originated from Africa. Accordingly, in spite of the differences in the tasting system among the various primate sub-orders evolved on different continental plates, sugars of the fruits of angiosperms were a major factor for shaping primate taste perception.

Taste perception of tannins, alkaloids and other secondary compounds

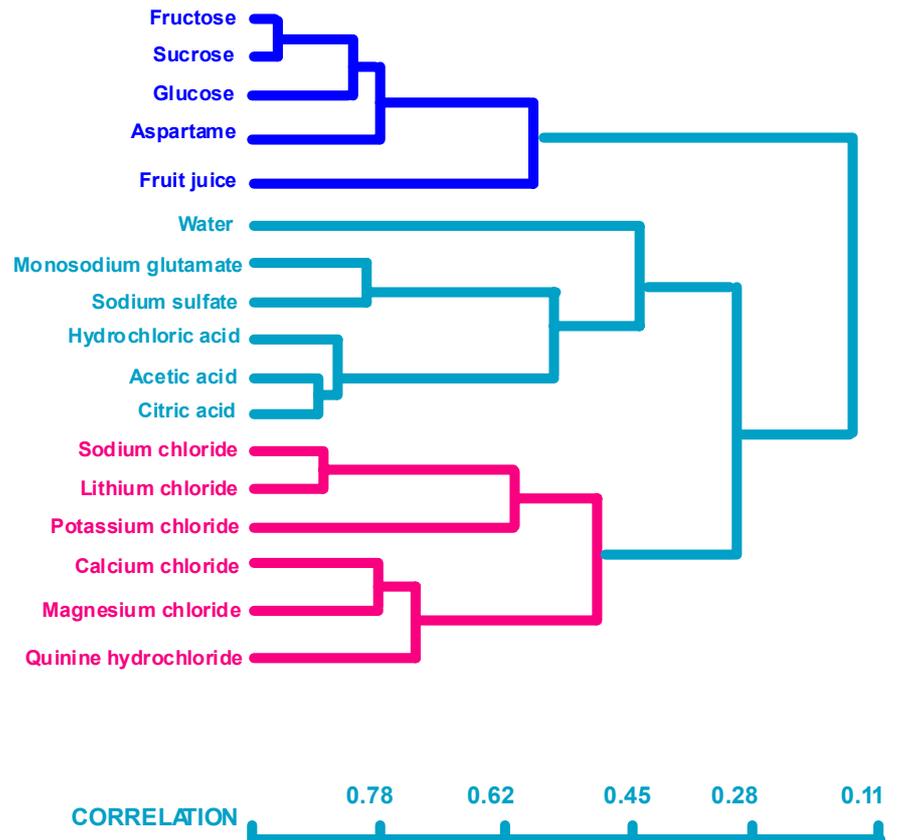
Besides sugars and other nutrients, foods plant also evolved toxic compounds such as alkaloids and tannins, that prevent overgrazing. The origin of some of these compounds might be as early as the first plants and animals left their aquatic environment for the terrestrial world. The selective pressure of invertebrates was certainly most important, owing to their long-lasting history and potentially devastating insect populations (Janzen 1978). Hence plants mutant with toxic substances (secondary compounds, not directly interfering with plant metabolism), being avoided by consumers, have a selective advantage, allowing large populations to colonize most environments.

Although in rainforests, where biodiversity is high, non toxic plants may persist (Simmen *et al.* 1999), primates and other vertebrates had to adapt to the potential toxicity of plants occurring in various environments. The covariation of taste perception of potentially toxic (quinine) and antinutrient (tannins) that is shown by the analysis of the data presented in this paper is an evidence of this adaptation.

As was shown by Scott and Mark (1987), the taste system encodes stimulus toxicity. The long distance between these perceptions and those of sugars in the additive trees (*Figures 1, 2*) emphasizes the dichotomy between primate taste perceptions, with a bipolarity resulting from two different kinds of evolutionary pressures. In behavioral terms, this dichotomy allows a functional adaptation with a gusto-facial reflex of avoidance of bitter and astringent compounds mirroring the gusto-facial reflex that accompanies the sweet taste (Steiner *et al.* 2001).

