Cow's face in Krishna's belly, style in the corolla tube and the Panglossian paradigm

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Historical and archaeological places with smart articulate tourist guides constitute an effective concoction for those of us craving to be intoxicated by the memories of the past glories of our civilizations. I derive additional pleasure in willingly succumbing to this addiction because of the interesting parallels that exist between history and evolutionary biology and the very transparent and illustrative metaphors these places offer to the complicated issues of natural selection. These metaphors also help lay bare the traps the adaptationists are likely to enter while explaining the evolution of biological designs. One such example from the temple at Somanathpur, Karnataka, has all the ingredients of such a trap and stands closely parallel to the problems associated with the studies such as that reported by Belavadi and his group in this issue[1].

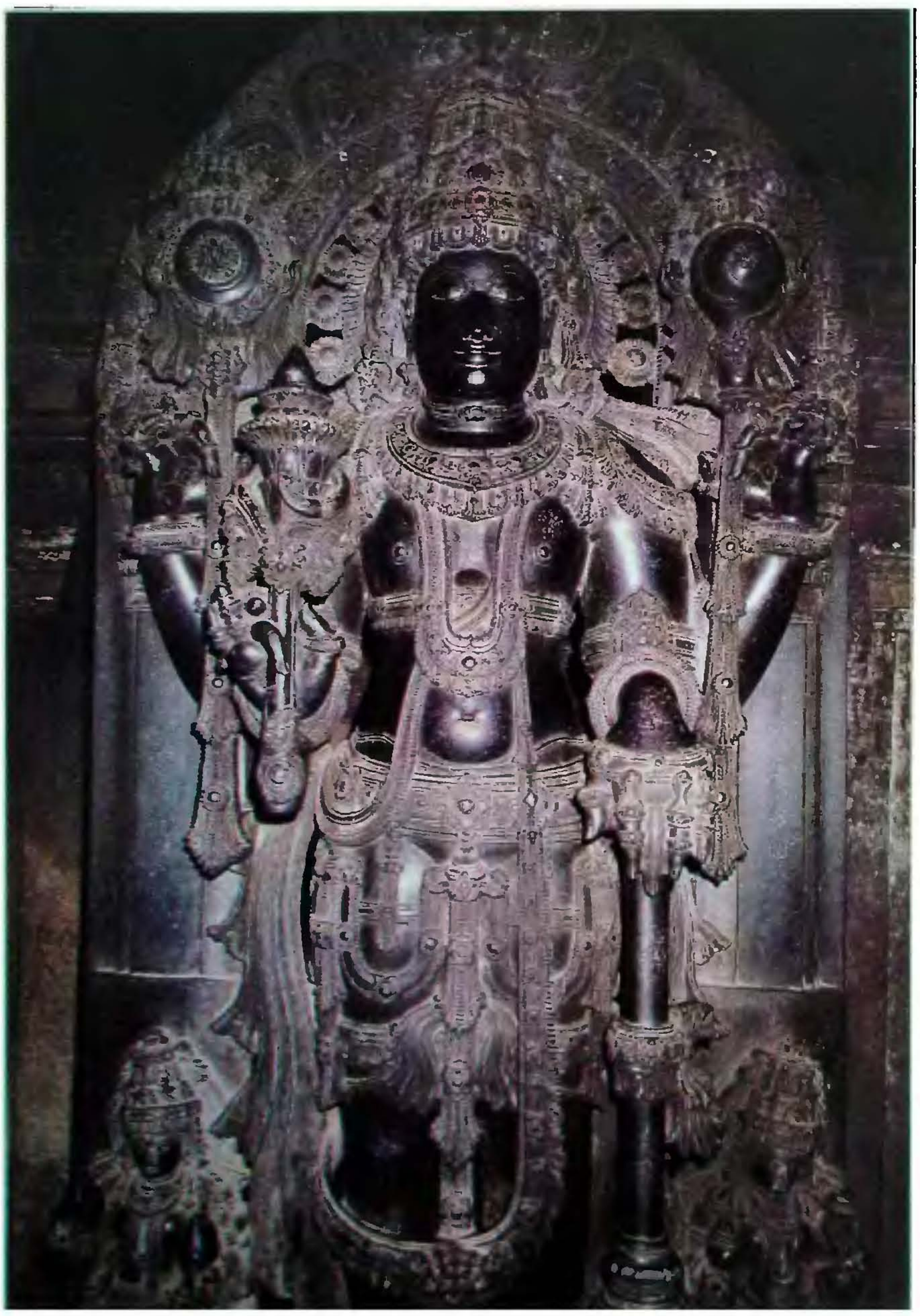

Figure 1 *a*. Statue of Lord Vishnu at Somanathpur temple.

