COMMENTS ON INERTIAL FEEDING.—Russell (1964) noted and re-emphasized (1967) that "inertial feeding" (Gans, 1961) would not be very effective in "underwater swallowing" by mosasaurs. The absence of a rejoinder and comments from colleagues suggest that the meaning of the concept should be amplified.

Animals may manipulate food objects through several strategies. Objects may be grasped and shifted to the desired position by a more or less continuous force application. This is exemplified when a monkey grasps a banana with its hand and lifts it to the mouth, when a chamaeleon shifts an insect from branch to jaw by a retraction of its tongue, or when the retraction of one side of a snake's dentigerous apparatus draws the prey off the teeth of the opposite side and further into the pharynx. Such a grasping manipulation requires that the structure holding the object be able to move relative to the portion of the animal toward which the object is to be shifted.

Numerous animals, including crocodiles, some turtles, and many lizards, cannot meet this requirement. Some of these lack limbs specialized for grasping and manipulation; others seem to lack the neuro-muscular control patterns requisite for utilizing limbs in this fashion. The tongue may be ineffective for such shifts, or the objects may be too large to be shifted by it. Yet such organisms do grasp objects between the tips of their jaws and then in some manner, shift them toward the esophagus; they generally effect such shifts by utilizing the inertia of the object.

The latter usage is here called inertial feeding. In this method, the jaws release the object and the head shifts to a new position while the object's inertia restricts its propensity to move. The accelerations imparted to the head by muscular effort must be sufficient to allow the animal to place the next grip on a more advantageous place. This implies a controlled shift in the relative positions of animal and object; the relative velocities and accelerations of head and object are hence of prime interest.

No difficulty will be achieved when the object is released to rest at zero absolute velocity on the ground (or afloat suspended in the water) while the head is being shifted. The relative velocity (of head and object) will then be equal to the absolute velocity of the head. Far more complex is the story when the food object is released in mid-air. Acceleration and velocity imparted to the head by muscular contraction must then be sufficient to overcome the effects of gravitational acceleration on the food object. Gravitational effects are often counteracted by imparting an upward acceleration to the object just prior to release. The downwardly directed action of gravitational acceleration is then counteracted by this "upward" kinetic energy. The time that it takes the prey object to travel upward and then back downward to the starting point is then available to shift the head to a new position.

When objects are to be moved backward into the mouth, there may be a similar induction of velocity; retraction of the head first accelerates the object in the direction of the pharynx; the head abruptly reverses thereafter to move forward. Relative displacement will then be maximized, but absolute velocity will be limited. A combination of these two movements is often seen when lizards of the genus *Varanus* manipulate eggs or engulf prey, or when crocodilians on land shift fish within their jaws.

The fundamental conditions are changed only slightly when the object or prey is being manipulated under water. As long as its density is approximately equivalent to that of the water its inertia will leave it suspended; thus a low velocity of the jaws may still achieve a sizeable relative displacement of jaws and prey object per snapping movement. If the food object is significantly denser or lighter than the suspending medium it will tend to move vertically. The velocity of such movement will be a function of the applied force (positive or negative buoyancy) and of the object's mass (determining its inertia). Water currents may change the magnitude and direction of the applied forces, but will not otherwise modify the picture.

Inertial feeding under water involves, of course, the need to overcome the frictional resistance (drag) of that medium, as this drag increases the forces needed to achieve significant accelerations of the head. Crocodilians often overcome this resistance by tossing small food objects (fish, etc.) into the air or lifting the head out of the water when manipulating prey (R. Allen, pers. comm.). Structural compensation may be achieved by reducing the size of the head and neck (sea snakes) or streamlining it (turtles and plesiosaurs); the former method also reduces the ratio of head mass to body mass (see below). Other animals have developed a long, slender snout whose sagittal cross section is less than its frontal one. Drag is then reduced by rotating the snout horizontally about an instant center located near the braincase or in the neck region. A shark will grasp prey loosely so that its laterally edged teeth are just in contact. Chunks are then cut or sawed off the prey, which is held by its own inertia, while the shark induces rotational vibrations around its long axis (Alexander, 1966).

Rotation of skull or body is of advantage as it involves rotational rather than translational inertia. Rotational inertia increases as the square of the distance between center of mass and center of rotation. Forms with a long, slender snout thus achieve maximum acceleration of grasping surface with minimum energy expenditure by rotating their head about an axis near its center of mass.

Mass in this context is that of the rotating system. It may include part of the nuchal musculature, rather than the head alone. Location of the instant center of rotation is further complicated when the animal is swimming or floating. Such animals often use shifts of the trunk and tail in order to impart the necessary momentum and controlled displacement to the head. Whatever the mechanism, the ingestion sequence does involve stabilization of prey by its inherent inertia between bites. This is the feeding method that Russell implied for mosasaurs; if he is correct, mosasaurs used inertial feeding.

It should be noted that a floating, swimming or flying animal must counteract a tendency for a general shift of its body while it manipulates prey with its head. The forces required to accelerate either food or the head will tend to induce equal reaction forces on the body and hence tend to shift it. Terrestrial forms can transmit such forces to the substratum utilizing their friction force reservoir (Gans, 1966). Suspended animals may counteract these movements by inducing equivalent but opposed forces with appendages. Alternately, or in combination with this, the animal has the evolutionary option of decreasing the ratio of head mass to body mass. The reaction to the force inducing major acceleration of the head will then produce a reduced acceleration of the trunk. The phenomenon is well documented by the structural shifts of turtles and some plesiosaurs, and the movements in question can be noted when a floating turtle is snapping at food.

Animals feeding in water have a third manipulative option; they can create either transient or steady-state currents. Water is relatively dense and the energy inherent within such currents causes them to impart momentum to entrained food objects and to accelerate these to velocities depending upon their inertia. Many vertebrates utilize variants of this method in the pattern long ago described as "Saugschnappen" (suction biting; Böker, 1937). In this the predator distends the buccal cavity and gapes widely, either simultaneously or immediately thereafter. The prey is then carried into the mouth by the inrushing water, e.g. in the mata-mata turtle (*Chelus fimbricata*), many chelyid and other aquatic turtles, and some fishes (Alexander, 1966).

Such manipulation by means of forces transmitted by a stream of water is, furthermore, used by certain animals that reverse the suction cycle, inducing transient currents by which they pump food objects into and out of the buccal cavity. In fishes and some salamander larvae, the objects are shifted past an array of teeth on which they impact and by which they may be shredded; in the turtle, *Malayemys trijuga*, the stream of water serves to peel fragments of a crushed snail's shell from its body, which remains restrained between the jaws. Yet another version of such aquatic manipulation of food objects is seen in neustophagia (*cf.* Belkin and Gans, 1968).

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