

son why limited morphological resemblances to the orang-utan should be more diagnostic of an ancestral relationship than were those to humans. The Tasmanian wolf (*Thylacinus cynocephalus*), a recently extinct marsupial carnivore, was classically thought to belong to the Australian dasyurids, but some paleontologists pointed to marked dental and basicranial resemblances to the extinct South American *Borhyaena* and argued for a close affinity between the two. Fossil albumin analysis revealed the Tasmanian wolf to be a dasyurid [7].

The older the fossil, the less likely on probability considerations alone that it has any modern descendants. Our immunological evidence of sirenian relationships strongly suggest relatively recent divergences of the manateids and dugongids and of Steller's sea cow and the dugong. These data should provide a useful framework for further interpretation of the sirenian fossil record.

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Swarm Raiding in a Myrmicine Ant

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Doryline ants (commonly known as army ants) are among the best studied social animals [1]. This can be attributed in large part to their dramatic raiding behavior. While the majority of doryline species forage in narrow columns, a few raid in broad swarms [1]. Swarm raiding, though rare, has been studied intensively [1, 2], and has long been recognized as one of the most impressive examples of coordinated group activity shown by animals [1]. To date swarm raiding has been found only in doryline ants. I report the dis-

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covery of massive swarm raiding in the myrmicine species *Pheidologeton diversus* (Jerdon); the raids of this highly polymorphic Asian ant (Fig. 1) are remarkably convergent with those of army ants.

P. diversus colonies have one or two stable trunk trails (i.e., relatively long-lasting orientation trails [3]), which extend 5–100 m from the nest. Trunk trails often remain in use for weeks, during which time ants move along them continuously, day and night. A variety of other ants, including certain

dorylines [4], also produce trunk-trail foraging routes.

The great majority of ants search for food solitarily [5]. This is also true for most species with trunk trails, since workers depart from the trails singly to search for food. However, in *P. diversus*, as in doryline ants, trunk trails serve as the departure points of raids: solitary foraging, inasmuch as it can be said to occur, is restricted to the advancing fronts of these raids (other than at the raid front, solitary ants rarely travel even 5 cm from a trail). Raids originate at any time of day and from any point along the trail; they advance for variable distances and then usually retreat. Raids are apparently influenced little by the courses of recently retreated raids, and will advance readily over previously unvisited ground [6].

A raid begins when ants abruptly move out from some point along a trunk trail or from the nest entrance and then advance at 10–20 cm/min in a narrow column. After the column extends between 0.5–3.0 m, the ants at its terminus spread out to form a narrow group, and progress begins to slow. A minority of these column raids further expand into larger, fan-shaped raids (Fig. 2) which sometimes advance at least 20 m. Within a narrow region along the advancing margin of these raids, ants move about in large numbers, forming a swarm. Behind this region, most ants move in a fan-shaped network of columns. The raid funnels back to a single, basal column, which lengthens as the raid progresses.

The raids of *P. diversus* can reach 6 m in width and contain tens of thousands of individuals. Such raids resemble those of swarm-raiding doryline ants, yet they advance slowly, usually 1.5–2.0 m/h, while doryline swarm raids often sweep ahead at 10–20 m/h [1]. A disparity in worker movement patterns probably accounts in large part for this difference. In contrast to doryline ants [1], workers at the raid front do not advance rapidly and directly on to uncharted territory and then retreat; rather they meander considerably, and without the rapid turnover characteristic of ants at a doryline raid front.

Whereas the recruitment techniques of other predatory ants allow the capture of agile prey up to at most a few times

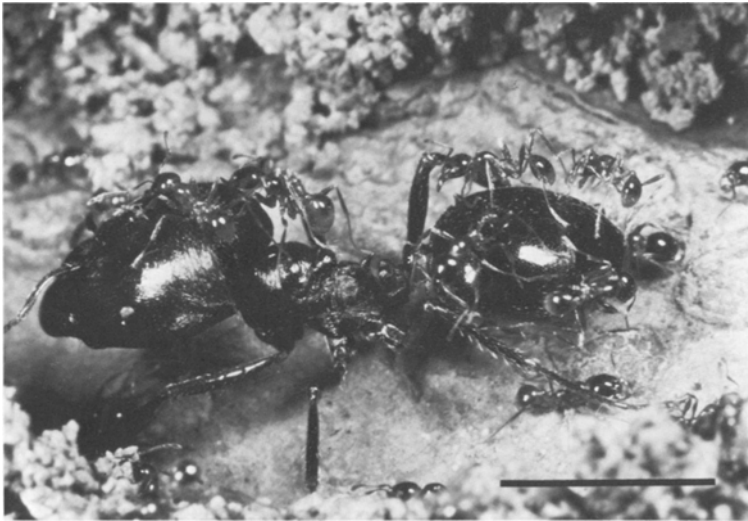


Fig. 1. *Pheidologeton diversus* foragers, including several minor workers riding on a large major (scale bar = 0.5 cm)

