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Paleoethological Inference: Therapsids as a Model System

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David Duvall



Brent M. Graves (left) received the B.S. degree in Biology from Central Michigan University in 1981. He is currently working on an M.S. in Zoology at the University of Wyoming, and his thesis deals with the behavioral and physiological ecology of alarm pheromone communication in prairie rattlesnakes. Brent Graves' general interests include the evolution of animal communication, functional morphology, and behavioral physiology. He is the author of several research reports and reviews. David Duvall, (right), one of the guest editors of this issue, earned A.B., M.A., and Ph.D. degrees, from the University of California, Berkeley, San Jose State University, and the University of Colorado, Boulder, respectively. Upon completion of his Doctorate in Biology at Colorado in 1980, he accepted a position as Assistant Professor of Zoology at the University of Wyoming. Although thoroughly immersed in research in the areas of behavioral and physiological ecology, the evolution of animal communication, evolutionary biology, and herpetology, David Duvall is committed to and involved in biology education. Currently, he is the General Biology Coordinator at Wyoming (a program which handles about 1,500 students per year) and a current member of *ABT's* Editorial Advisory Board. He is the author of several research reports and reviews.

Prior to the appearance of any dinosaur, the terrestrial fauna of the late Paleozoic was dominated by reptiles whose ancestors would one day be known as mammals. Classification of these "mammal-like reptiles" into the orders Pelycosauria and Therapsida describes an evolutionary relationship, the latter animals being more advanced and grading directly into mammals. Ecologically, the mammal-like reptiles have been broadly grouped into herbivorous forms, exemplified by *Lystrosaurus* (fig. 1) and *Styracocephalus* (fig. 2), and carnivorous forms such as *Trochosaurus* (fig. 2) and *Blattoidealestes* (fig. 2). While both groups radiated evolutionarily under numerous circumstances, mammals are believed to have stemmed from a carnivorous therapsid lineage. Paleontologists, those who study fossils, and biologists have come together to study such ancient animals forming the field of learning known as paleobiology. Central to the goals of paleobiology is elucidation of taxonomy and life histories and processes of ancient species, primarily through application of the principles of uniformitarianism, the comparative method, and inheritance relationships between fossil and living organisms.

As a branch of paleobiology, paleoethology seeks to study the behavior of ancient animals by building inferential cases for hypothesized behavior patterns. Although such ancient behaviors can never be directly observed, indirect evidence can strongly support certain possibilities. Animals come to function effectively in their respective communities and habitats through the evolution of physiological, morphological, and behavioral adaptation. Knowledge of behavioral components of an animal's overall biology can aid in developing a clear understanding of how that organism lived and can help to discern evolutionary trends and processes. In studying biology today the relatively minuscule number of extant species available for study represents but a small portion of the species that have lived and shaped the current biosphere. Therefore, inferentially supported hypotheses about ancient animals can greatly increase our understanding of evolution and behavior.

Methods of Study and Inference

The concept of uniformitarianism (Simpson 1970) is often represented by the aphorism "the present is the key to the past," which states effectively that events and processes occurred in the same manner in the past as they do currently (and vice versa). Using this concept, we can develop propositions about extinct organisms, based upon physical and biological facts that can be studied in the present. For example, one might assume that gravity existed in the past and exerted force on mass in the same way that it does today. Or, if a fossil mammal skull contains a central cavity, we can propose that this space was occupied by

