

Conflict in the Hypaxial Musculo-Skeletal System: Documenting an Evolutionary Constraint¹

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SYNOPSIS. The identification and demonstration of an evolutionary constraint is suggested to be a four step process: 1) recognition of a possible mechanism of constraint, 2) formation of an historical scenario of the consequences of the constraint, 3) elucidation of the causal mechanism in the modern analog or model, and 4) phylogenetic correlation of the constraint with the proposed effect in extant lineages. Steps 1 and 2 represent the formation of two interdependent hypotheses, and steps 3 and 4 are tests of those hypotheses.

This approach is illustrated with an example from the musculo-skeletal system of tetrapod vertebrates. Consideration of the anatomy and mode of locomotion of lizards led to the hypothesis that they may not be able to run and breathe at the same time. Analysis of the pattern of ventilatory airflow of lizards supports this hypothesis. Tidal and minute volume increase above resting levels during slow walking (*i.e.*, speeds below 10% of maximum running speed), but decline rapidly at higher speeds. Furthermore, electromyographic monitoring of the hypaxial muscles indicates a clear conflict between locomotor and ventilatory functions. Key anatomical characters, suggested to be responsible for the conflict, can be traced back to the earliest tetrapods. The organization of the two extant lineages that do breathe while running (*i.e.*, birds and mammals) suggests that the evolution of an ability to breathe during locomotion required modifications of the ancestral configuration that separate locomotor and ventilatory function.

INTRODUCTION

During the past decade, constraints on evolutionary processes have received increased attention from biologists (Gould, 1980, 1989; Alberch, 1982; Wake, 1982; Maynard Smith *et al.*, 1985). Developmental mechanisms, properties of the materials of which organisms are constructed, ancestral phenotypes and conflicts between two or more functions are often as important, or more important, than natural selection in directing the course of evolution. Despite a great amount of discussion of this subject, a review of the literature shows that we still have relatively few examples in which the causal link between a postulated constraint and its effect on phenotypes has been established and the consequences of the constraint tested in a phylogenetic context.

The relative lack of explicit examples of constraint may be partially the result of the perspective of evolutionary biologists, which has until recently been heavily biased

towards the role of natural selection (Gould and Lewontin, 1979). However, it may also be the case that evolutionary constraints are often difficult to envision and once envisioned relatively difficult to quantify. During the past five years I have adopted an approach to investigate a mechanical conflict between two functions, which I believe may be generally applicable to the analysis of evolutionary constraints.

The first, and possibly most elusive, step toward evaluation of a constraint is its initial recognition. To date, the most compelling examples have been uncovered, not by intentional searches for constraints, but through serendipity. Recognition of a potential constraint typically results from three kinds of observations. First, one might realize that a group of organisms displays a limited range of the theoretically possible phenotypes. For example, the observation that there are no insects larger than a few grams in body mass leads one to consider physical limitations on size. Second, one might observe a pattern that appeared to be nonadaptive. An example of this might be the weak bone tissue of juvenile birds and mammals (Carrier and Leon, 1990). Weak skeletal tissue is likely a liability in animals that must actively locomote, but may be a consequence of the very rapid growth that

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birds and mammals undergo. Third, the actual mechanism of constraint might come to the attention of an investigator before any consideration of its phenotypic consequences. One might realize, for example, that the physical properties of exoskeletons place limits on the maximum size of organisms with this organization (Currey, 1967).

The second step is the formation of an historical hypothesis, based on the proposed constraint, to explain a pattern of observed phenotypes. For example, the mechanical coupling of lung ventilation and feeding in salamanders has been suggested to constrain specialization in prey capture (Roth and Wake, 1985). Typically in salamanders, the mouth and hyobranchial systems are critical to both lung ventilation and feeding. Those salamander species with highly specialized tongues are lungless. The scenario of Wilder and Dunn (1920) suggests that to decrease buoyancy in the swiftly moving water of mountain streams some species experienced selection for reduced lungs. Less emphasis on lung ventilation opened the possibility for specialization in prey capture and elaboration of tongue structure and function.

The third step involves testing the hypothesized source of the constraint in a model. This is critical to the construction of a convincing argument, but is often neglected. The proposed cause of a constraint often can be tested in a modern analog; that is, in a species that displays the features suggested to be responsible for the constraint. If an appropriate analog does not exist, the constraint can be modeled through simulation. This may take the form of an actual physical model or it might require computer simulation.

The fourth step involves phylogenetic correlation of the constraint with its proposed effects in modern lineages (Lauder, 1981, 1982). This is a test of the historical hypothesis. There are two kinds of potentially testable predictions. Modern species that have retained characters suggested to be responsible for a constraint are expected to display the associated phenotype or range of phenotypes. In contrast, species that have circumvented the constraint are expected to have apomorphies that make this possible.

I did not set out initially with the intention of following a particular approach to the analysis of evolutionary constraints. Instead, the nature of the problem and the skepticism of colleagues led me to adopt one. The individual steps of this approach are not new to evolutionary biology. Indeed, Lauder and Liem (1989) recently proposed a similar approach. However, the four steps do seem to represent the basic elements required for the identification and demonstration of a constraint. Analysis will rarely proceed in the sequence outlined above. Indeed, analysis is an interactive process, in which information gained at one stage facilitates progress at other stages. In this paper I illustrate this approach with an attempt to identify a possible constraint on sustained locomotion in tetrapods. My intent is to illustrate the steps involved and to provide an example of the kinds of questions we can hope to answer.

PROPOSED CONSTRAINT

In 1984, while thinking about how lizards breathe, I began to wonder if they might be unable to run and breathe at the same time. The argument was as follows: 1) Lizards are aspiration breathers; that is, they breathe by actively moving their ribs to change the volume of the thoracic cavity. 2) All of the hypaxial muscles and most of the epaxial muscles of lizards attach directly or indirectly to their ribs. 3) Some of these trunk muscles are likely to be used during locomotion to bend the body from side to side or to stabilize the trunk against the vertical and horizontal components of the propulsive force. 4) The locomotor action of these muscles will likely interfere with the ventilatory action of the muscles responsible for breathing. This line of reasoning suggested a simple conflict between two functions that are presumably produced by the same musculo-skeletal complex.

HISTORICAL HYPOTHESIS

The most intriguing aspect of this hypothesis is its historical implications. Information from the fossil record suggests that the earliest tetrapods were similar to modern lizards in certain key aspects of their locomotor and ventilatory anatomy (Carrier,

1987a). In animals such as *Ichthyostega* and *Eryops*, the presence of large complete ribs with latero-posterior orientations suggests that early tetrapods were aspiration breathers (Gans, 1970). The sprawling posture and aquatic heritage of the early tetrapods suggest that lateral bending of the trunk increased stride length of propulsive force. In addition, their dorsal vertebrae had little or no development of transverse processes (Romer, 1956). Thus, as in lizards, the hypaxial muscles and the bulk of the epaxial muscles must have attached to the ribs. If it were true that the anatomical configuration of lizards makes it impossible for them to run and breathe at the same time, then early tetrapods would likely have had the same restriction.

