der Saeugethiere von Paraguay* (Schweighauserschen, Basel, 1830); A. de W. Bertoni, *Rev. Soc. Cient. Paraguay* **4**, 3 (1939).
5. *Platygonus* examined by R.M.W. (present location, number of specimens, and provenance) are: American Museum of Natural History, 4, Papago Springs Cave, Arizona (Rancholabrean); 1, Snake Creek Formation, Nebraska (Hemphillian); 9, Edson Quarry, Kansas (Hemphillian); and 7, Cherokee Cave, Missouri (Rancholabrean). Carnegie Museum, 15, Welsh Cave, Kentucky, and 5, Guy Wilson Cave, Tennessee (Rancholabrean). U.S. National Museum, 8, including holotype, *P. cumberlandensis* Gidley, Cumberland Cave, Maryland (Irvingtonian); 1, Hagerman Formation, Idaho (upper Pliocene); 1, Melbourne, Florida (Pleistocene); and 1, holotype, *P. alemanii* Dugès, Moroleón, Guanajuato, Mexico (Pleistocene). Specimens of *T. pecari* and *D. tajacu* from throughout their ranges have been studied.
6. J. E. Guilday, H. W. Hamilton, and A. D. McCrady [*Ann. Carnegie Mus.* **43**, 249 (1971)] illustrate sagittal sections of skulls and discuss the unique sinuses of *Platygonus*.
7. F. Ameghino, *An. Soc. Cient. Argent.* **58**, 186 (1904).
8. C. Rusconi, *An. Mus. Nac. Hist. Nat. 'Bernardino Rivadavia'* **36**, 122 (1929–1931).
9. ———, *Rev. Mus. Hist. Nat. Mendoza* **2**, 231 (1948).
10. G. G. Simpson, *Am. Mus. Novit. No. 1408* (1944), p. 29.
11. G. E. Meade, *Contrib. Geol. 1944, Univ. Texas Publ. 4401* (1945), p. 529.
12. Fieldwork in 1973 and 1974 was supported by grants to R.M.W. from the National Geographic Society and the University of Connecticut Research Foundation. Fieldwork by P.M. in 1972 and 1973 was supported by the University of California Museum of Vertebrate Zoology. In addition to those supporting our fieldwork, we thank officials of the government of Paraguay for interest in our work, especially Ing. Hernando Bertoni, Ministro de Agricultura y Ganadería; Ambassador G. W. Landau and his staff at the U.S. Embassy in Asunción; our hosts, R. J. Eaton at Juan de Zalazar and O. Netto at Rincón Charrua; J. W. Lovett, J. Balbuena, and J. Gonzalez for field assistance; and the following curators for their aid in R.M.W.'s examination of specimens: M. C. McKenna, R. H. Tedford, and K. Koopman of the American Museum of Natural History; M. Dawson, J. E. Guilday, and D. A. Schlitter of the Carnegie Museum of Natural History; and C. E. Ray and F. C. Whitmore, Jr., of the U. S. National Museum.

* Present address: Museum of Zoology, University of Michigan, Ann Arbor 48104.

10 February 1975; revised 7 April 1975

## Locomotory Adaptations in a Free-Lying Brachiopod

Abstract. Magadina cumingi *inhabits an environment of high current energy and mobile sediments by using its pedicle in Pogo-stick fashion as an elevating device. This type of progression is associated with pedicle musculature different from that of attached and other free-lying forms, and some diagnostic differences in muscle attachment areas are evident in preservable hard parts.*

Brachiopods are known to be attached to the substrate (by pedicle or cementation) or to be free-lying (with a reduced or atrophied pedicle) and with other various stabilizing and tethering devices, such as differential weighting or spines (*1*). *Magadina cumingi* (Davidson 1852), the only known Recent member of the terebratellid subfamily Magadinae, is free-lying but possesses a pedicle which is not used as a means of permanent attachment to the substrate. The pedicle is long and retractile so that when it is fully withdrawn into the body cavity its anterior end lies close to the intestine; posteriorly it bears four to six fingerlike processes (Fig. 1). The histological structure of the pedicle of *M. cumingi* does not differ from that described for other articulate, attached brachiopods and, since the processes are extensions of the main shaft of the pedicle, they contain no muscular or nervous tissue. Two pairs of muscles, the dorsal and ventral adjustors, act antagonistically to extend and retract the pedicle. The ventral adjustors have small tendonous attachments to the pedicle and wide fibrous attachments to the ventral valve; the dorsal adjustors are fibrous for their full lengths, their attachments to the pedicle forming a cradle-like structure around its antero-ventral segment.