However, primate food choices result of a trade-off between positive reactions to beneficent compounds, and the occurrence of secondary compounds in most natural food items. Taste thresholds for quinine are extremely low (highest taste acuity) among primate species living in the

FIGURE 3. Degree of similarity in the response profiles of the neurons of the primary taste cortex of *Macaca fascicularis* (data from Scott and Plata-Salamán 1999).



least diversified environments, where toxic alkaloids are present in most plants (Simmen *et al.* 1999). Among the most common plant secondary compounds, tannins are extremely frequent, even in the most diversified rainforests. In maturing fruits, tannins concentration progressively decrease, together with an increase of sugar content. The taste of tannins is generally repulsive (who never experienced an unripe persimmon?), but for some primates, a high concentration can be tolerated. This is the case of the sifaka (*Propithecus verreauxi*) in Madagascar, who can tolerate food plants with a high tannin content. For chimpanzees, the juice of plant parts containing up to 5 g of tannin can be eaten. The most amazing result was obtained when testing gorillas, who not only tolerate 10 g per liter of tannins, but also appreciate and preferentially eat such solutions (Simmen, Charlot 2003).

The Evolutionary status of perception of salts, acids and other substances

Several other taste signals can be observed in the primate taste repertory, that are not necessary eliciting clear-cut reactions of preference or aversion. In the pioneer approach of Schiffman and Erickson (1971), the subtle variations between the tastes of various salts (as perceived by human subjects) were presented as an evidence that the "basic tastes" are not necessary to explain taste responses.

The results obtained by Scott and Plata-Salamán (1999) when recording directly the activity of the neurons of the primary taste area of the brain of a Macaque provide a

unique example of the detailed reaction inside the brain of a primate, when solutions are applied on its tongue. These results (Figure 3), not only show a dichotomy in the hierarchical cluster corresponding to those presented and discussed in the present paper (sugars opposed to a group of bitter tasting substances), but also allow to locate the signals elicited by several acids and salts at an intermediate position.

Indeed, the compounds used in such studies, generally not included in these purified forms in the diet of primates, can be considered as chemical probes allowing to understand the fundamentals of taste perception. The converging results of the various approaches, showing correlations between different signals involve that any taste signal (even that of pure fructose) is a "complex signature" made of several individual receptors and taste fibers firing simultaneously (Hladik *et al.* 2002b).

Various acids elicit quite distinct signals (Figure 3), and sourness can be perceived differently by various primate species, according to their dietary specialization. For instance, in the rainforest of Sumatra, where most fruits eaten by gibbons (*Hylobates lar*) are extremely acid (with a pH as low as 1.5), orangutans (*Pongo pygmaeus*) and macaques (*Macaca fascicularis*) eat larger proportions of fruit with a pH between 4 and 5, and the langurs (*Presbytis thomasi*) avoid most acidic fruit. For this latter species, a decrease of the pH in the stomach might damage the symbiotic microorganisms that allow fermentation in the forestomach (Ungar 1995).