If the early tetrapods could not breathe during locomotor activity, they would have been unable to sustain continuous locomotion. Disruption of ventilation would have forced a reliance on anaerobic metabolism. Anaerobic metabolism can be sustained only for brief periods; tens of seconds to a few minutes, depending on the intensity of the activity. Added to this respiratory limitation would have been the increased cost of movement on land. The energetic cost of transport (*i.e.*, cost per unit distance) in modern walkers is, on average, ten times greater than that of swimming fishes (Tucker, 1975). Consequently, early terrestrial locomotion would likely have been restricted to brief episodes of progression, interspersed with recovery periods during which the dominant activity was vigorous breathing.

As tetrapod communities became more complex, predator-prey interactions would have selected for improved locomotor performance and more effective mechanisms of prey capture and escape. Several tetrapod groups appear to have retained the ancestral constraint on simultaneous running and breathing and have remained relatively immobile. For example, turtles and salamanders are poorly equipped to run from predators, and instead have specialized in mechanical or chemical systems of defense. Lepidosaurs also appear to have retained the constraint, but have specialized in burst locomotion, dependent on anaerobic metabolism. In contrast, birds and mam-

mals can sustain vigorous locomotion. Both groups have derived features that appear to decouple locomotor and ventilatory functions. Derived features such as diaphragmatic muscles, large transverse processes on the dorsal vertebrae, bounding and bipedal gaits, and upright posture may make simultaneous running and breathing possible.

MODERN ANALOG

At this stage in the investigation, there were two related hypotheses: one suggested a mechanical conflict between two musculoskeletal functions, and a second hypothesis proposed historical implications of this conflict. To test the hypothesis that animals with sprawling posture and small transverse processes could not run and breathe at the same time, I returned to the group of animals from which the idea had arisen.

Running and breathing in lizards

As a first step in elucidating the nature of the proposed constraint, I measured lung ventilation in four species of lizards as they walked and ran on a solid track (Carrier, 1987b). Demonstrations of breathing during locomotion would have refuted the hypothesis.

The four species tested did increase ventilation above resting levels while walking slowly. However, in all four species, tidal volume decreased dramatically as speed increased above the maximum aerobic speeds (Fig. 1). (The maximum aerobic speeds of these lizards are actually quite slow, representing only 5 to 10% of maximum running speed.) Minute ventilation (tidal volume \times breath frequency) also increased above resting levels at the very slow speeds that these animals can sustain, but dropped off sharply at higher speeds (Fig. 1).

This trend toward reduced ventilation is further enhanced when ventilation during locomotion is compared to ventilation that occurs immediately after the cessation of locomotor activity (*i.e.*, recovery ventilation; Fig. 1). The rate of metabolism immediately following activity should more closely approximate activity metabolism than does resting metabolism. Consequently, ventilation during recovery is the

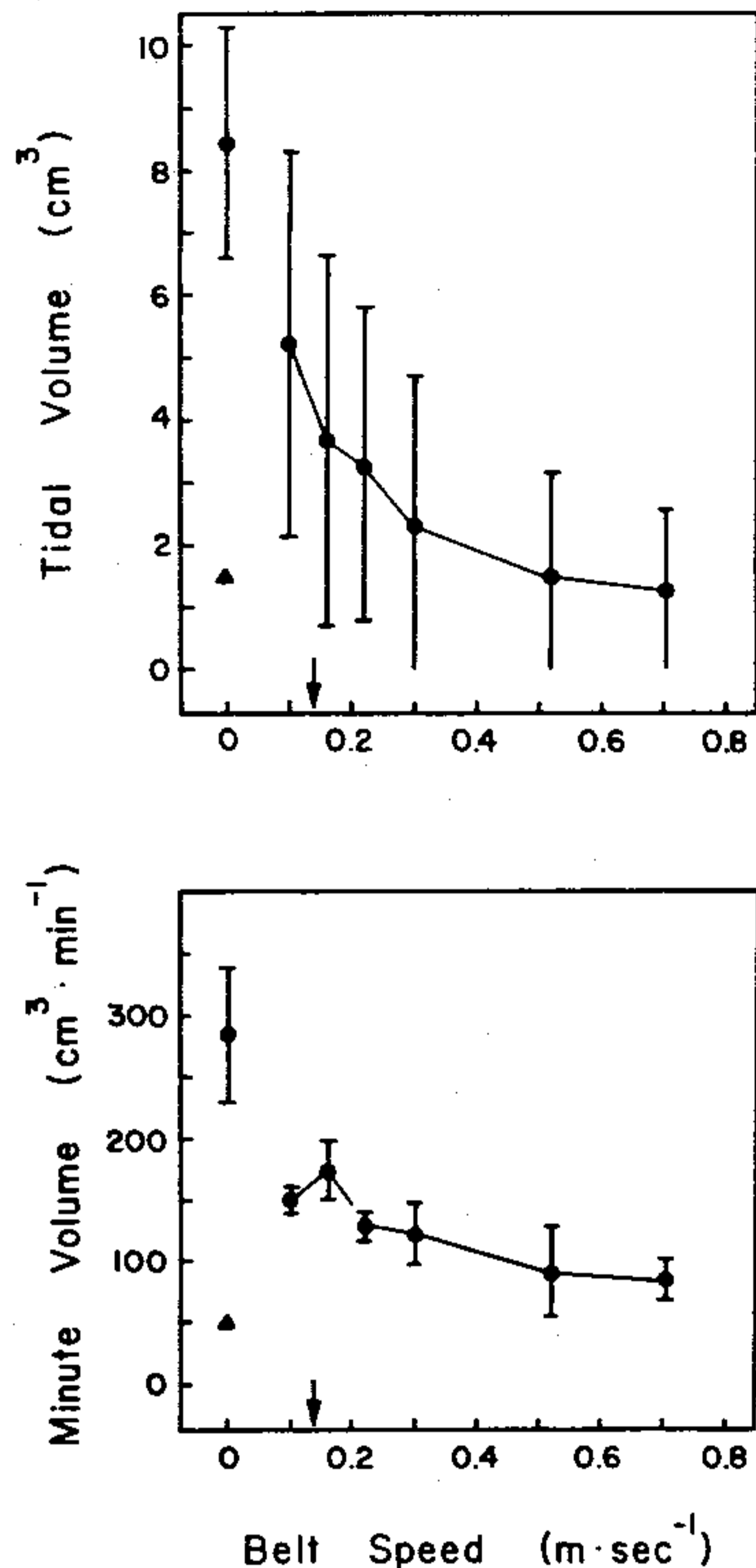


FIG. 1. Means and standard deviations of tidal and minute volume plotted against belt speed for a single individual of *Iguana iguana* walking on a treadmill. Means were calculated from all breaths that occurred during the test period, including the larger breaths that occurred during frequent pauses in locomotor activity. The dot and triangle at zero velocity represent recovery and pre-run ventilation respectively. The arrow on the ordinate indicates the reported maximum aerobic speed (Gleeson *et al.*, 1980). Modified from Carrier, 1987b.