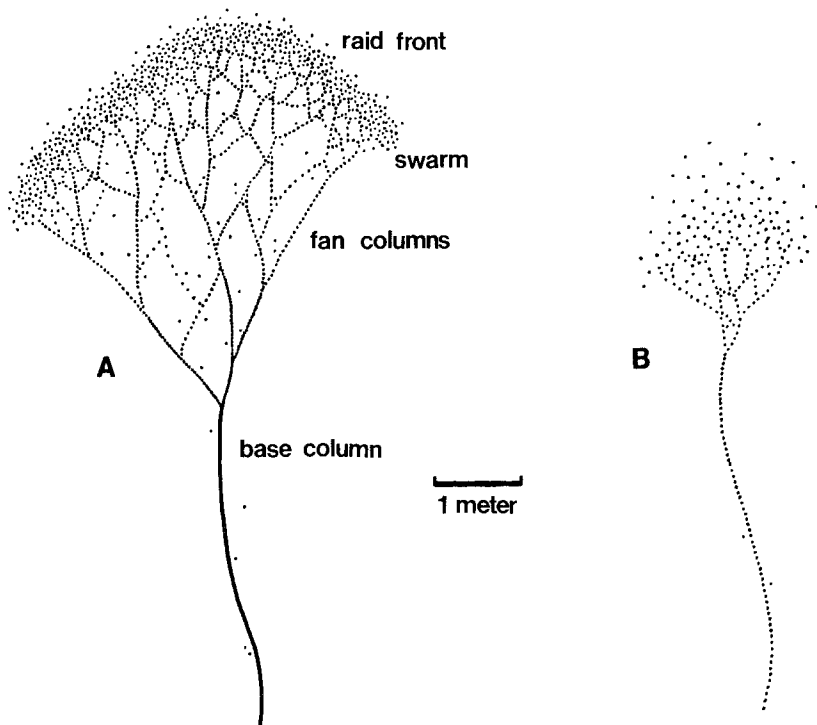


Fig. 2. Two extremes in the raiding pattern of *P. diversus*. In pattern A, worker density is high and concentrated at a well defined raid front. Raids of this description vary from 2 to 6 m across. Pattern B is characteristic of most smaller raids. Workers are relatively spread out, so that, in extreme cases, scattered individuals advance as much as 50 cm ahead of other ants

the body weight of individual foragers, *P. diversus* and dorylines capture relatively formidable prey, including prey having dry weights hundreds or thousands of times greater than that of the ants participating in prey capture. In *P. diversus*, common prey include cock-

roaches, centipedes, orthopterans, and earthworms up to 10 cm in length. Workers rush at prey encountered during the advance of a raid, piling on until the quarry is securely pinned down and can be torn apart.

As the raid advances, the ground tra-

versed is covered repeatedly by many individuals within the swarm. This leads to the ferreting out of an impressive variety of foods other than difficult prey. For example, the ants also catch smaller prey, even such tiny, elusive insects as collembolans and fruit flies. And, unlike doryline ants, which have diets composed almost entirely of animal material [1], in *P. diversus*, seeds, nuts, and fruits form an important part of the diet: usually almost half the material carried to the nest is of vegetable origin [6].

A variety of ants other than *P. diversus* and doryline ants have been referred to as "raiding" or "group raiding" ants. These include slave-making ants, cerapachyine ants, and certain ponerine ants, all of which attack other ant colonies or formidable prey. In *P. diversus* and doryline ants, workers search in groups for live prey and other food, while, with few known exceptions [7], the foragers of these other raiding ants search for prey and other food solitarily and then recruit workers over a distance to it. The difference is fundamental: the raids of both *P. diversus* and doryline ants are not directed toward specific food sources. Indeed, this feature is the crux of the army ant foraging strategy.

Doryline ants foraging in swarm raids are characterized by their large colonies, relatively broad diets, and the efficiency with which they kill massive prey [8]. Tropical Asia lacks epigaeic doryline species of this description, although such ants are conspicuous in Africa (i.e., some *Dorylus* spp.) and Central and South America (i.e., *Eciton burchelli* and *Labidus praedator*). In Asia, *P. diversus* and probably some other related *Pheidologeton* species have apparently preempted this army ant niche.

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and E.O. Wilson (pp. 248-251 of: Caste and Ecology in the Social Insects. Princeton Univ. Press 1978). Although workers search for food separately, in many species recruitment must occur before the retrieval of an intractable food item can begin

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class T4) send their axons to bulbar/spinal motor systems (for review see [1]). This was supported by anatomical [5] and neurophysiological [4] evidence. The present study is a first attempt to investigate the internuncial network between tectal output neurons and bulbar/spinal motoneurons in paralyzed toads *Bufo bufo*. From the medial reticular formation (and adjacent positions) – a projection field of tectal descending fibers [3] – we have extracellularly recorded different types (a-i) of visual sensitive neurons:

(a) Movement-specific neurons with excitatory receptive fields (ERFs) of $\approx 40^\circ$ diameter located in the visual field of the ipsi- or contralateral eye showing maximum activity in a central area of $10-15^\circ$. The response properties of these neurons resemble configurational sensitivities of tectal class T5(1), T5(2), T5(3), or thalamic TH3 neurons [1]. Some are very sensitive to irregular movements. – (b) Neurons with ipsi- or contralateral frontal ERFs of $60-180^\circ$ showing selectivity to stimulus