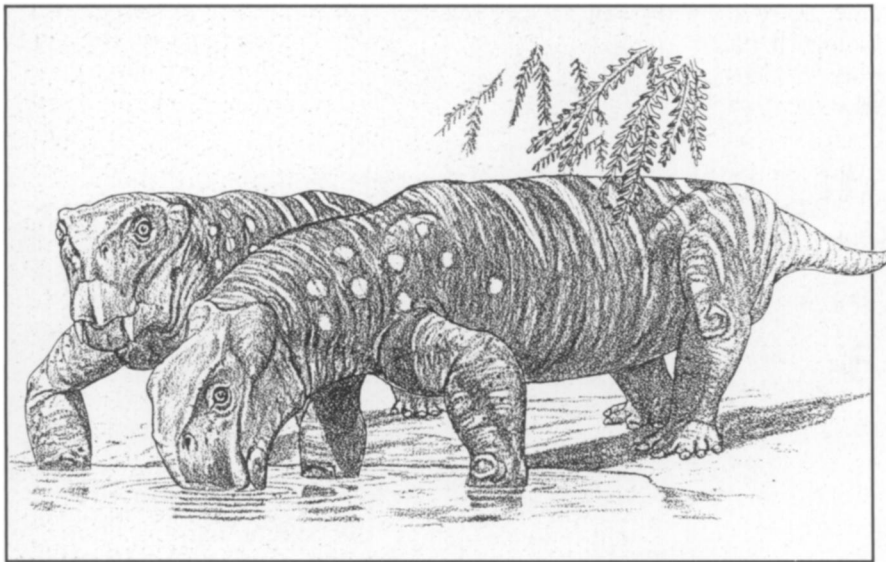


FIGURE 1. A restoration of *Lystrosaurus*, an early Triassic herbivorous therapsid which had a worldwide distribution. Because of its dentition and incompletely ossified feet, *Lystrosaurus* is thought to have been amphibious and fed on shallow freshwater plants. Developed by Gregory Paul, and reprinted with permission.

a brain.

Especially useful in paleobiological inference is taxonomic uniformitarianism (Lawrence 1971) which proposes that associations between biological aspects of fossilized animals can be made with observable characteristics of closely related extant taxa. The premise here is that structures with similar form and occurrence in uniform but separate environments probably served similar functions. Such syllogistic logic allows one to deduce likely functions associated with particular structures. For example, ichthyosaur fossils are found in marine deposits, and although reptiles, they appear superficially like modern porpoises. Therefore, paleobiologists have interpreted other aspects of ichthyosaur biology, such as feeding and locomotion, to be similar to that of extant porpoises.

Analogy and homology are additional, useful concepts for clarifying evolutionary relationships and trends (Atz 1970; Romer and Parsons 1977). A homologous feature is one which is present in different taxa due to inheritance from a common ancestor. In contrast, analogous features are those which have evolved independently in different taxa. Examples might include the tails of monkeys and horses as homologous features, with the wings of birds and butterflies as analogues.

The comparative method can also be used to discern evolutionary trends — and likely selective pressures which have shaped them. When one examines groups of animals, certain behavioral and morphological similarities and differences become apparent. It is assumed that such features are the result of functional changes correlated with environmental conditions and the mode of life under which the animal has evolved. For instance, the ichthyosaur's limbs have become fin-shaped to aid in pelagic swimming, while those of its reptilian cousins are designed for terrestrial locomotion.

Why Study Therapsids?

An assemblage of fossils of rich variety and in good condition can enhance the range and quality of information obtainable through the use of these methods. A group ideally suited for such inference is the mammal-like reptiles, especially the more advanced therapsids. In their evolution from truly reptilian forms to mammals, therapsids comprise the only well-documented transition from one vertebrate class to another. Indeed, therapsid evolution is better portrayed in the fossil record than for almost any other animal taxa (Kemp 1982). And because many aspects of vertebrate physiology manifest themselves in skeletal structure, certain "soft" anatomical, ethological, and even ecological characteristics of these animals can sometimes be inferred.

From the earliest point of reptilian evolution, two distinct lineages are apparent. One branch includes the cotylosaurs, dinosaurs, birds, and all living reptiles. The other, the mammal-like reptiles, includes the pelycosaurs and their more advanced derivatives, order Therapsida. Initially appearing in the late Permian (about 230 million years ago), therapsids existed until the mid-Jurassic (about 160 million years ago) (fig. 3). These vertebrates radiated to fill a wide variety of ecological niches and were the dominant terrestrial vertebrates for an extremely long duration. As the Jurassic period waxed, dinosaurs probably appropriated therapsid ecological roles, facilitating their demise, and leaving only mammalian descendants of the latter as representatives of the mammal-like reptile evolutionary line.