most appropriate comparison for a test of the hypothesis that locomotor movements limit breathing. Compared to breathing during recovery, tidal volume was greatly reduced even during slow walking (Fig. 1). Because of an increase in breathing frequency during locomotion, minute volume did not decrease as rapidly as tidal volume. However, minute ventilation during locomotor activity was less than that recorded

during recovery at all speeds greater than the maximum aerobic speeds (Fig. 1).

Several findings suggested that the reduced ventilation was a consequence of the proposed constraint. First, there was a strong temporal correlation between locomotor activity and the disruption of lung ventilation. Second, tidal volume was inversely related to stride frequency. The largest breaths that occurred in a running sequence corresponded to strides of relatively long duration or to brief pauses in the locomotor movements (Fig. 2). These consistent temporal correlations seemed too rapid to invoke anything but a mechanical coupling. Third, minute volume was inversely related to running speed, suggesting that breathing became more difficult as the locomotor effort increased.

These observations support the idea that a constraint on simultaneous running and breathing does exist in lizards. However, demonstration of such a constraint requires a knowledge of the activity of the hypaxial muscles in both lung ventilation and locomotion. This information was not available for lizards or for any other tetrapod. Consequently, I studied the activity of the hypaxial muscles of the green iguana, *Iguana iguana*.

Ventilatory activity of the hypaxial muscles

Four hypaxial muscles produce lung ventilation in green iguanas (Carrier, 1989). The anterior segments of the intercostal muscles are the only hypaxial muscles that display electromyographic activity during inspiration. Expiration is associated with electromyographic activity in the transversalis and retrahentes costarum. The external oblique, internal oblique, rectus abdominus, pubic abdominus and posterior segments of the two intercostal muscles are not active during breathing. Thus, the majority of the hypaxial musculature is not involved in lung ventilation.

Locomotor activity of the hypaxial muscles

At the initiation of this investigation there were three competing hypotheses concerning the role that the hypaxial muscles might

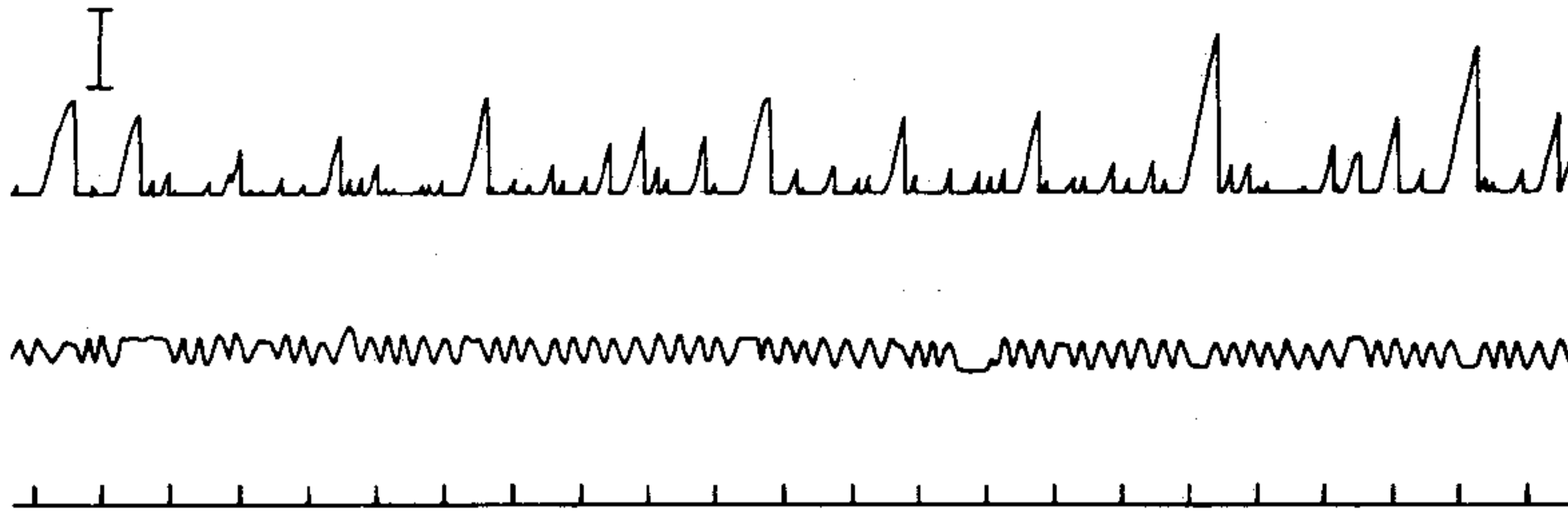


FIG. 2. Sample recording of breathing during treadmill locomotion of an individual of *Varanus exanthematicus*. The upper trace is a measure of inspiratory tidal volume. The vertical scale after the first breath equals 10 cm^3 . The second trace records lateral bending of the trunk. Each wave cycle of the trace equals one locomotor cycle. The lizard was walking at approximately its maximum aerobic speed. Notice that the larger breaths correspond to brief pauses in the locomotor movements. Modified from Carrier, 1987b.

play in the locomotion of limbed tetrapods (Carrier, 1990). First, these muscles might effect the lateral bending of the trunk, which is so prominent in lizard locomotion. If the hypaxial muscles were primarily responsible for this, muscles with a longitudinal component to their fiber orientation would be expected to be active on the side of the trunk to which the trunk was flexing (*i.e.*, contralateral to hind support) but not on the other side. Second, the hypaxial muscles might act to stabilize the trunk against the horizontal and vertical components of the propulsive force (Fig. 3). To resist the horizontal component of the propulsive force, muscles with a longitudinal orientation would have to be active contralateral to hind support. The vertical component induces long-axis torsion in the trunk. Resistance to torsion requires radially directed tensile elements. Consequently, muscles with fibers oriented obliquely in the caudoventral direction would have to be active contralateral to hind support, whereas muscles with obliquely oriented fibers in the caudodorsal direction would have to be active ipsilateral to hind support (Fig. 3). Third, the hypaxial muscles might not be involved in locomotion. Instead, lateral bending of the trunk and stabilization of the trunk might be produced solely by the epaxial muscles. If this were true, little or no activity would be recorded from the hypaxial muscles during locomotion.

