Dynamics of brachiating siamang [Hylobates Symphalangus (S syndactylus)]

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were transformed to large organelles with multilayer cristae. These organelles often had an irregular form (Fig. 1*d*). They were 1.2–1.5 μm long whereas normal mitochondia are 0.5–0.6 μm long. The whole interior chamber of these mitochondria was filled with densely packed parallel cistae lying transversely to the long axis of the organelle.

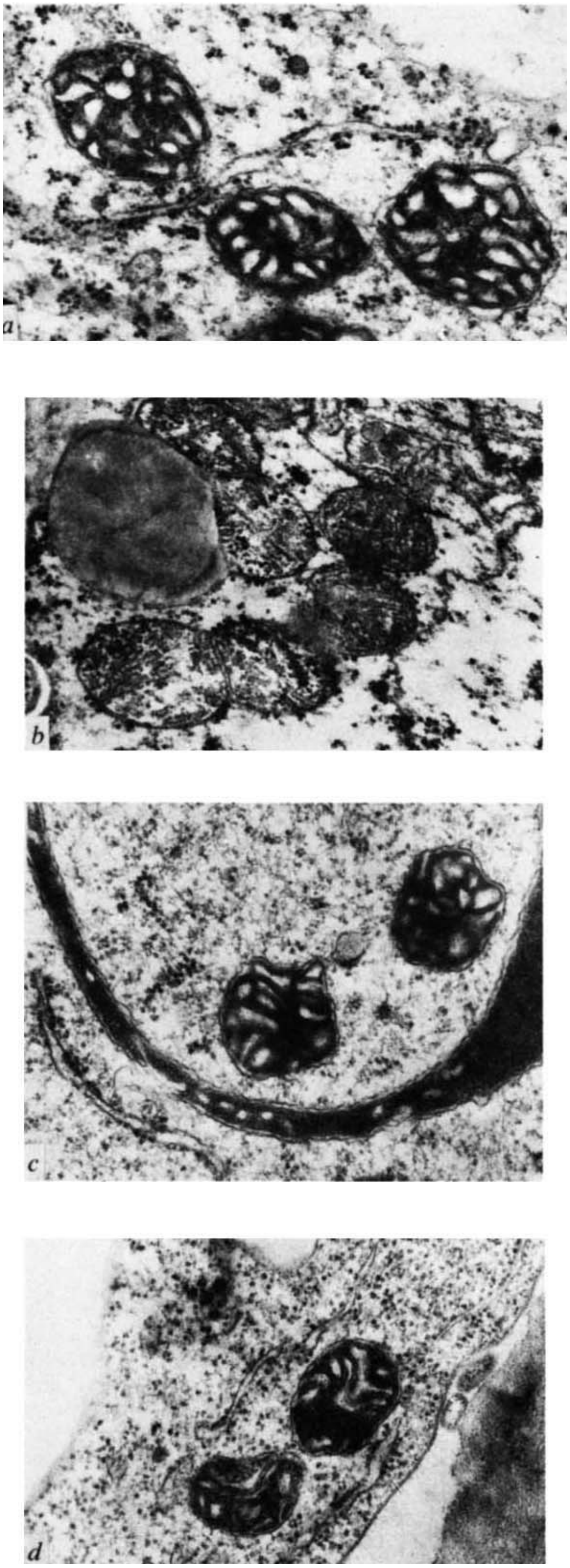

Fig. 1 Ultrastructure of mitochondria in cells of rice roots and coleoptiles in aerobic and anaerobic conditions. *a*, Root, 9 d after growth in aerobic conditions; *b*, root, 6 d of aerobic growth, then 3 d of growth in anaerobic conditions; *c*, coleoptile, 9 d of aerobic growth; *d*, coleoptile, 6 d of aerobic growth, then 5 d of growth in anaerobic conditions.

Such mitochondria have not, as far as we know, been described yet in plant cells, for which layers of parallel cristae are not characteristic[10]. They are found in animal cells performing especially active work (cells of flight muscles in insects, myocardium of mammals)[11].

The appearance of these mitochondria, extremely unusual for plants, can hardly be attributed to the beginning of organelle degradation; it rather points to hypertrophy of the mitochondrial apparatus, arising in rice coleoptiles cells because of shortage in oxygen supply.

It is interesting that the mitochondria of leaves, which in contrast to coleoptiles do not start growing in the absence of O_2 revealed unexpectedly high resistance to anoxia: 3–5 d exposure of plants to nitrogen did not lead to their destruction.

High resistance of rice coleoptile cells to anaerobiosis is thus reflected not only in their ability to preserve mitochondrial apparatus when growing in strictly anaerobic conditions but also in especially active development of a number of mitochondrial cristae, possibly promoting more complete extraction of traces of oxygen from an environment which almost completely lacks it.