Because of these evolutionary relationships and the rich therapsid fossil fauna available to us, this group provides not only a unique window into the phylogeny of an interesting group of extinct animals, but also a means of considering patterns of large-scale morpho-

logical, physiological, and behavioral change. We will examine a number of aspects of therapsid biology, with emphasis placed on ethological characteristics that can be inferred from available evidence, and how such hypotheses are constructed and supported or refuted (see Colbert 1958). Specifically, we will discuss two examples of how morphological and related considerations help to provide insights into the behavior and physiology of therapsids. First, metabolic rate and associated activity patterns, and second, the possible existence and uses of vomeronasal organ will be explored. These examples were chosen for their wealth of relevant data and by no means cover the range of possibilities for paleoethological inference.

Metabolism and Activity Patterns

Many aspects of typically mammalian behavior can be related directly to endothermy and associated high activity levels. Significant to inference about "active therapsids" is extensive fossil evidence for elevated metabolic rates, perhaps approaching those of mammals. When metabolic rate increases, cellular energy demands increase proportionally and a higher rate of oxygen delivery to tissues is required. Extant mammals

satisfy this respiratory requirement in part through use of a diaphragm. Muscular contractions of the diaphragm increase the size of the thoracic cavity, causing a negative pressure to develop in the lungs, which causes air to be sucked in. If we hypothesize that therapsids did have elevated metabolic rates and a diaphragm to aid in oxygen intake, how might we support or refute such an idea? If there is some skeletal feature associated with possession of a diaphragm in mammals, its presence in therapsids would indirectly support our hypothesis. Therapsid rib structure provides such a feature (Brink 1957).

Ribs support the trunk of vertebrates but are critical for breathing as well. Without ribs the body cavity would collapse under negative pressure developed during respiration. Ribs of ectothermic reptiles occur along the entire length of the trunk (Romer 1966), and in conjunction with costal muscles, increase trunk volume to maximize inhalation effectiveness. Mammals, however, have thoracic ribs only and none in the abdominal region. When the diaphragm contracts and straightens to increase the volume of the thoracic cavity, the abdominal cavity must necessarily be compressed. Therefore, ribs in the abdominal area would counteract the actions of the diaphragm by restricting abdominal distension in response to pressure from the



FIGURE 2. A restoration of some late Permian therapsids. Two wolf-sized predators, *Trochosaurus* (50kg), feeding on the herbivorous *Styracocephalus* (100kg) while the carnivorous *Blattoidealestes* (2kg) darts around looking for scraps. Developed by Gregory Paul, and reprinted with permission.

diaphragm. Hence, these ribs have been lost in mammals, allowing the abdomen to work in coordination with the diaphragm, rather than against it.

What types of ribs are present in fossilized therapsid specimens? Most possessed reptilian type rib structure. However, in the more advanced cynodont therapsids, typified by *Thrinaxodon liorhinus* (fig. 4), a differentiation between thoracic and abdominal ribs occurs precisely at the location where the diaphragm is found in mammals (Brink 1957). Thus, our hypothesis that therapsids possessed a diaphragm is supported inferentially for the more advanced therapsids. More important, our primary hypothesis, that therapsids possessed an elevated metabolic rate and were quite active behaviorally, is supported more generally. Before any selective pressure for evolution of a diaphragm could have occurred, some degree of increased metabolic rate must have been characteristic of these mammal-like reptiles.

Other features of therapsid fossils suggest elevated metabolism. For example, the biomechanics of therapsid locomotion can be determined from bone structure (Kemp 1982). Locomotion efficiency greatly increased when the pelvic girdle rotated to place limbs under the body rather than to the sides in a sprawling manner. This arrangement afforded more power to the hind limbs for speed and moved the feet closer together resulting in increased maneuverability. Associated with the latter, we find vertebral column modifications, and all such structural and locomotory modifications of cynodonts would have allowed these predators to more actively capture prey, avoid predators, and proceed through routine activities. Histological observations of the bones of virtually all therapsids indicate a marked difference from other reptiles, as well. The Haversian canal system and cortex vascularization are well developed and growth rings are absent. Therapsid bones are identical to mammalian bones in these regards and these features have been attributed to endothermic physiology (Ricqlès 1974).