Locomotor activity of the hypaxial muscles of green iguanas supports the hypothesis that they stabilize the trunk against hor-

izontal and torsional forces on the axial skeleton (Fig. 4). The most dramatic illustration of this is the activity of the internal intercostal muscle (Fig. 5). This muscle has two regions of different fiber orientation. The lateral portion, which is oriented in the caudodorsal direction, is active ipsilateral to hind support as would be expected if it were resisting torsion. In contrast, the ventral portion of this muscle has a longitudinal orientation and is active contralateral to hind support, as would be expected if it were acting to stabilize the trunk against the horizontal component of the propulsive force. Thus, the hypaxial muscles of green iguanas do appear to stabilize the trunk against the horizontal and vertical components of the propulsive force. Whether this pattern will hold for other tetrapods remains to be determined. However, these findings suggest that the demands of locomotion may provide an explanation of the basic organization of the hypaxial musculature in limbed tetrapods.

Constraint on simultaneous running and breathing

The locomotor activity of the hypaxial muscles of iguanas does conflict with breathing (Fig. 6). To effect inspiration, the two intercostal muscles on one side of the body contract synchronously with the two intercostal muscles on the other side of the trunk. Similarly, the two expiratory muscles are activated bilaterally. However, during locomotion these four muscles, as well as the other hypaxial muscles, are activated first on one side of the trunk and then on

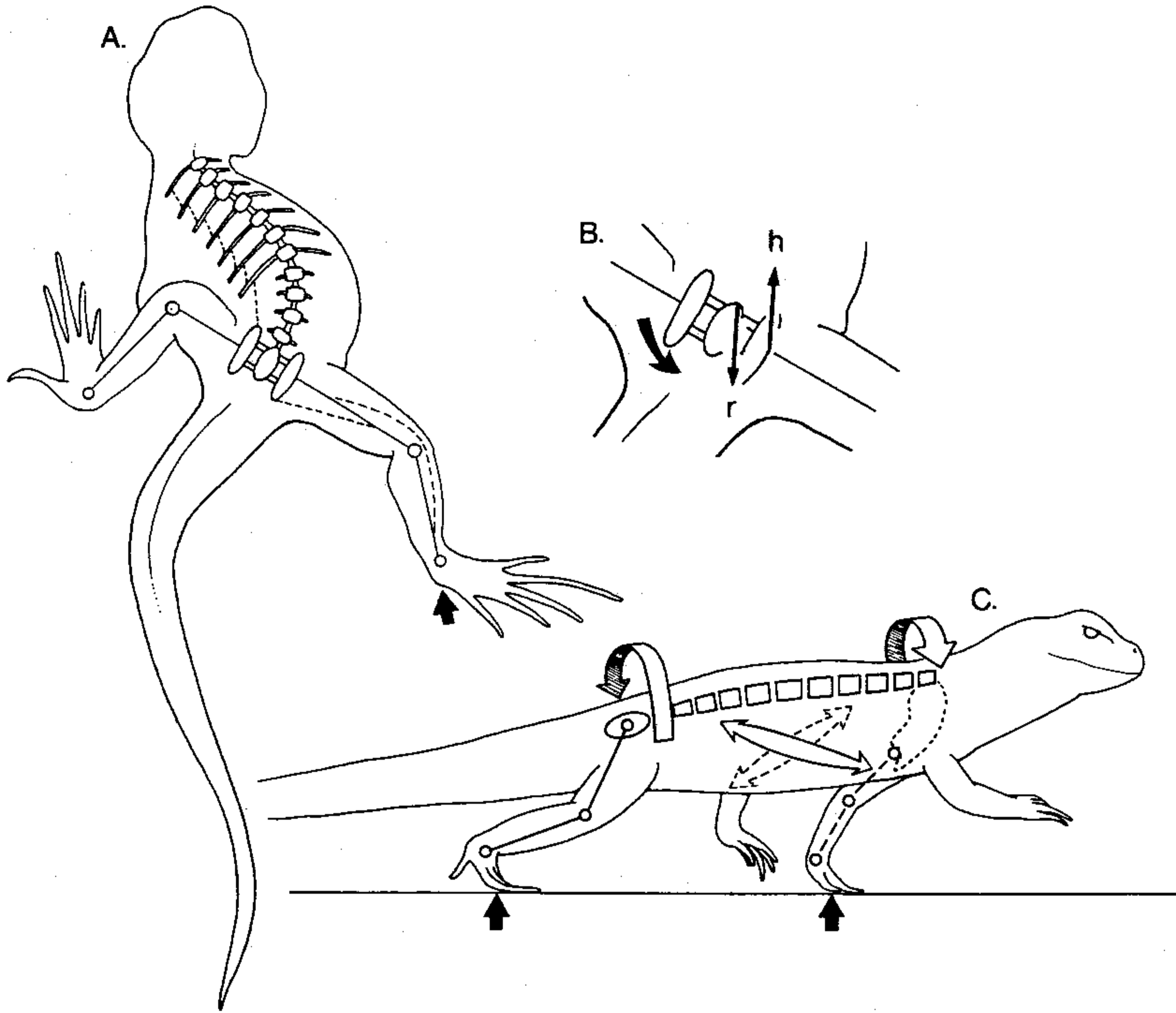


FIG. 3. Schematic representation of the moments imposed on a trunk during locomotion. A) The lizard is exerting a force against the ground with the right hind leg. The inertial mass of the animal resists the propulsive force with a reaction force that acts rearward through the centra of the vertebrae. B) This reaction force (r) and the horizontal component of the propulsive force (h) at the hip joint, produce a couple that tends to rotate the pelvis. In this case, the couple causes the pelvis to rotate counter clockwise. To stabilize the pelvis against these forces, muscles on the left side of the trunk with a longitudinal orientation (dashed lines in A) must be active. C) The lizard is supported by diagonal limbs, which impose long-axis torsion on the axial musculo-skeletal system. To stabilize the trunk against long axis torsion, hypaxial muscles with oblique orientations are necessary. The solid arrow indicates the orientation of muscles that must be active on the side of the body ipsilateral to hind support. The dashed arrow indicates the orientation of muscles that must be active on the side of the body contralateral to hind support. From Carrier, 1990.

the other. A single hypaxial muscle on one side of the body acts synergistically with its counterpart on the other side to produce ventilation, but acts antagonistically to its counterpart to effect locomotion. Thus, the reduced ventilation observed in running lizards does result from a conflict between the two functions.