Observations with scuba equipment in the tide race (surface velocities up to 250 cm sec$^{-1}$) of Backstairs Passage, South Australia, at a depth of 40 m showed that most animals lie obliquely (ventral valve uppermost) partially buried in the substrate so that only their anterior halves are visible; other living animals were observed lying on the substrate surface. The substrate consists of a planed-off surface of bedrock covered with a thin layer of sediment made up of coarse sand, small flat pebbles, and biogenic carbonates. These sediments form drifts in the lee of the sparse reef outcrops or of any small obstructions and contain the highest population densities observed (20 to 80 m$^{-2}$) of *M. cumingi*. Between one tide and another sediments in given areas in Backstairs Passage may vary in depth by several centimeters.

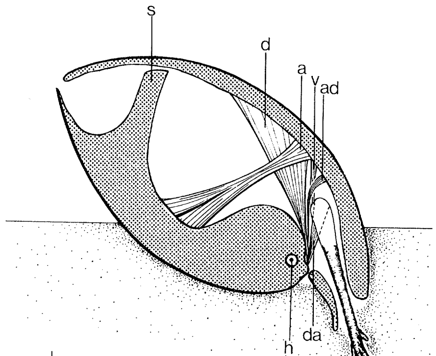

Fig. 1. *Magadina cumingi*. Semidiagrammatic sagittal section to show the extended pedicle and muscles of the left-hand side, ventral valve uppermost; *a*, adductor muscle; *ad*, accessory diductor muscle; *d*, diductor muscle; *da*, dorsal adjustor muscle; *h*, hinge axis; *s*, septal pillar; *v*, ventral adjustor muscle.

The shell of *M. cumingi* is differentially weighted and the accessory diductor muscles lie alongside the anterior section of the retracted pedicle so that their contraction is always accompanied by an elevation of the animal on the pedicle. These morphological features together with the nature of the pedicle and its musculature thus provide a picture of an animal which can automatically right itself if shifted by current action, in which opening of the valves is accompanied by an extension of the pedicle, and in which the more powerful activation of the pedicle by the adjustor muscles (together with added frictional resistance to the substrate provided by the processes of the pedicle) can lift the animal to or nearer to the surface of the substrate. Elevation of the animal seems to be the principal function of the pedicle. It is doubtful if the pedicle could serve any direct anchoring function since its posterior processes provide considerable resistance to penetration of a layer of sediment. It is possible, however, that an extended pedicle could function effectively, for animals lying in different positions on the surface of the substrate, as a stabilizer or as a lever.

The morphological characters contingent upon such a relationship between *M. cumingi* and its substrate in a high-energy environment are:

1) The absence of median pedicle muscles attaching the pedicle to the valve permits the pedicle to be fully retractile.

2) The attachments of the dorsal adjustor muscles are sited more posteriorly than is the case in attached or other known free-lying brachiopods—that is, flanking the cardinal process instead of lying anterior to it on hinge plates or on the valve floor. In this position the dorsal adjustors lie more nearly parallel to the pedicle so that a greater component of the total muscle force is available to move the pedicle in and out.

3) The diductor muscles are of greater size than those of attached species. The angle of insertion of the diductors is governed by the length of the pedicle, a long pedicle and a small angle of insertion requiring large ventral attachments for the muscles to operate efficiently.

4) Differential thickening governs the correct orientation of the shell and holds it in a stable position. The valves of *M. cumingi* are heavily thickened and, since the dorsal adjustor muscles are attached posteriorly, the greater part of the massive platform formed by the fused cardinalia has no function other than to provide weight. This extensive thickening combined with the large area occupied by the diductors reduces the size of the mantle

cavity relative to the body cavity; this constitutes a limiting factor to lophophore size which may relate to the early loop phase characteristic of this particular species.

5) Shell outline, degree of convexity, cardinal margin, and characters of the beak [differentiated as "bouchardiform" by Thomson in 1915 (*2*)] all combine to produce an animal with a shape apparently well adapted to live in close association with constantly shifting sediments of a coarse sandy type.

Some terebratulid genera show great morphological conformity with *M. cumingi*; for example, *Australiarcula* (Cretaceous). Some differ in adult loop patterns and in the degree of secondary thickening (while retaining its differential character) but show the characteristic beak and muscle scar patterns; for example, the Tertiary genera *Magadinella* (Australia), *Rhizothyris* (New Zealand), and *Tanakura* (Japan). Others are functionally similar while displaying differences in some morphological characters; for example, *Bouchardia* (Recent, Brazil) possesses a cardinal process of very different shape but situated in the same position relative to the dorsal insertions of the adjustor muscles. It is conceivable that other functional replicas may be found in genera such as the Cretaceous terebratulids *Trigonosemus*, *Sympithyris*, and *Terebrirostrata*; in *Onychotreta* (Orthida, Silurian); and in *Cardiarina* (Rhynchonellida, Carboniferous), all of which possess open, transapical foramina allied with a prominent or elongate beak. Now that the assumption has proved incorrect that an open foramen of adequate size implies permanent attachment to a substrate, studies of these and other genera may give hints of the existence of other types of brachiopod progression.