Geological information supports a hypothesis of elevated therapsid metabolic rates. Bakker (1974) notes that Permian deposits in which dinocephalians (see fig. 3) were fossilized were formed at about 60° latitude. Therefore, dinocephalians, which were probably too large to find suitable hibernation sites, probably needed to produce enough heat to remain active during temperate seasons.

Also associated with homeothermy might be a role for insulation for retaining heat and sweat glands for dissipating heat. Evidence for a specialized type of hair, vibrissae, is present on some cynodont skulls (Watson 1931). Brink (1957) has argued that prior to development of such specialized hairs, ordinary body hair must have been present in ancestral therapsids. Similarly, pits in the snouts of certain cynodonts have been interpreted as housing specialized skin glands. If such specialized skin glands were present in cynodonts, less complex skin glands may have been present in therapsid progenitors.

Essential to an increased metabolism are means by which greater amounts of energy can be obtained and assimilated. As noted previously, increased locomotion efficiency and oxygen intake would aid in chasing and securing prey. Hence, the differentiation of teeth into incisors, canines, and multi-cusped postcanine teeth that is characteristic of the cynodonts may have played a related role. Such an increase in complexity, compared with typical reptilian homodont (undifferentiated) dentition, indicates that greater mastication of food may have occurred before swallowing. Thus, a greater surface area of food particles would have been available for digestive enzymes to act upon, and consequently, assimilation of food energy could have occurred more rapidly.

Also associated with mastication of food is the secondary palate. This bony structure partly to entirely separates the oral and nasal cavities in therapsid fossil skulls from late Permian time on. A secondary palate would be advantageous to animals with such a high

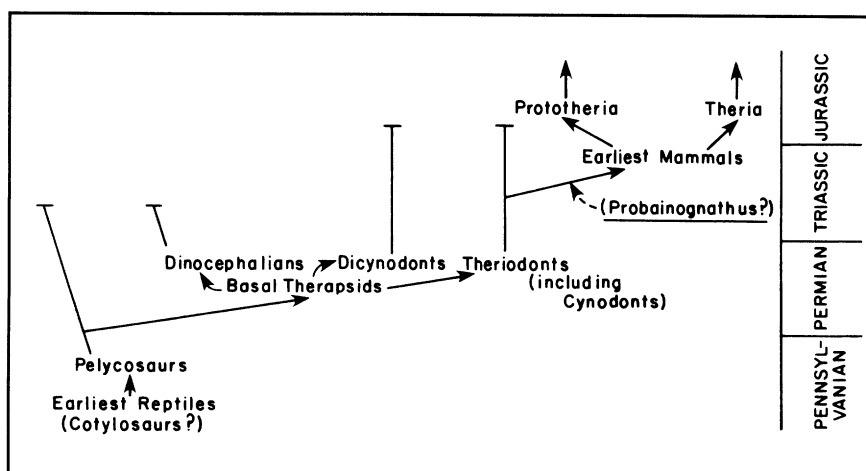
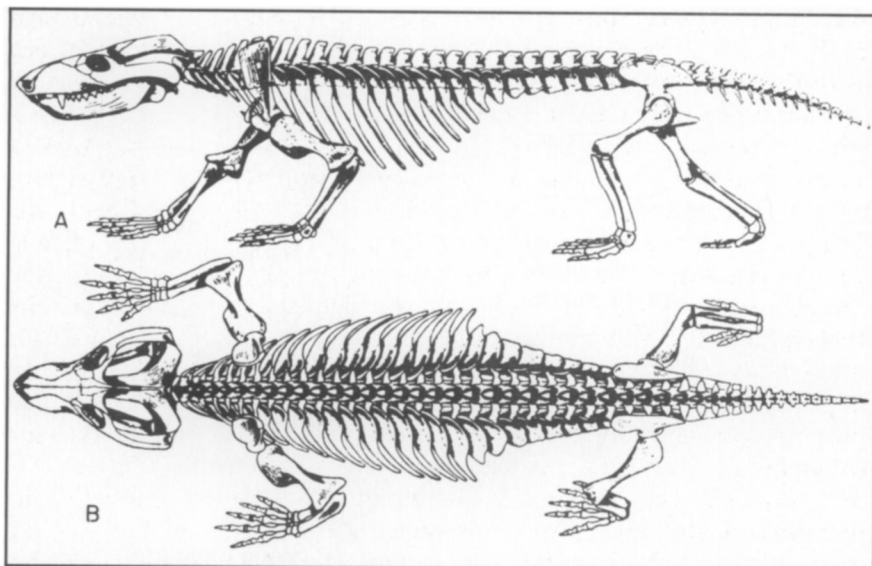