Cow's face in Krishna's belly

In one of the three shrines of Somanathpur temple built by Vishnuvardhana, the Hoysala king during 13th century, there is a famous statue of Lord Vishnu, undoubtedly one of the most beautiful carvings I have ever seen (Figure 1 *a*). Introducing this statue, the tourist guides generally throw a challenge to the visitors to recognize *Gomukha* or the cow's face in the body of the statue. When we give up he covers the statue above the neck and below the waist, and draws our attention to the chest and belly. We then

Figure 1 *b*. *Gomukha* or the cow's face visible on the chest and belly of the statue.

begin to witness a perceptive magic as the cow's face springs out from the chest and the belly (Figure 1 *b*); the nipples in the chest appear like eyes and the naval cavity as the mouth of the cow's face. On a closer examination, a lot more becomes apparent – the ornamented horns, the nose string, etc. We are told that the sculptor 'designed' *Gomukha* because Lord Krishna, one of Vishnu's reincarnation, was a cow boy; thus a purpose is attributed to the design we perceive.

But strangely, on exiting the shrine we begin to perceive a cow's face on almost

every other male statue in the temple – with varying degrees of perfection, though[2]. We then tend to feel that the *Gomukha* in the Vishnu statue may not be a uniquely carved feature but merely represents one of the variants of the permitted proportions of the basic design of chest and belly of the male human body. That the tourist guides assign a meaning to it and a purpose to the sculptor could be purely a postmortem attribution. A strong suspicion starts haunting: could this *Gomukha* design have emerged purely due to the design constraints of the human body with the sculptor having no intentions whatsoever?

The Darwinian explanation of the emergence of biological designs faces similar difficulties while attributing adaptive basis to their evolution. It is a challenging task to delineate the role of selection in shaping the designs from that of the design constraint *per se* spinning off an advantage. Gould and Lewontin[3] cautioned adaptationists of such false attribution of spin-off functions to the process of natural selection. They traced this attitude to the blind faith in natural selection that it is 'near omnipotent' in shaping the organic design. This faith, perpetuated by Wallace and Weismann, views natural selection to be such a powerful force in shaping the organic form and behaviour that the constraints are thought to hardly hinder its sweeping actions. The faith in the power of natural selection is so ordained that it is not uncommon for us to come across statements such as 'Natural selection guides the trait . . . *the way it guides everything else*'[4] in the literature on evolutionary biology. An important and a dangerous consequence of this faith is that 'fundamental' adaptationists are likely to perform an 'inverse explanation'[3] such as suggesting that the nipples and the naval cavity of Vishnu statue are carved so as to create the *Gomukha* effect. Gould and Lewontin warned that 'Any one who tried to argue that the structure exists because' of the perceived purpose (*Gomukha effect*) 'would be inviting the same ridicule that Voltaire heaped on Pangloss: "Things cannot be other than they are . . . . Everything is made for the best purpose. Our noses were made to carry spectacles, so we have spectacles" . . . .' Today the term *Panglossian paradigm* has become synonym with this false attribution of the spin-off functions to natural selection.

Style in the corolla tube

The work by Belavadi and his group reported in this issue[1] constitutes an interesting example to demonstrate the important ingredients of the Panglossian paradigm. But at the same time the system appears amenable for, at least partly, dissecting out the spin-off from the selection process. Belavadi and his group observed that the corolla tube of cardamom flower containing the nectar is longer than that of the proboscis of their major pollinators, the honey bees. Nevertheless honey bees were found capable of extracting the nectar from levels much deeper than their proboscis could reach.