The same aspects of body organization that lead to a conflict between running and breathing in lizards appear to have been present in the earliest tetrapods. Thus, our

earliest terrestrial ancestors were probably unable to breathe during locomotor activity, and would therefore, have been unable to sustain locomotion more rapid than intermittent slow walking.

CORRELATION IN EXTANT LINEAGES

There are two kinds of predictions that can be used to test an historical hypothesis of a constraint. First, members of a lineage that have ancestral characters suggested to be responsible for a constraint should dis-

play the associated phenotype. In the example discussed here, species that have retained the ancestral configuration of sprawling posture and small transverse processes are predicted to be unable to run and breathe at the same time. Second, members of the same lineage that do not display the phenotype associated with the constraint should have derived characters that provide a means of circumventing the constraint. Thus, groups that can breathe during locomotion are predicted to have derived characters that separate locomotor and ventilatory functions. These two tests represent opposite sides of the same coin. However, either could potentially falsify the hypothesis.

We have information on ventilation during locomotion in three groups of extant tetrapods: mammals, lizards and birds. Although both birds (Funk *et al.*, 1989) and mammals (Bramble and Carrier, 1983; Hornicke *et al.*, 1983) breathe during high speed locomotion, and the ventilation of lizards decreases as speed increases above that of a slow walk (Carrier, 1987b). Each of these three groups represents an independent test of the hypothesis, and each provides support for the hypothesis (Fig. 7). Lizards have retained the ancestral characters that are suggested to limit simultaneous running and breathing. Thus, the observation that their ventilation is greatly reduced during moderate and rapid locomotion supports the suggestion that early tetrapods were unable to do both simultaneously. Because mammals and birds do breathe during locomotion, the hypothesis predicts that they will possess derived characters that separate, or decouple, locomotor and ventilatory functions. Early members of the two lineages that gave rise to birds and mammals had sprawling posture and small transverse processes (Romer, 1956). During the late Permian and early Triassic periods, members of both lineages independently developed suites of characters that appear to separate locomotor and ventilatory functions (Carrier, 1987a).

The means by which the lineages of birds and mammals circumvented the constraint are convergent to a large extent. Both groups developed large transverse processes, which transfer the locomotor forces produced by

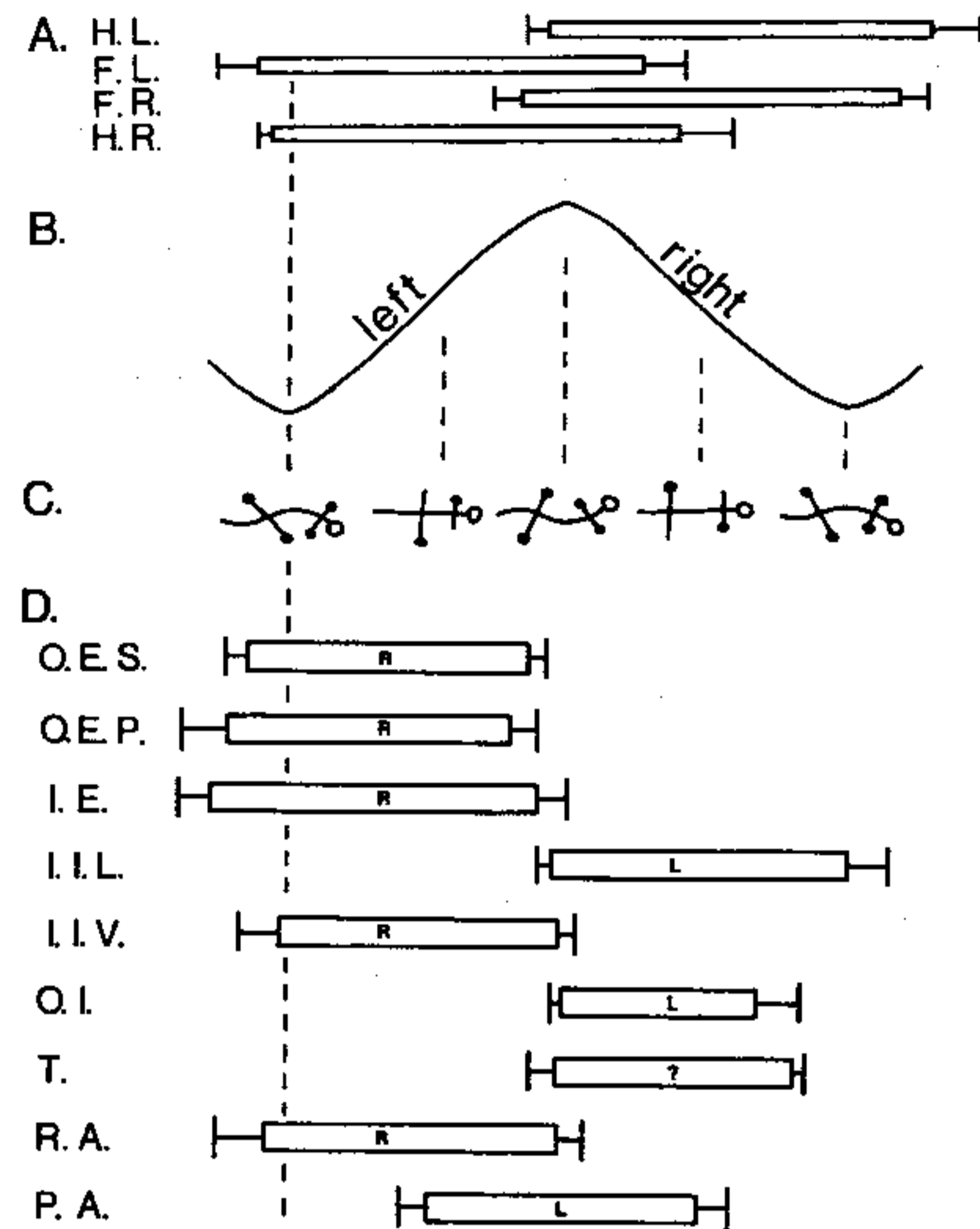


FIG. 4. Onset and offset times of the hypaxial muscles on the left side of the body during walking in *Iguana iguana*. A) Summary of foot support relative to trunk bending. B) Trace of lateral bending of trunk. The trunk is bending to the left when the trace is deflected upwards. C) Schematic representation of trunk bending and foot support. Solid circles represent feet in contact with the ground. D) Means and standard deviations of the activity of the hypaxial muscles relative to trunk bending during walking. The R or L in each activity box represents the phase of hind limb support in which activity was predicted to occur, based on the hypothesis that the hypaxial muscles act to stabilize the trunk against the horizontal and vertical components of the propulsive force. Seven of the eight muscles, for which predictions could be made, match the predictions. I.E., intercostales externi; I.I.L., intercostales interni lateralis; I.I.V., intercostales interni ventralis; O.E.P., obliquus externus profundus; O.E.S., obliquus externus superficialis; O.I., obliquus internus; P.A., pubic abdominis; R.A., rectus abdominis; T., transversalis. Modified from Carrier, 1990.