FIGURE 3. A dendrogram showing tentative relations of basal reptiles, mammal-like reptiles, and mammals. Redrawn and modified from Duvall, King, and Graves 1983. Originally redrawn and modified from J.A. Ruben 1981, with permission.

FIGURE 4. Lateral and dorsal views of a reconstructed skeleton of *Thrinaxodon liorhinus* showing differentiation of thoracic and lumbar vertebrae. Reproduced from Brink 1957, with permission.



rate of metabolism, in that breathing could be continued while food was being chewed. Ethmoturbinals, bony ridges within the nasal cavity, are present in cynodonts as well as mammals. Along with the secondary palate these would increase surface area within the nasal cavity and could have functioned to warm, moisturize, and cleanse air prior to its movement into the lungs, all useful when respiratory rates are elevated in association with increased metabolic rate.

Integration of the above information yields a framework with which to build a model of therapsid activity patterns. Especially in the advanced cynodonts, behavior patterns likely were approaching the mammalian grade. Predatory therapsids were probably actively foraging (as opposed to ambush style), quick and agile hunters (Geist 1972). Movement could be sustained rather than occurring in short bursts, and activity times would not be restricted to periods of daily or seasonal warmth. An elevated metabolism would have freed these animals from dependence on solar radiation, opening the door to the ecological possibilities of a nocturnal activity pattern. Such adaptations were probably important in preparing the therapsids for further evolutionary modification eventually producing true mammals.

Clearly, much can be inferred and supported by fossil and comparative evidence about physiological aspects of therapsids. Furthermore, behavioral characteristics associated with such physiological adaptations can be inferred through analogy to animals which exhibit similar adaptations. At first glance it would seem that little evidence to elucidate behavioral biology could be extracted from the fossil record. However, once inferential limits are placed on such hypothesis building, certain features of therapsid behavior can be explored reasonably. Such limits to inference can be narrowed, widened, or modified altogether, as new evidence comes to light.

Therapsid Chemical Communication

Communication is the cutting edge by which social behavior and interaction are mediated. For example, an ethologist may qualitatively and quantitatively describe action patterns observed when animals interact. Whether these behaviors are classified as courtship, agonistic, parental, or otherwise, will depend on what information is communicated, the type of interaction exhibited, and its selective function. Animals may convey such information via a number of signaling modes, such as visual, auditory, tactile, or chemical. We will focus on the chemical channel of communication, however, since much fossil and comparative evidence is available for use in paleoethological hypothesis building.

Tetrapods (i.e., amphibians, reptiles, birds, and mammals) generally possess two organs for odor detection which exhibit differing morphological, developmental, functional, and histological properties. Almost all tetrapods have functional nasal olfaction, a sense dependent upon stimulation of chemical receptors in the nasal mucosa. Kemp (1982) hypothesizes that this sense of smell was well developed in certain therapsids and was associated with increased surface area in the nasal cavity. Ethmoturbinals and elongation of the snout due to development of a secondary palate, as discussed above, would be associated with such a sensory adaptation.

Another structure for odor detection is the vomeronasal or Jacobson's organ. The vomeronasal organ (VNO) has been shown to be especially important to tetrapods for chemical signal detection in a variety of social contexts (Burghardt 1970; Doty 1976). Hence, evidence for the presence of a VNO in therapsids carries with it numerous implications for social chemical communication and interaction.

