

quencies. This procedure is necessary to demonstrate causal propagation in the so-called rotating-wave approximation made by Fermi. But when this approximation is not made and one works with the full electromagnetic field, properly retarded signalling is no more difficult to demonstrate in QED than in classical electrodynamics<sup>6</sup>. This result is hardly surprising, as the Maxwell equations for the Heisenberg-picture field operators have the same formal structure as in classical electrodynamics<sup>7</sup>. One obtains exactly the results of myself and Knight<sup>8,9</sup> and therefore, as a special case, the result of Fermi<sup>10</sup>. Regarding Hegerfeldt's theorem<sup>11</sup> which "shows there is a small probability that atom B will 'notice' the decay of A long before the interval  $R/c$  has elapsed"<sup>11</sup>, it should be noted that the theorem as stated does not even require the presence of a second atom. Its relevance to interatomic signalling seems dubious at best. Fermi's calculation, far from being "in error", exemplifies his inimitable, direct and pragmatic style.

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1. Maddox, J. *Nature* **367**, 509 (1994).
2. Serber, R. *Phys. Rev.* **48**, 49 (1935).
3. Uehling, E. A. *Phys. Rev.* **48**, 55 (1935).
4. Fermi, E. *Rev. mod. Phys.* **4**, 87 (1932).
5. Kikuchi, S. Z. *Phys.* **66**, 558 (1930).
6. Power, E. A. in *Physics and Probability* (eds Grandy, W. T. Jr & Milonni, P. W.) (Cambridge Univ. Press, 1993).
7. Milonni, P. W. *The Quantum Vacuum* (Academic, Boston, 1994).
8. Milonni, P. W. & Knight, P. L. *Phys. Rev. A* **10**, 1096 (1974).
9. Milonni, P. W. & Knight, P. L. *Phys. Rev. A* **11**, 1090 (1975).
10. Milonni, P. W. Los Alamos National Laboratory preprint (1994).
11. Hegerfeldt, G. C. *Phys. Rev. Lett.* **72**, 596 (1994).

## Ape family tree

STR — The recently discovered *Dryopithecus* partial cranium CLL-18000 is reported to have several derived features of the zygomatic bone<sup>1</sup>, including three zygomaxillary facial foramina on its frontal process, which establish this taxon as a primitive member of a *Pongo* clade excluding African apes and humans<sup>1</sup>. But crania of extant hominoid primates are highly variable<sup>2</sup> and polymorphic for zygomaxillary facial foramina numbers (table). In a Liberian chimpanzee cranial sample, the character state of three foramina per side in any combination, unilaterally or bilaterally, occurs in 22.8% of the specimens, approximately one in four.

These findings are reinforced by a survey of Asian hominoids: *Pongo pygmaeus*, *Symphalangus syndactylus*, and *Hylobates* spp. Phenotypes differ in various complex ways but a few patterns are clear. *Pongo* is so highly variable for this epigenetic feature that its numerical range encompasses

### FREQUENCY DISTRIBUTION OF ZYGOMAXILLARY FORAMINA IN EXTANT HOMINOIDEA

Taxon	Numbers of foramina (right side)								
	N	1	2	3	4	5	6	7	8
<i>Pan troglodytes</i>	250	87	138	24	1	0	0	0	0
<i>Pongo pygmaeus</i>	89	9	17	25	19	12	4	1	2
<i>Symphalangus syndactylus</i>	11	2	6	3	0	0	0	0	0
<i>Hylobates muelleri funereus</i>	19	9	6	3	1	0	0	0	0
<i>H. lar entelloides</i>	20	0	9	5	3	2	1	0	0
<i>H. lar carpenteri</i>	17	0	3	8	3	3	0	0	0

All observations comprise specimens collected in the wild, with Liberian *Pan troglodytes* curated at the Frankfurt Anthropological Institute and Asian hominoids curated in the Department of Mammology at the US. National Museum of Natural History (Smithsonian). Numbers of zygomaxillary facial foramina are given for the right side only, corresponding to the preserved region of CLL-18000.

all other extant hominoid genera as well as the CLL-18000 specimen attributed to *Dryopithecus*. However, even with the wide range of variation subdivided into just two character states, *Pongo* exhibits a lower percentage of specimens with three or more foramina than does at least one taxon, *Hylobates lar carpenteri*, in a reportedly plesiomorphous genus<sup>1</sup>. Because all extant hominoid taxa are polymorphic for zygomaxillary facial foramina, the number of foramina in any individual, extant or fossil, is unreliable as an indicator of phylogenetic relationship. Taken alone, the numbers of zygomaxillary facial foramina in CLL-18000 do not provide support for removing *Dryopithecus* from a position ancestral to extant African Hominoidea and humans, because the fact that a specimen has two or three zygomaxillary facial foramina does not necessarily indicate whether it is primitive or derived. Instead, the character state present in ancestral hominoids was probably the same as that encountered in all extant taxa closely related to them: a polymorphism of considerable phenotypic complexity.

Assignment of CLL-18000 to a *Pongo* clade was also based on reported robustness of the specimen's zygomatic bone as well as the location of foramina relative to the orbital margin<sup>1</sup>; subsequent work<sup>3</sup> adds low position of the frontozygomatic suture and low position of the glenoid fossa relative to the external auditory meatus to the characters reportedly shared by CLL-18000 and *Pongo*. When these features are illustrated and described in sufficient detail, and shown to be shared with other *Dryopithecus* specimens, it should be possible to structure further tests of hypotheses concerning the phyletic position of the intriguing Can Llobateres hominoid material.

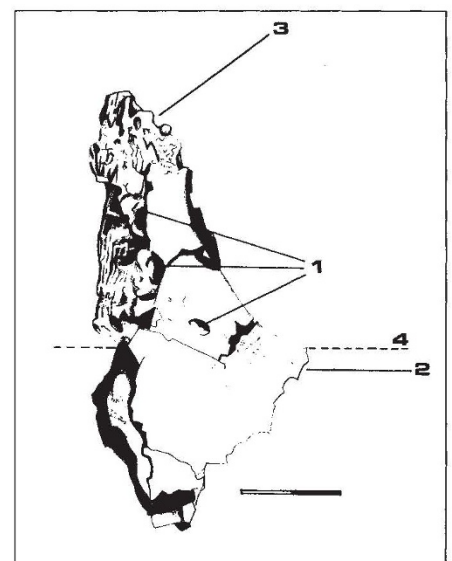
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MOYÀ-SOLÀ AND KÖHLER REPLY — We fully accept the principle that variability renders certain morphological characters inappropriate for assessment of phylogenetic relationships of isolated specimens. Our hypothesis that *Dryopithecus* is a primitive member of the *Pongo* clade would certainly be questionable if based exclusively on numbers of zygomaxillary facial foramina, which do indeed show some variation.

In fact, we referred in our paper<sup>1</sup> to a combination of characters, observed only in *Pongo* among extant hominoids. The zygomatic of *Pongo* is clearly distinguished from those of African apes and hylobatids by a unique association of morphological characters: elevated average number of foramina (typically three); foramina situated above the inferior orbital rim and relatively close to the frontozygomatic suture; zygomatic very broad and robust; and zygomatic flat and anteriorly oriented.

As reported in our paper<sup>1</sup>, the zygomatic of CLL-18000 shows the same com-



Right zygomatic of *D. laietanus* (CLL-18000) from Can Llobateres (Spain). 1, Zygomatic foramina; 2, zygomaxillary suture; 3, frontozygomatic suture; 4, lower limit of the orbit. Scale bar, 1 cm.