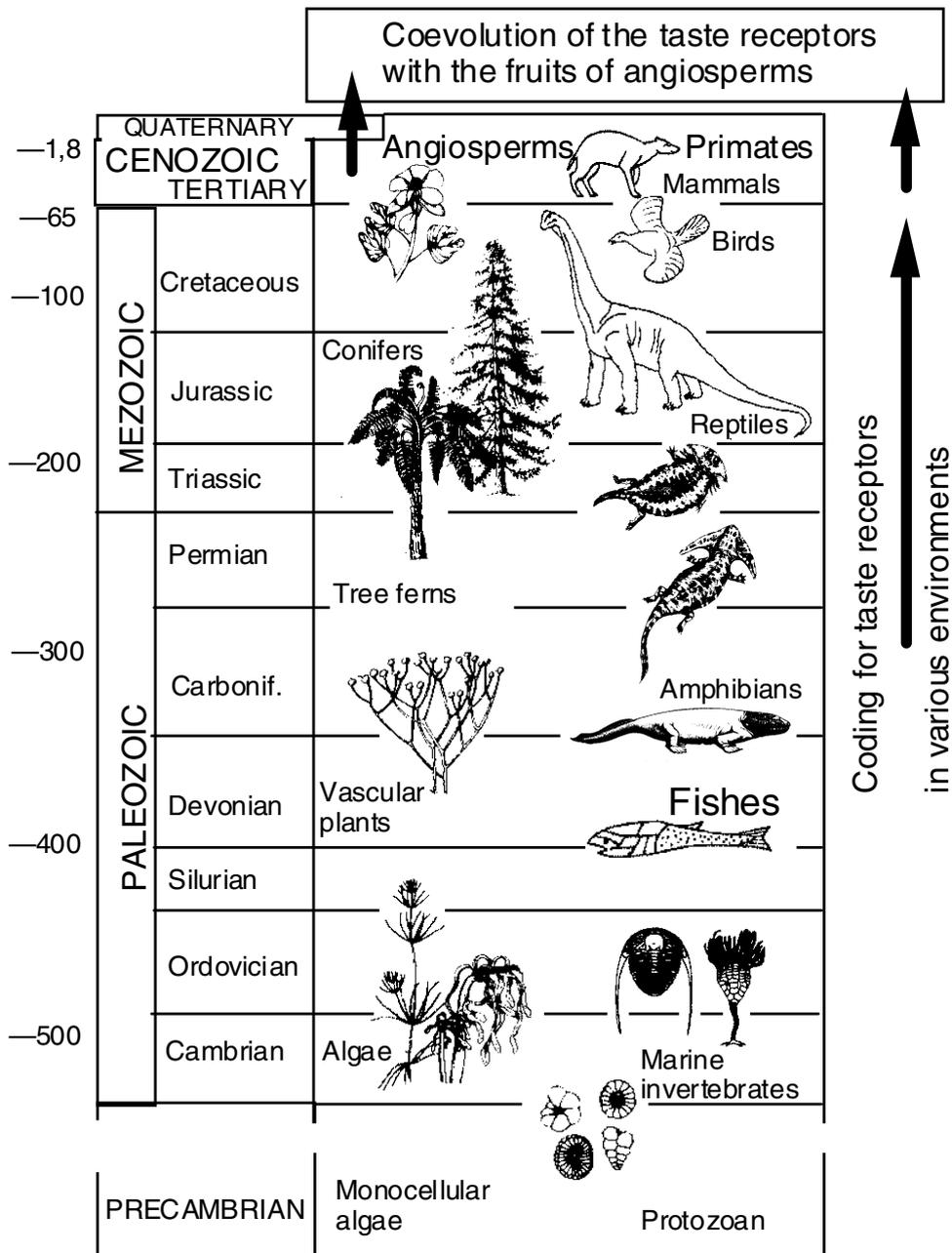


FIGURE 4. The parallel evolution of animals and plants (age in million years). During the Cenozoic, the primate taste responses coevolved with the angiosperms bearing fleshy fruit with increasing amounts of sugars. Prior to this coevolution, the genes coding for taste receptors were probably homologous of those of fishes and reptiles, still occurring in the skin of several extant freshwater fishes and allowing responses to various soluble substances including salts.

Since we also perceive salts (and particularly sodium chloride), we have to face a dilemma about the evolutionary origin of what is generally described as an evident adaptation to a physiological necessity to balance our diet with sodium. The major issue is that almost all wild primate species never experienced the "salty taste", because salt concentration in all food samples subjected to analyses revealed a salt concentration below taste threshold (Hladik, Simmen 1996). Accordingly, during the 65 millions years

of primate radiation, including the last millions of year when the *Australopithecus* and *Homo* genera were present in tropical environments, it is most likely that no experience of a "salty taste" could have allowed a coevolutionary process resulting in the present possibility of all primate species to recognize a salty solution.