The VNO is present in either adult or embryonic

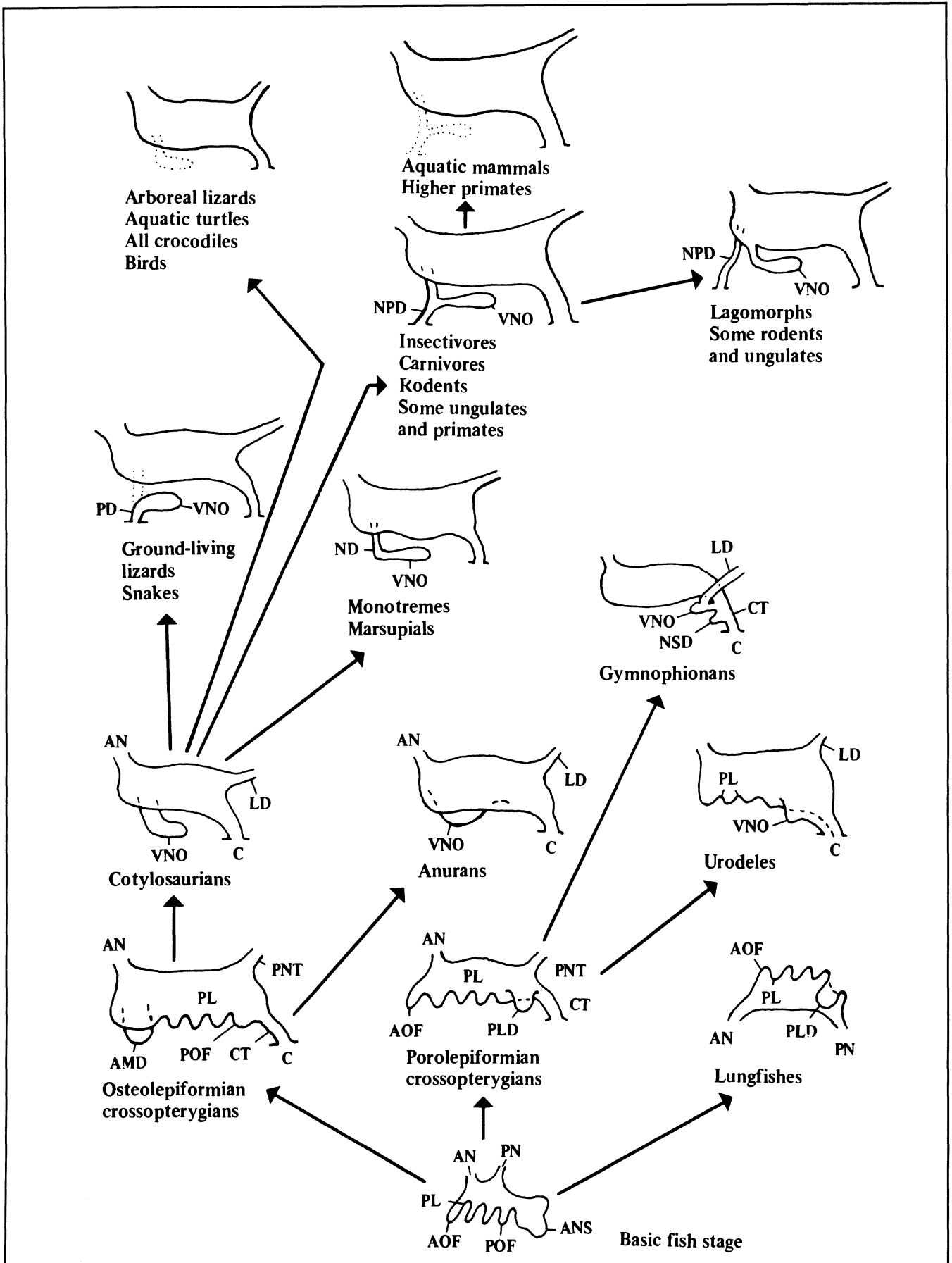


FIGURE 5. Diagram of the morphological evolution of nasal and vomeronasal structures. Redrawn and modified from Bertmar 1981, with permission. Explanation of abbreviations: vomeronasal organ (VNO), nasal ducts (ND), nasopalatine ducts (NPD), palatine ducts (PD). See Bertmar (1981) for further explanation.