the epaxial muscles from the ribs to the vertebral column. Both groups developed upright posture (*i.e.*, limbs positioned under the body), which reduces the lateral and torsional components of the propulsive force. Both groups lengthened the pelvis longitudinally, which may also stabilize the trunk during locomotion. Additionally the lineage that gave rise to mammals evolved a diaphragmatic muscle and bounding (asym-

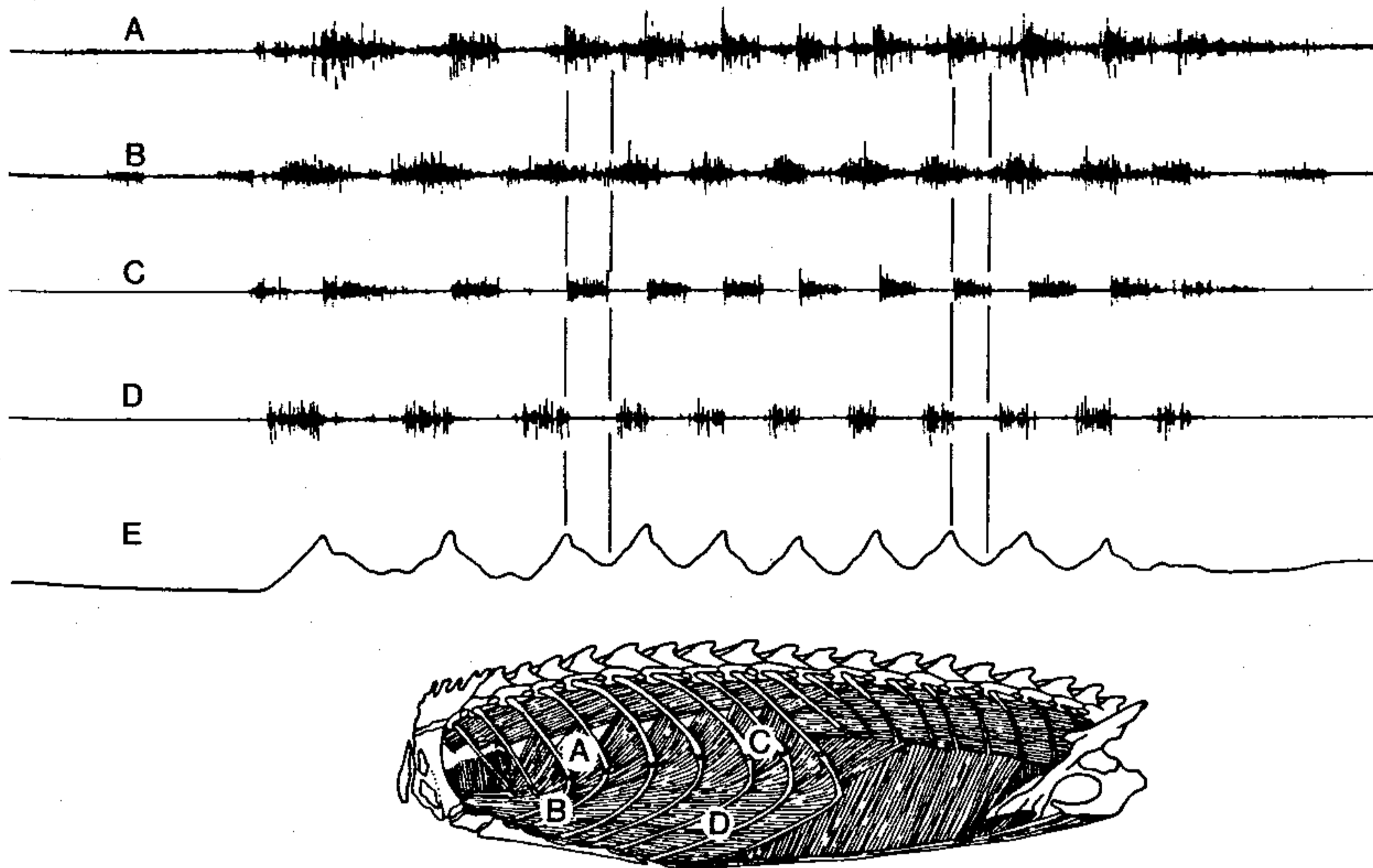


FIG. 5. Electromyographic recordings of two separate patterns of activity in the internal intercostal muscle of *Iguana iguana* during walking. The recordings are from the left side of the trunk, and the site for each electrode (A–D) is marked on the diagram of the muscle. Anterior is to the left. Trace (E) is the recording of trunk bending. An upward deflection of the trace indicates bending of the trunk to the left. The lateral portion of the left internal intercostal (sites A and C) is active ipsilateral to hind support, as the trunk bends to the right, and the ventral portion (sites B and D) is active contralateral to hind support, as the trunk bends to the left. From Carrier, 1990.

metrical) gaits, and the lineage that gave rise to birds adopted bipedal locomotion. All of these apomorphies may be argued to facilitate lung ventilation during locomotion.

CONCLUSION

There are three conclusions that can be drawn from this analysis of the locomotor-ventilatory system of tetrapods. First, the evidence clearly indicates that there is a mechanical constraint on simultaneous running and breathing in modern lizards. Second, the fossil record and the configuration of the extant tetrapods suggest that the earliest tetrapods were also not able to run and breathe at the same time. Third, tetrapod lineages that did evolve a capacity for sustained locomotion (e.g., birds and mammals) had to change from the ancestral configuration in ways that circumvented this initial constraint.

The analytical approach outlined here is applicable to many types of constraint. In cases where a constraint is suspected to be due to functional or structural aspects of the organism an approach that attempts to elucidate the causal mechanism should be applied. Additionally, every effort should be made to evaluate the hypothesis in a phylogenetic context as has been advocated by Lauder (1981, 1982) and more recently by Lauder and Liem (1989). Although determination of the causal mechanism and testing in a phylogenetic context will not be easily accomplished or even possible in many cases, both are required for a compelling argument.