To explain such perceptions of salts in their diversity, we have to return to the evolutionary history of primates and other vertebrates (Hladik *et al.* 2002a). The genes

coding for salt taste receptors were certainly present in early fish species, allowing to react to water salinity (Figure 4). Taste receptors do exist in the skin of various extant freshwater fishes, as a kind of external "tongue" allowing to react to the composition of water; and salt sensitivity of a fish such as the minnow (*Phoxinus Phoxinus*) is 180 times better than human sensitivity (Penzlin 1977). As for other genes coding for physiology and morphology (such as the leg with five digits, transmitted to amphibians, reptiles and mammals), genes coding for taste receptors probably derived from those of fishes. In the mucosa of the mouth of amphibians, reptiles and early mammals, these chemoreceptors had to be adapted to the various compounds of the environment, especially to avoid the noxious compounds such as tannins that were present in the plants as soon as they colonized the lands. It now appears that such primitive taste receptors had to combine their responses to cope with the changes in the composition of plant species, hence the complexity of the present taste signals. When primates coevolved with angiosperms, selection of sets of chemoreceptors adapted to sugars and alkaloids using this primitive gustatory system.

Such chemoreceptors, initially responding to salts, still have the capacity to respond to sodium chloride. Although wild primates have no experience of salty foods (or quite exceptionally), they have kept their ability to respond to salt. And this was certainly a marvelous discovery for one of the first *Homo* spp. who tried to add to his food (especially to cooked food) this white deposit found along a sea shore. It was probably the first additive used to improve food taste. Afterwards, in human civilizations, the salty taste was becoming so important and so obvious as a "basic" taste that it might be difficult for physiologists not to stick to the obsolete theory of the four "basic tastes", rather than to a mere dichotomy based on the evolutionary background.

Considering again the genus *Homo* (Figure 5), to highlight what has been inherited from our ancestors, we included in the additive tree, the result obtained with Propylthiouracil (PROP), a peculiar chemical not found in natural habitats, which particularly interested taste physiologists. Indeed, the genetic coding of the response (involving a single gene) allows to discriminate between "tasters" and "non-tasters" (the PROP status), in humans and in some other primates (Reed *et al.* 1995). Variations in PROP sensitivity are linked to sensitivities to some other compounds, and thus, indirectly linked to food preferences (Pasquet *et al.* 2002).

But sensitivity to PROP is largely independent from sensitivities to quinine and tannins. This suggests that the gene coding for PROP sensitivity was not directly involved in primate evolution, as for salts. Such perceived tastes can be considered as responses from our peripheral taste receptors according to a long lasting evolutionary history, the whole set of receptors allowing adaptation to a variety of plant products.

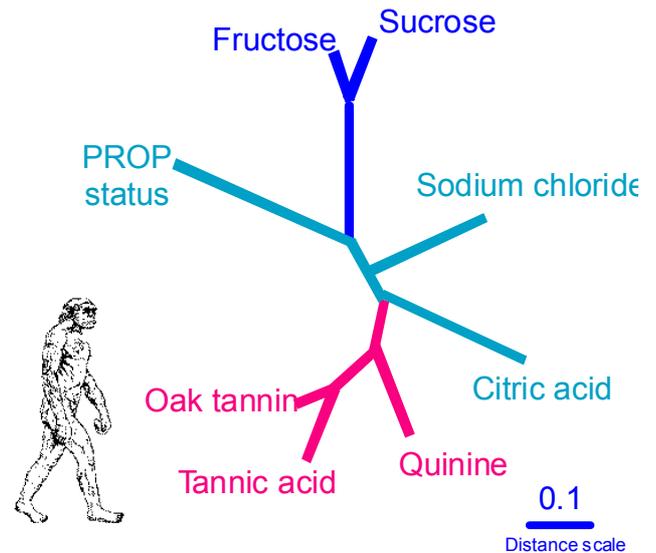


FIGURE 5. The present aspect of taste responses in the genus *Homo*: additive tree (stress<0.001) showing the relationships between taste recognition thresholds for 412 human subjects, including relationships to PROP status.

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Claude Marcel Hladik
 Bruno Simmen
 Patrick Pasquet
 Eco-Anthropologie et Ethnobiologie
 CNRS and Muséum National d'Histoire
 Naturelle
 4 Avenue du Petit Château
 91800 Brunoy
 France
 E-mail: hladik@ccr.jussieu.fr