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Dynamics of a brachiating siamang [*Hylobates (Symphalangus) syndactylus*]

The slow brachiation which is characteristic of the siamang [*Hylobates* (*Symphalangus*) *syndactylus*] and to a lesser extent the smaller gibbons [*Hylobates* (*Hylobates*) spp.] is often described as pendulum-like[1,2]. This comparison is apt because both the pendulum and the gibbons rotate about a fixed overhead fulcrum and make use of gravitational acceleration to effect movement. Beyond these basic observations, there have been few attempts to elucidate the mechanical aspects of this unique form of locomotion[2,3]. Analysis of 16 mm cine films of free-ranging and captive siamangs and gibbons reveals details of their locomotor behaviour that can be interpreted as precise adaptations for maximising the forward momentum gained from pendular movement.

This study is based on excerpts from several thousand feet of 16 mm film of wild siamang in Pahang, Malaysia and 100 feet of 16 mm film of captive siamang and gibbons on semi-natural islands in the Zoo Negara, Malaysia. Film was shot by the author with a Beaulieu R16B camera at speeds between 24 and 64 f.p.s.

The slow brachiation of the siamang involves a repeated series of movements. A representative cycle (Fig. 1) can be analysed in terms of two distinct phases involving the coordinated movements of trunk and legs as well as arms. The downswing phase begins as the animal releases the trailing hand. As the body swings forward and down with the legs extended, the free forelimb remains extended and sweeps through an arc behind the body. The upswing begins as the siamang flexes both legs and the free forelimb; midway through the upswing the forelimb is extended for the next grasp. During a complete swing, the trunk rotates through approximately 180° about a vertical axis.

In this form of locomotion, there are three ways in which the siamang can maximise its forward momentum: by maximising the change in kinetic energy on the downswing; by minimising the loss of kinetic energy on the upswing, and by minimising any lateral components in its momentum. Analysis of the siamang's posture in different phases of a single swing shows how the postural changes are adapted to maximise forward momentum in all three ways.

The total kinetic energy, and hence the maximum velocity acquired during the downswing, is proportional to the distance between the animal's centre of mass and the centre of rotation (in this case its hand). In a frictionless system, the increase in kinetic energy is proportional to the change in height of the centre of mass during the downswing ($\frac{1}{2}\ mv^2 = \frac{1}{2}\ lw^2 = mg\Delta h$). For a given arc ($\alpha$) of rotation, the vertical displacement of the center of mass increases with the distance between the centre of mass and the centre of rotation [$\Delta h = \Delta r(\sin\ \alpha)$]. The siamang increases this distance on the downswing by extending its legs and its free arm (Fig. 1).

On the upswing, the siamang minimises the loss of momentum due to gravitational deceleration by approximating its centre of mass to the centre of rotation. This is accomplished by flexion of the legs and the free arm (Fig. 1). By decreasing the moment of inertia, this redistribution of mass should increase the rotational velocity of the siamang. This increase in velocity can be seen in stop-frame analysis.

For all of the kinetic energy acquired on the downswing to be converted into forward momentum, the centre of mass should travel in the same vertical plane as the centre of rotation. The siamang is able to limit lateral motion of the centre of mass between handholds by extensive rotation at the wrist, elbow, and shoulder (Fig. 1*b*).

In the motion of a simple pendulum all of the kinetic energy acquired on the downswing is subsequently changed to potential energy on the upswing so the pendulum retraces its path indefinitely. In a single swing of the siamang, the kinetic energy lost on the upswing is less than that acquired on the downswing because of the input of potential energy resulting from the redistribution of mass on the upswing. By the mechanisms described above, the siamang could theoretically acquire a net momentum from each swing.

In most forms of locomotion, an animal must exert a propulsive force against the environment in order to acquire a forward momentum. Although the brachiation of the siamang as described above probably involves some energy expenditure in supporting the body, only with the rotation of the trunk about the hand is there a suggestion of any work being performed against the superstrate. In instances when siamangs do not utilise this pumping mechanism, active rotation and brachial flexion appear to become more important. Further studies involving electromyography could possibly determine the nature of the muscular activity involved.

The analysis above illustrates a way in which a slowly brachiating siamang could maximise his net forward momentum from gravitational acceleration without exerting any propulsive force against the environment. In the same way that a child on a swing can increase the kinetic energy of that system by 'pumping', the siamang is able to maximise the kinetic energy of a single cycle by appropriately timed redistribution of its mass.

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b

FIG. 1 *a*, Lateral view of a brachiating siamang, *b*, anterior view of a brachiating siamang. Figures rendered from tracings of 16 mm film stopped at intervals of ⅛s.