They attribute this to the evolution of the style of appropriate thickness within the corolla tube. They argue that given a constant diameter of the corolla, as the thickness of the style increases, the effective diameter of the cavity in the corolla tube decreases. This creates a capillary effect and the liquid rises purely by adhesive and cohesive forces. Further, bees also 'suck' the nectar with a stomodeal pump in their pharynx, which might also cause the column of the nectar to rise in the corolla tube especially because the nectar is 'sticky'. It is likely that the thickness of the proboscis also adds to create this capillary effect by reducing the effective diameter of the corolla tube – a possibility that Belavadi's group does not consider. Thus the style and proboscis together render the nectar at much deeper levels available to the bees. Obviously, when the bee departs, the proboscis is taken out and the nectar level falls much lower than that the bee can apparently reach (Figure 2). Belavadi's group views the capillary effect due to style as an adaptation by the plant. They suggest that the evolution of style in the corolla tube with the appropriate thickness is a consequence of selection to favour bees drawing nectar such that the pollinators' visits to the flowers are sustained. This adaptationist view suffers from the regular traps of the Panglossian paradigm just as that of *Gomukha* in the Vishnu's statue.

Constraints of design or designed by natural selection?

Both the archaeological and the cardamom designs could arise by any of the following alternate processes:

a. *Emergent patterns from the basic design*: The function of the style (cow's face on statue) has not been shaped by natural selection (sculptor) but emerges purely as a spin-off of the basic design of the system.
b. *Tinkering the design*: Natural selection (sculptor) has fine tuned the basic design such that the required function (shape) has been achieved.
c. *Breaking the constraints*: Natural selection (sculptor) has mutated the basic design to arrive at the useful pattern.

The cow's face does not seem to have emerged by mutating the basic design. In a very preliminary analysis[5] based on certain proportional features of the body, it has been shown that the chest and the belly of the Vishnu statue do not differ significantly from those of other male statues in the temple. The first alternative is also unlikely because most observers perceive the *Gomukha* distinctly on the Vishnu statue than on others and the probability that such a rare variant would occur purely by chance on the idol where it does convey a meaning is dismally low to believe that it is a rare coincidence. Therefore the design appears to have emerged due to an intended tinkering of the basic design by the opportunistic sculptor.

Unfortunately it is not always possible to demonstrate that the selection has indeed operated on biological designs

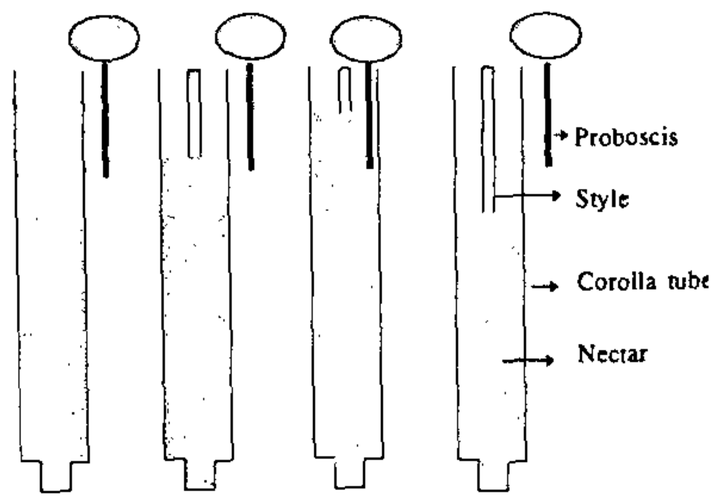

Figure 2. The nectar level in the corolla tube of cardamom (*a*). When the style is introduced, the nectar level rises not purely due to the physical displacement but also due to the adhesive and cohesive forces (*b*). When the proboscis is introduced, again for similar reasons, the nectar might raise to a new level from where the bee sucks through a pumping process (*c*). However when the proboscis is taken out, the nectar falls to level much below that of proboscis (*d*).