Neurophysiological Data Regarding Motor Pattern Generation in the Medulla Oblongata of Toads

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The command system hypothesis of prey-catching behavior in toads suggests that several classes of neurons in the optic tectum, specialized for *identification* (e.g., class T5(2)), *localization* (e.g., class T1(3)), and *arousal* (e.g.,

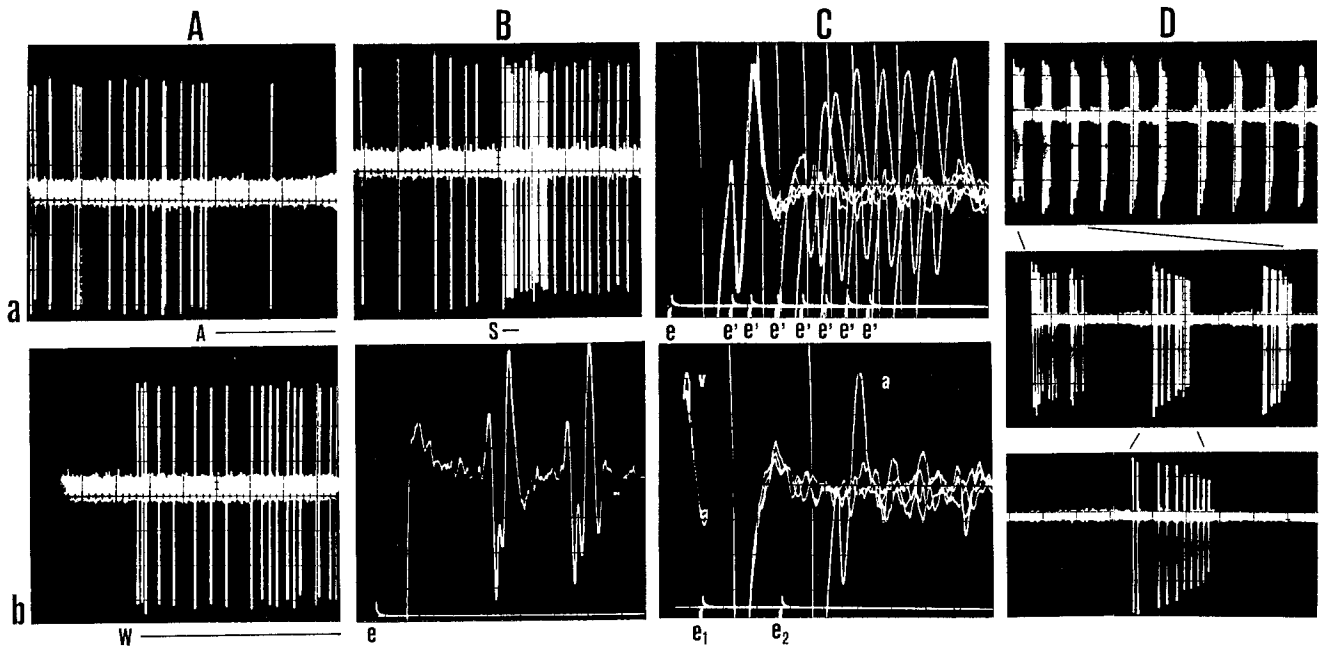


Fig. 1. Types of visually sensitive neurons recorded from the toad's medial reticular formation in the medulla oblongata. A) Spontaneously active neuron which is inhibited during and shortly after a $2^\circ \times 8^\circ$ stripe was moved in "antiworm" (A) configuration (a); in the silent period (b) the neuron can be activated if the same stripe is moved in "worm" (W) configuration (time scale: 1 s/Div). B) Spontaneously active neuron whose activity is increased (a) during and following stimulation with a $8^\circ \times 8^\circ$ moving square (S); the post-stimulus activity may last up to 10 s (time scale: 1 s/Div). The same neuron can be activated synaptically following electrical stimulation (e) with a negative square wave impulse of 0.1 ms and $15 \mu\text{A}$ applied to the contralateral optic tectum (b) (time scale: 2 ms/Div). C) Antidromic activation of a cell by an electrical impulse (e) of 0.1 ms and $10 \mu\text{A}$ applied to the ipsilateral spinal cord between the 2nd and 3rd ventral root (a); in response to electrical double stimuli (e, e') the neuron followed down to stimulus intervals of less than 2.5 ms (a, eight superimposed traces). No antidromic (a) spike was recorded in experiments, in which a visually (v) elicited spike triggered immediately the electrical stimulus, e_1 , at a delay of 1 ms (b); collision between v and a occurred at a critical spike-stimulus interval of 2.8 ms, but not at 3.2 ms (cf. e_2) (b, three superimposed traces). Time scale (a, b): 1 ms/Div. D) Neuron that exhibits cyclic burst activity initiated by short visual stimulation; time scale: 2 s/Div (above), 0.5 s/Div (middle), 0.2 s/Div (below)