stages of every tetrapod studied in this regard. For example, the VNO is absent in adults, although present in embryos, of crocodylians, birds, some bats, manatees, cetaceans, and some primates (including humans). All other tetrapods possess VNOs as adults. Such phylogenetic continuity suggests that the VNO is homologous in vertebrates, with some common ancestor(s) having possessed the trait (Bertmar 1981, Duvall 1983). Because mammals and reptiles both possess VNOs, given the homology of this structure, and since therapsids gave rise to mammals, it follows that therapsids also possessed VNOs. Yet beyond this, can evidence be obtained from the fossil record to support the inferential hypothesis that therapsids had VNOs? To answer this query we must employ the comparative method by examining the anatomy of this structure in extant and fossil tetrapods (the later to the extent possible).

The VNO is generally positioned above the mouth in the palatal region and may connect with the mouth, nasal cavity, or both in extant tetrapods (fig. 5). This oral and/or nasal connection is achieved through a palatine duct, a nasal duct, or a nasopalatine duct. Chemical cues are introduced into the VNO via such ducts. Hence, fossil evidence for these may be taken as likely evidence for VNOs in therapsids.

In mammals the nasopalatine ducts pass through incisive foramina as they travel from the nasal to the oral cavity. Incisive foramina are features of the secondary palate and so are preserved in many therapsids that have derived a secondary palate. Examination of virtually all cynodont skulls verifies that if a secondary palate is present, incisive foramina are identifiable (Duvall 1983; Duvall, King, and Graves 1983). The therapsid septomaxilla of the nasal cavity has been found to possess grooves that further suggest the presence of VNOs (Cluver 1971; King 1981; Duvall 1983).

Concurrent with fossil evidence for VNOs, what can be determined with respect to sources of chemical signals? Substances which possess chemical signal function are usually thought to have evolved from some more general metabolite (Weldon 1983), a process termed "chemical preadaptation" (Duvall 1983). Examples of such metabolites include urine, feces, sweat, and saliva. Presumably therapsids could produce saliva, and they surely produced digestive wastes. As noted earlier, therapsids may have possessed specialized snout glands as well as generalized skin glands. Therefore, it seems certain that therapsids had the ability to produce chemical signals.

Chemical Communication and the Evolution of Parental Care

Now assuming that therapsids had the ability to produce and detect chemical signals, how might these

have been used? Since some therapsids were approaching the mammalian physiological grade, as argued above, other features of their biology probably evolved concurrently. For example, chemical communication may have been useful in the evolution of a variety of social actions such as in spacing and mating, for instance, and perhaps even in parental care.

While approaching the mammalian grade, evolution of parental care was associated with increased metabolic rate, decreased body size, and reduced developmental state of young at birth (Hopson 1973). As young therapsids became more altricial (i.e., helpless at birth) and smaller in size, any advantage parents could provide to young might become critical. Perhaps a mother-young association after birth was first maintained in order for the young to make use of the mother's body heat (produced as a byproduct of elevated metabolism) for aid in thermoregulation. In such early stages of evolution of parental care young would still be precocial (i.e., able to take care of themselves at birth) and therefore, quite mobile. Hence, for whatever reason that parental care became more prominent in therapsids, it could not have evolved unless some mechanism existed by which the young could detect and orient toward the mother.

As stated earlier, the concept of uniformitarianism can be used to strengthen inferences concerning the behavior of ancient species. Intraspecific chemical signals, called pheromones, mediate aggregation in many extant reptiles and mammals (Shorey 1976; Duvall 1983; Duvall, King, and Graves 1983; Graves and Duvall 1983) and could have helped maintain therapsid mother-young proximity as well. For example, Mykytowycz and Ward (1971) have demonstrated a mother-young aggregation pheromone in wild rabbits. Similarly, neonatal rats (Hofer, Shair, and Singh 1976; MacFarlane *et al.*, 1983) and kittens (Kovach and Kling 1967) utilize olfactory cues to orient and attach to the mother's venter. Also, newborn marsupials migrate to the mother's pouch relying on olfaction (the only developed sensory system at birth) to do so (Griffiths, McIntosh, and Coles 1969; Griffiths 1978). Hunsaker and Shupe (1977) suggest that it is vomeronasal olfaction specifically which mediates such orientation by the young to the mother.