JOYCE R. RICHARDSON
JEANETTE E. WATSON
*National Museum of Victoria,*
*285-321 Russell Street,*
*Melbourne, 3000 Victoria, Australia*

### References and Notes

1. M. J. S. Rudwick, *Living and Fossil Brachiopods* (Hutchinson, London, 1970), pp. 1–199.
2. J. A. Thomson, *Trans. N.Z. Inst.* **47**, 392 (1915).
3. Supported by a grant from the Australian Research Grants Commission.

17 March 1975

## Far-Field Acoustic Response: Origins in the Cat

Abstract. *Short-latency evoked potentials recorded from the vertex of adult cats in response to click stimulation (the far-field acoustic response) were analyzed in a series of lesion experiments to determine the origins of each component. The resultant data indicate that the primary generator of potential 1 is the acoustic nerve; of potential 2, the cochlear nucleus; of potential 3, neurons of the superior olivary complex activated by projections crossing the midline; of potential 4, neurons of the ventral nucleus of the lateral lemniscus and preolivary region activated equally by crossed and uncrossed projections; and of potential 5, neurons of the inferior colliculus activated primarily by crossed projections.*

In human subjects, a series of evoked potentials with submicrovolt amplitudes can be recorded from disk electrodes placed on the scalp vertex and earlobe within 10 msec of click stimulation (*1*). This sequence of waves, which are separated by intervals of approximately 1 msec, has been tentatively correlated with activation of the brainstem auditory nuclei and thus has been termed the "far-field" acoustic response (*1*). Such a measure of brainstem auditory function could provide a sensitive and objective neurological measure that would be particularly useful among populations unable to respond appropriately in conventional audiological testing, such as in cases of severe mental retardation, as well as among patients with central hearing problems or with acute head trauma for which the locus of pathology is unknown. In the cat, similar recording procedures result in a series of evoked potentials at latencies that are slightly shorter than those recorded in the human but also show successive delays of approximately 1 msec (*2, 3*). These evoked potential components emerge separately in the kitten during the first 2 weeks after birth and progressively increase in amplitude and decrease in latency until an adult profile is attained at 1 to 2 months of age (*4*). The decrease in latency of one far-field response component has similarly been correlated with development in human infants (*5*). Thus, the far-field response could also represent a powerful tool for observing functional maturation within the brainstem auditory pathway. However, neither the clinical nor experimental potential of the far-field acoustic response can be fully exploited until an anatomical identification has been made of the generator loci primarily responsible for each of the short-latency waves.

The latencies of the far-field acoustic response components in the cat have been correlated with the latencies of auditory responses recorded from brainstem areas by Jewett (*2*). In this study, the far-field peak 1, with a latency similar to the $N_1$ response at the round window, was interpreted as a reflection of acoustic nerve discharge. Far-field peak 2 was correlated with the latency of the cochlear nucleus evoked potential; peak 3, with the latency of potentials recorded in the region of the superior olivary complex; peak 4, with the latency of potentials recorded on either side and within the inferior colliculus; and peak 5, with the latency of potentials recorded within and rostral to the inferior colliculus. In order to extend these data and more clearly identify the primary origins of each far-field potential component, the present series of lesion experiments was performed on ten adult cats.

Prior to surgery, the cat was anesthetized with sodium pentobarbital (35 mg per kilogram of body weight) and placed in a stereotaxic frame with hollow ear bars. The skull was exposed and a stainless steel screw was secured at the vertex for the far-field recordings. A second reference lead was attached to the pinna of one ear. Click stimuli of 0.1-msec duration and 10-khz frequency were generated by a Wavetek 112 audiooscillator and delivered through B & K 4144 condenser microphones attached to the end of each ear bar. At the other end of the ear bar, click intensity was measured at 70 db sound pressure level (referenced to 0.0002 dyne/cm$^2$), or approximately 50 db human sensation level, by lengthening the click duration to 400 msec to allow for the slow response time of the calibrator (General Radio sound intensity meter 1565A). Clicks were presented at 10 per second and the resultant response was led from the recording electrodes to a Grass P511 amplifier (30 to 3 khz band pass, 100,000 gain). The amplified response was fed into an averager (Enhancetron 1024) and the average of 600 successive responses was plotted with an *x*-*y* plotter. A series of control recordings was routinely made with binaural and monaural clicks before any lesion was made. After each lesion, the same series of recordings was repeated and at least 1 hour was allowed for stabilization of the recordings before a subsequent lesion was made. Precollicular decerebration was carried out by first aspirating the occipital lobes and then sectioning the brainstem rostral to the inferior colliculi with a blunt spatula. Hemostasis was facilitated in all procedures by Gelfoam and Oxycel. In another type of preparation, the inferior colliculi were aspirated or undercut bilaterally under visual control. In some preparations a sagittal midline section of the brainstem from the level of the colliculus to that of the cochlear nucleus was carried out with a blunt spatula held in a stereotaxic carrier to interrupt all crossed projections. A coronal brainstem section or hemisection