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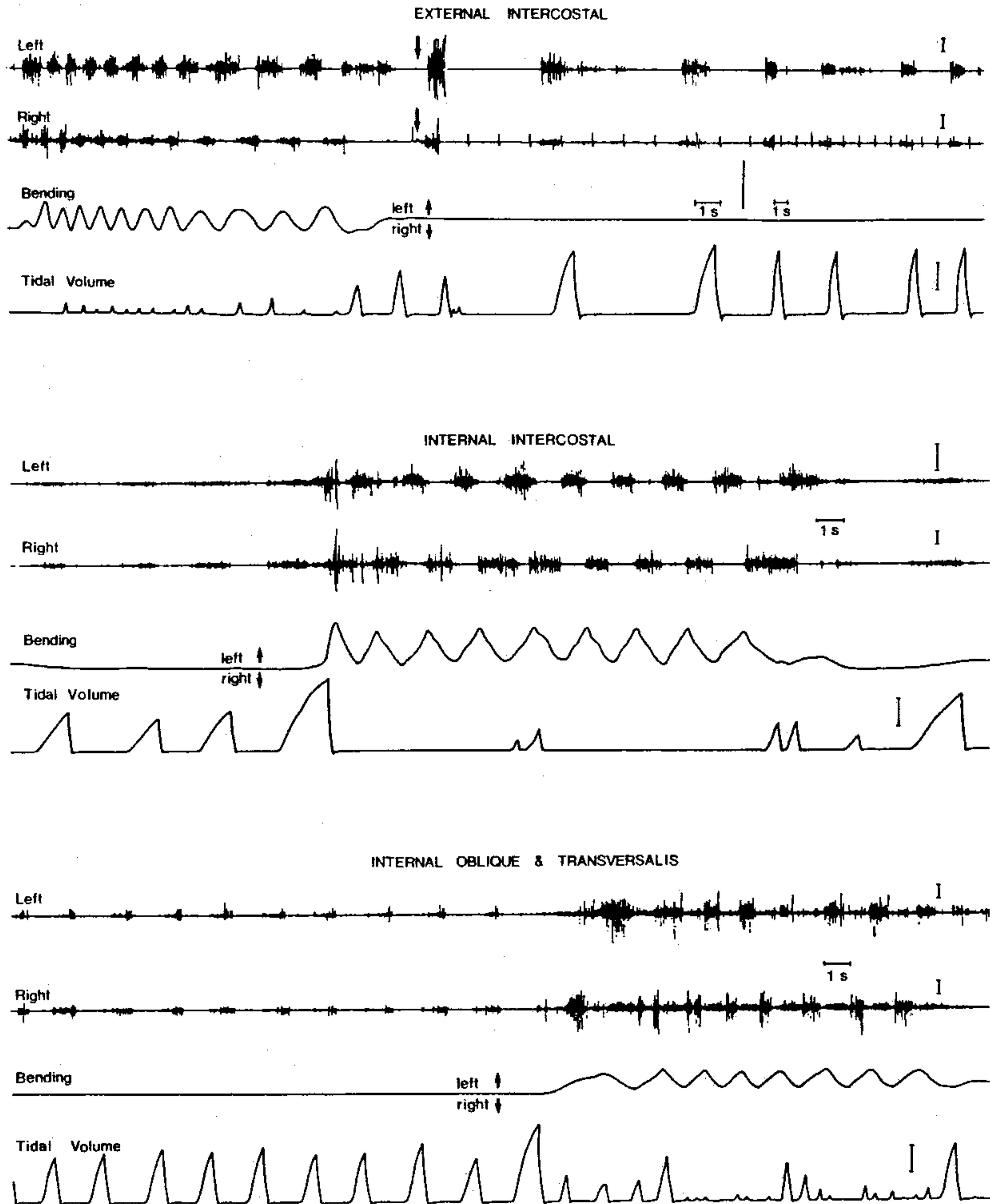


FIG. 6. Comparison of locomotor and ventilatory activity of three ventilatory muscles of *Iguana iguana*. In each recording, the top two traces are electromyographic signals of the muscles from the left and right sides of the trunk. For the external and internal intercostal muscles the electrodes were placed between sternal ribs 1 and 2. For the transversalis muscle the electrodes were placed in the region of sternal rib 5, and recorded activity from both the internal oblique and transversalis muscles. The vertical bar at the end of each trace represents 50 μ V. The arrows pointing to the traces of the external intercostal represent the time at which the gain on the recording amplifiers was increased 5-fold, to enhance visualization of ventilatory activity. In each recording, the third trace represents a recording of movements of the trunk during walking. The trunk is bending to the left as the trace is displaced upwards. Each wave cycle represents one locomotor cycle. The animal is stationary when the trace is flat. In each recording, the fourth trace represents a recording of inspiratory tidal volume. The vertical bar represents 5 cm^3 .