A possible source for aggregation signals that may have been used by therapsids is simple skin glands of the venter (where young likely would gather for most efficient thermoregulation). Detection of such exudates by therapsid young may have been mediated by VNO olfaction as are many intraspecific chemical signals by extant vertebrates. Furthermore, chemical cues are often delivered to ducts leading to the VNO by actions of the tongue and lips in extant tetrapods. Therapsids possessed tongues and are thought to have had muscular, dextrous lips as well (Geist 1972). Hence, it is likely that therapsids obtained chemical signal infor-

mation in a similar manner.

Lactation is a highly evolved parental investment mechanism that has been suggested to have arisen in therapsids (Brink 1957; Lillegraven 1979; Graves and Duvall 1983). Once young were licking an aggregation secretion from skin glands of their mother's venter, selective pressures could have caused modification of the secretion for nutritive purposes. But if an aggregation secretion had little nutritive value, as primitive skin gland secretions likely did, why would young have started to lick them from the mother's venter in the first place? It is likely that pheromones cemented the bond between therapsid young and their mothers initially, and secondarily facilitated the evolution of lactatory (milk feeding). Young therapsids may have introduced chemical aggregation signals into their VNOs via an oral or even a nasal route using tongue and lip movements. Hence, tongue and lip dexterity for more efficient acquisition of secretions could interact evolutionarily with nutritive and moisture providing qualities of the mother's secretions. Refinement of secretory glands and behavioral actions for obtaining their products could then proceed through a morphological-ethological coevolution. Such an evolutionary, "positive feedback loop" between behavior of young and maternal venter gland structure could have led to what we now observe as lactation and suckling in extant mammals.

Behavior may be the limit of what can be hypothesized in paleobiology, and indeed, only patterns which can be inferred from fossil morphology are accessible. Therefore, though behavioral actions themselves do not preserve in the fossil record (but see Seilacher 1967), certain possibilities can be hypothesized and evidence gathered to argue for or against them. Even so, parsimony should guide any inferential hypotheses built along these lines. Still, much more can be obtained from the fossil record than long lists of specimens, descriptions of each, and taxonomies. Knowledge of the biology of extant life forms, available fossil faunas, and the comparative method can be very helpful in piecing together substantive inference about the lives of ancient organisms. Well-preserved and rich fossil faunas, such as the therapsids, are, of course, helpful also.

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An Overture

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hand, such an exercise is fulfilling because, as biology teachers ourselves, we realize the importance of maintaining a close relationship to the basic literature, which undoubtedly strengthens the quality of presentations we develop and offer in the classroom. Ultimately, our hope is that biology teachers find this volume useful in this context.

Finally, we wish to thank Alan J. McCormack, Editor of *The American Biology Teacher*, for his friendship and inspiration in getting this project off the ground, and Diana W. Baber, ABT's Managing Editor for skilled assistance as well. Mrs. Mary David deserves thanks for typing the many manuscripts we directed her way.

David Duvall and William A. Gern
Guest Editors

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Working with test development and advisory committees your primary responsibility will be to develop and review tests and related materials in biological science, as well as other science fields, to comply with EETS guidelines and clients' specifications. You'll arrange and conduct meetings, help develop workshops, and occasionally address professional groups on topics relating to test development and measurement. You'll also assist other senior staff members in the coordination of program and project responsibility. Supervision of 1 or 2 support staff.

To qualify for this challenging position you'll need at least 4 years related experience (teaching especially desirable). A background in test statistics and measurement is preferred. Must hold a Master's degree in a field related to the biological sciences, or its equivalent in a combination of education and experience. Hands-on familiarity with computers or word processors is desirable.

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