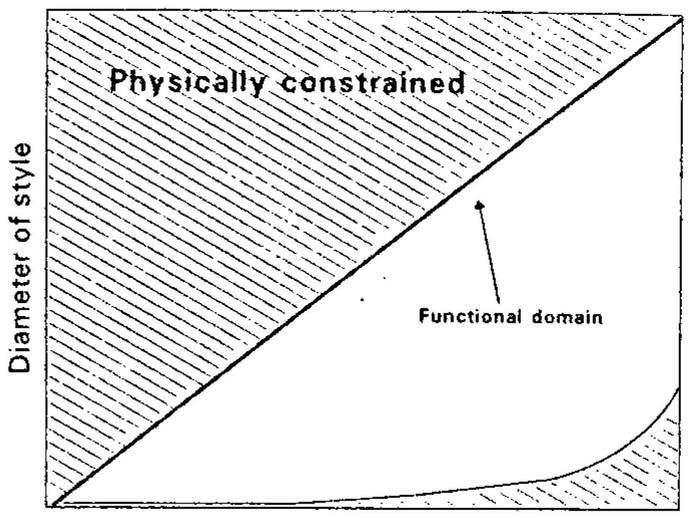

Figure 3. The physical constraints for the evolution of style and corolla diameters. Owing to the floral designs of the angiosperms, the style thickness shall always be less than that of the corolla, such that the upper left portion of the space (above the solid line) is physically constrained. Wider corollas are likely to be longer with long styles. In order to bear their own weight, the long styles have to be thicker as well such that the lower portion of the space below the curve is also physically constrained. The angiosperms have to occupy the space in between the diagonal and the curve. The functional advantage of the style as envisaged in the cardamom arises only in the shaded area because in this space the effective diameter of corolla is small enough to raise the liquid by adhesive forces. But any given plant species might occupy this space purely by chance or by their historical constraints and not necessarily by the 'design' of natural selection.

such as style and corolla in cardamom. The style constitutes the innermost whorl of the flowers and is contained within that of corolla in the angiosperms. Thus there is a basic design that limits the range of possibilities permitted for the relative diameters of the corolla and the style; the style has to be always less thicker than the corolla. All the angiosperms can only occupy the morphospace where style is smaller than corolla and the rest of the space is physically constrained (Figure 3). Further, styles and corollas that are too thin may not be able to support themselves and hence physical constraints limit certain other combinations of style and corolla diameters as well (below the curved line in Figure 3).

Obviously, there is a limited range of possibilities of corolla and style thickness and some of these, as spin-off, might result in raising the level of nectar as seen in the cardamom. These combinations occupying the functional domain of the morphospace (shown as the shaded area in Figure 3) could occur purely without any selection operating and cardamom flowers could represent one such combination. When bees start using this design, the cardamom plant accrues advantage as a spin-off and not by design of natural selection. In other words, the observed diameters of present-day cardamom might have arisen purely by chance and not by design. Note that this is different from the selection operating on the chance mutations. Darwinian evolution emphasizes selection of the best among the chance variants but does not generally recognize the constraints *per chance* offering fitness without selection[6].

Alternatively, it is also likely that the corolla and style of ancestors of cardamom occupied a non-functional domain that does not offer any advantage to the plant and selection has shaped them to move to the functional domain to derive advantage. It is indeed difficult to resolve this issue unless the immediate ancestors of cardamom are available. It would in fact be interesting to plot a set of random species on this morphospace to examine if there is more density of plant species in the functional domain than in the non-functional domain. A higher density of plants in the functional domain might suggest the role of natural selection in shaping the diameters of the corolla and style. But in the specific case of cardamom it may be difficult to delineate the two alternatives if the ancestors also fall in the functional domain.

Precisely for these reasons, it would be relishing to relate the examples from historical and archaeological contexts. In fact Gould and Lewontin's example of spandrels from San Marcos[3] is more illustrative than biological examples could be. But I have found that our students have more difficulty relating the spandrels than *Gomukha* to the Panglossian paradigm probably because of a lack of exposure.

While explaining the evolution of biological design, the constraints, both physical and phylogenetic are often recognized but 'are usually dismissed as unimportant or else and more frustratingly, simply acknowledged and then not taken to heart and invoked'[3]. Thus it is difficult to visualize the extent to which our interpretations in evolutionary biology are in the Panglossian style. But it is important that we need to be wary of such interpretations and if we are not, we may not be any more objective than the tourist guides attributing functions to all of their personal perceptions.

1. Belavadi, V. V., Venkateshalu and Vivek, H. R., *Curr. Sci.*, 1997, **73**, this issue.
2. For example, readers are invited to examine the dancing Krishna's statue printed in *Sunday*, 8–14 July 1997, p. 36.
3. Gould, S. J. and Lewontin, R. C., *Proc. R. Soc. London*, 1979, **B205**, 581–598.
4. Joshi, N. V., *Curr. Sci.*, 1997, **72**, 771.
5. Veena, T., *Avalanche Meetings I*, 1991, **1**, 78 (unpublished).
6. I should hasten to confess that Belavadi's group does not propose that the placement of style in the corolla in itself is a naturally selected feature but that their relative sizes probably are. But what is not generally recognized by adaptationists is that even these features could also be a consequence of constraints operating on the design with the fitness advantage merely being a spin-off.

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