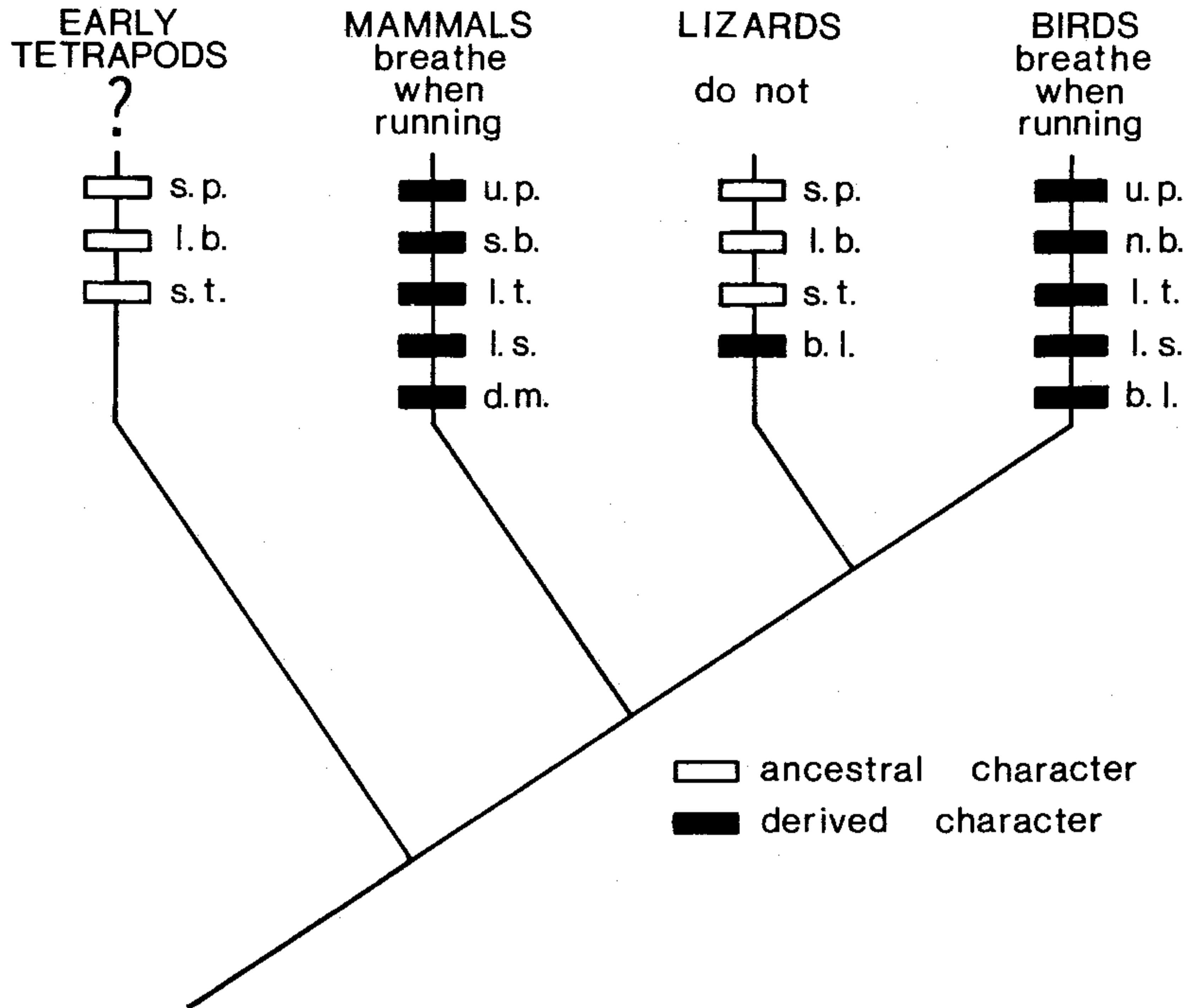


FIG. 7. Phylogenetic distribution of characters associated with the coupling of locomotor and ventilatory functions in tetrapods. Only those extant groups for which we have information on ventilation during locomotion are included. Open bars represent ancestral characters that are suggested to result in a conflict between locomotion and ventilation. These characters have been retained in lizards, but have been modified in birds and mammals. Solid bars represent derived characters that are suggested to separate locomotor and ventilatory function. We do not know if early tetrapods could breathe during locomotion. However, the distribution of characters suggests that they could not. b.l., bipedal locomotion; d.m., diaphragmatic muscle; l.b., lateral bending of the trunk during locomotion; l.s., lateral stability of trunk; l.t., large transverse processes on vertebrae; n.b., no bending of trunk during locomotion; s.b., sagittal bending of trunk during locomotion; s.p., sprawling posture; s.t., small transverse processes on dorsal vertebrae; u.p., upright limb posture.

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REFERENCES

- Alberch, P. 1982. Developmental constraints in evolutionary processes. In J. T. Bonner (ed.), *Evolution and development*, pp. 313-332. Springer-Verlag, New York.
- Bramble, D. M. and D. R. Carrier. 1983. Running and breathing in mammals. *Science* 219:251-256.
- Carrier, D. R. 1987a. The evolution of locomotor stamina in tetrapods: Circumventing a mechanical constraint. *Paleobiology* 13:326-341.
- Carrier, D. R. 1987b. Lung ventilation during walking and running in four species of lizards. *Exp. Biol.* 47:33-42.
- Carrier, D. R. 1989. Ventilatory action of the hypaxial muscles of the lizard *Iguana iguana*: A function of slow muscle. *J. Exp. Biol.* 143:435-457.
- Carrier, D. R. 1990. Activity of the hypaxial muscles

- during walking in the lizard *Iguana iguana*. *J. Exp. Biol.* 152:453-470.
- Carrier, D. R. and L. R. Leon. 1990. Skeletal growth and function in the California Gull. *J. Zool. London* 222:375-389.
- Currey, J. D. 1967. The failure of exoskeletons and endoskeletons. *J. Morphol.* 123:1-16.
- Funk, G. D., I. J. Valenzuela, G. N. Sholomenko, J. D. Steeves, and W. K. Milsom. 1989. Effects of changes in locomotor intensity, hypoxia and hypercapnia on locomotor-respiratory synchrony during walking/running in Canada geese. *J. Exp. Biol.* 147:343-360.
- Gans, C. 1970. Respiration in early tetrapods—the frog is a red herring. *Evolution* 24:1177-1184.
- Gleeson, T. T., G. S. Mitchell, and A. F. Bennett. 1980. Cardiovascular response to graded activity in the lizards *Varanus* and *Iguana*. *Am. J. Physiol.* 239: R174-179.
- Gould, S. J. 1980. The evolutionary biology of constraint. *Daedalus* 109:39-52.
- Gould, S. J. 1989. A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. *Evolution* 43:516-539.
- Gould, S. J. and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proc. Roy. Soc. London B* 205:581-598.
- Hornicke, H., R. M. Meixner, and U. Pollmann. 1983. Respiration in exercising horses. In D. H. Snow, S. G. B. Persson, and R. J. Rose (eds.), *Equine exercise physiology*, pp. 7-16. Burlington Press, Cambridge.
- Lauder, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. *Paleobiology* 7:430-442.
- Lauder, G. V. 1982. Historical biology and the problem of design. *J. Theor. Biol.* 97:57-67.
- Lauder, G. V. and K. F. Liem. 1989. The role of historical factors in the evolution of complex organismal functions. In D. B. Wake and G. Roth (eds.), *Complex organismal functions: integration and evolution in vertebrates*, pp. 63-78. John Wiley & Sons Ltd., New York.
- Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. Developmental constraints and evolution. *Quart. Rev. Biol.* 60:265-287.
- Romer, A. S. 1956. *Osteology of the reptiles*. University of Chicago Press, Chicago.
- Roth, G. and D. B. Wake. 1985. Trends in the functional morphology and sensorimotor control of feeding behavior in salamanders: An Example of the role of internal dynamics in evolution. *Acta Biotheor.* 34:175-192.
- Tucker, V. A. 1975. The energetic cost of moving about. *Am. Sci.* 63:413-419.
- Wake, D. B. 1982. Functional and developmental constraints and opportunities in the evolution of feeding systems and urodeles. In D. Mossakowski and G. Roth (eds.), *Environmental adaptation and evolution*, pp. 51-66. G. Fisher, New York.
- Wilder, I. W. and E. R. Dunn. 1920. The correlation of lunglessness in salamanders with a mountain brook habitat. *Copeia* 84:63-68.