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The opisthotonic posture of vertebrate skeletons: postmortem contraction or death throes?

Cynthia Marshall Faux and Kevin Padian

Abstract.—An extreme, dorsally hyperextended posture of the spine (opisthotonus), characterized by the skull and neck recurved over the back, and with strong extension of the tail, is observed in many well-preserved, articulated amniote skeletons (birds and other dinosaurs, pterosaurs, and at least placental mammals). Postmortem water transport may explain some cases of spinal curvature in fossil tetrapods, but we show how these can be distinguished from causes of the opisthotonic posture, which is a biotic syndrome. Traditional biotic explanations nearly all involve postmortem causes, and have included rigor mortis, desiccation, and contraction of tendons and ligaments. However, examination of the process of rigor mortis and experimental observations of drying and salinity in carcasses of extant animals show that these explanations of the ''dead bird'' (opisthotonic) posture account for few or no cases. Differential contraction of cervical ligaments after death also does not produce the opisthotonic posture. It is not postmortem contraction but perimortem muscle spasms resulting from various afflictions of the central nervous system that cause these extreme postures. That is, the opisthotonic posture is the result of ''death throes,'' not postmortem processes, and individuals so afflicted assumed the posture before death, not afterward. The clinical literature has long recognized that such afflicted individuals perish from asphyxiation, lack of nourishment or essential nutrients, environmental toxins, or viral infections, among other causes. Accepting the actual causes of the opisthotonic posture as perimortem and not postmortem provides insights into the causes of death of fossilized specimens, and also revises interpretations of paleoenvironmental conditions of many fossil deposits. The opisthotonic posture tells us more about the circumstances surrounding death than about what happened after death. Finally, the opisthotonic posture appears to have a phylogenetic signal: it is so far reported entirely in ornithodiran archosaurs (dinosaurs and pterosaurs) and in crown-group placentals, though the distribution in mammals may expand with further study. It seems important that the opisthotonic posture has been observed extensively only in clades of animals that are known or thought to have high basal metabolic rates: hypoxia and related diseases would be most likely to affect animals with high oxygen use rates.

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Introduction

The disposition of fossil bones can be studied in many ways that produce different kinds of useful paleoecological information: the scattering of skeletons by currents and scavengers (e.g., Weigelt 1927; Bickart 1984; Davis and Briggs 1998), the selective gnawing of bones by predators (Buckland 1824; Dart 1925), and the pathologies of injury and bone disease (Rothschild and Martin 1993) are only a few. Here we investigate traditional explanations for a well-known death position of many articulated skeletons (i.e., those that are not obviously disarticulated by wind, water, or other animals). As we hope to show, there is a correct and clinically uncontroversial interpretation of the causes of this posture, and it can provide new insight into the causes of death and the paleoenvironmental conditions involved in many fossil vertebrate deposits.

A pronounced and diagnostic death posture in tetrapods, in which the head and neck are reflexed over the back of the animal, is known in the medical literature as opisthotonus (Gr., *tonos* = tightening; *opistho* = behind, suggesting extreme extension), or (more generally and archaically) *tetanus dorsalis*, a stiffening of the vertebral column (Fig. 1). The tail, if sufficiently long and flexible, is typically drawn over the body. In both cervical and caudal series, the opisthotonic posture is characterized by a gradual curvature, reflecting the

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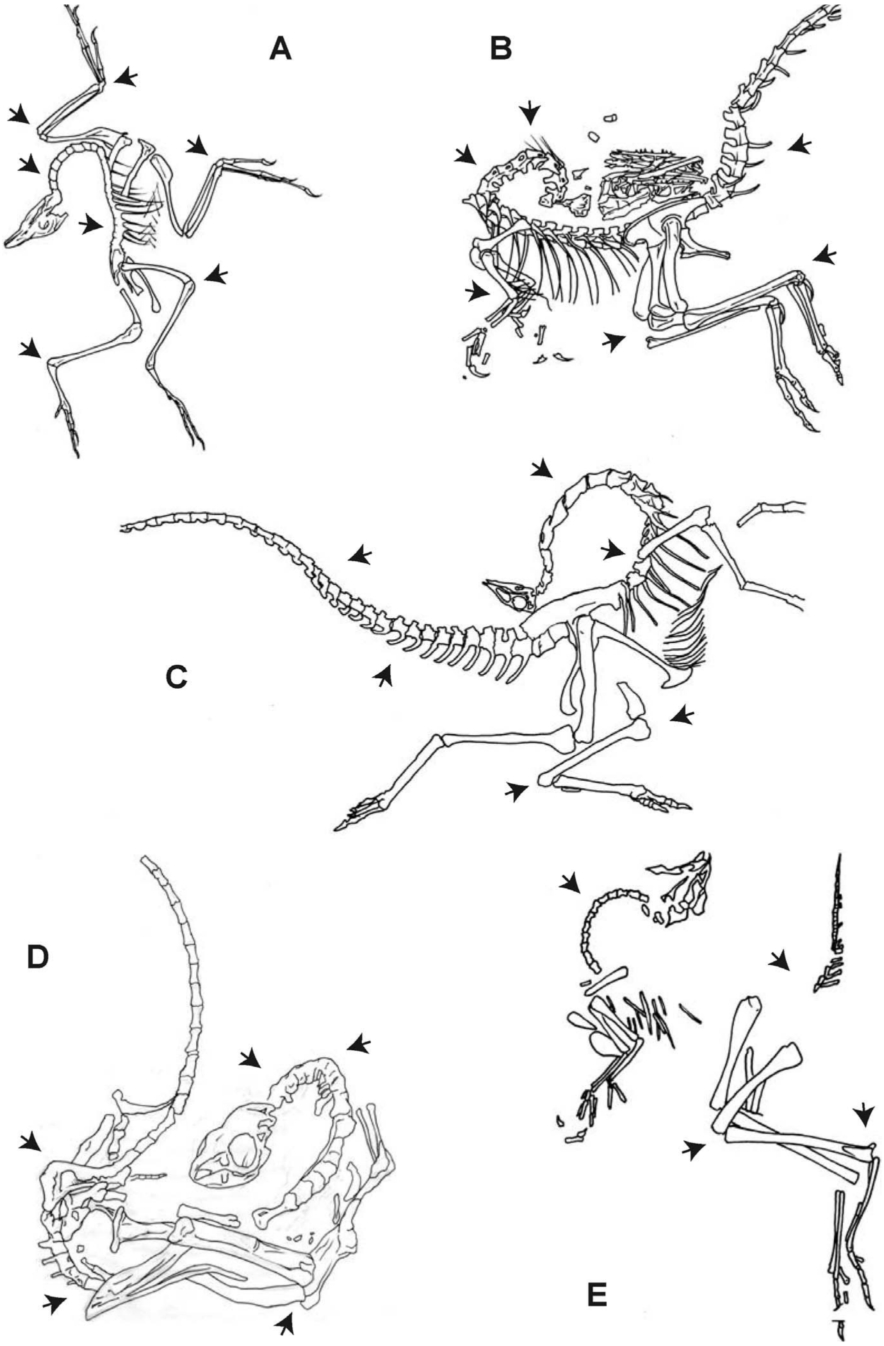
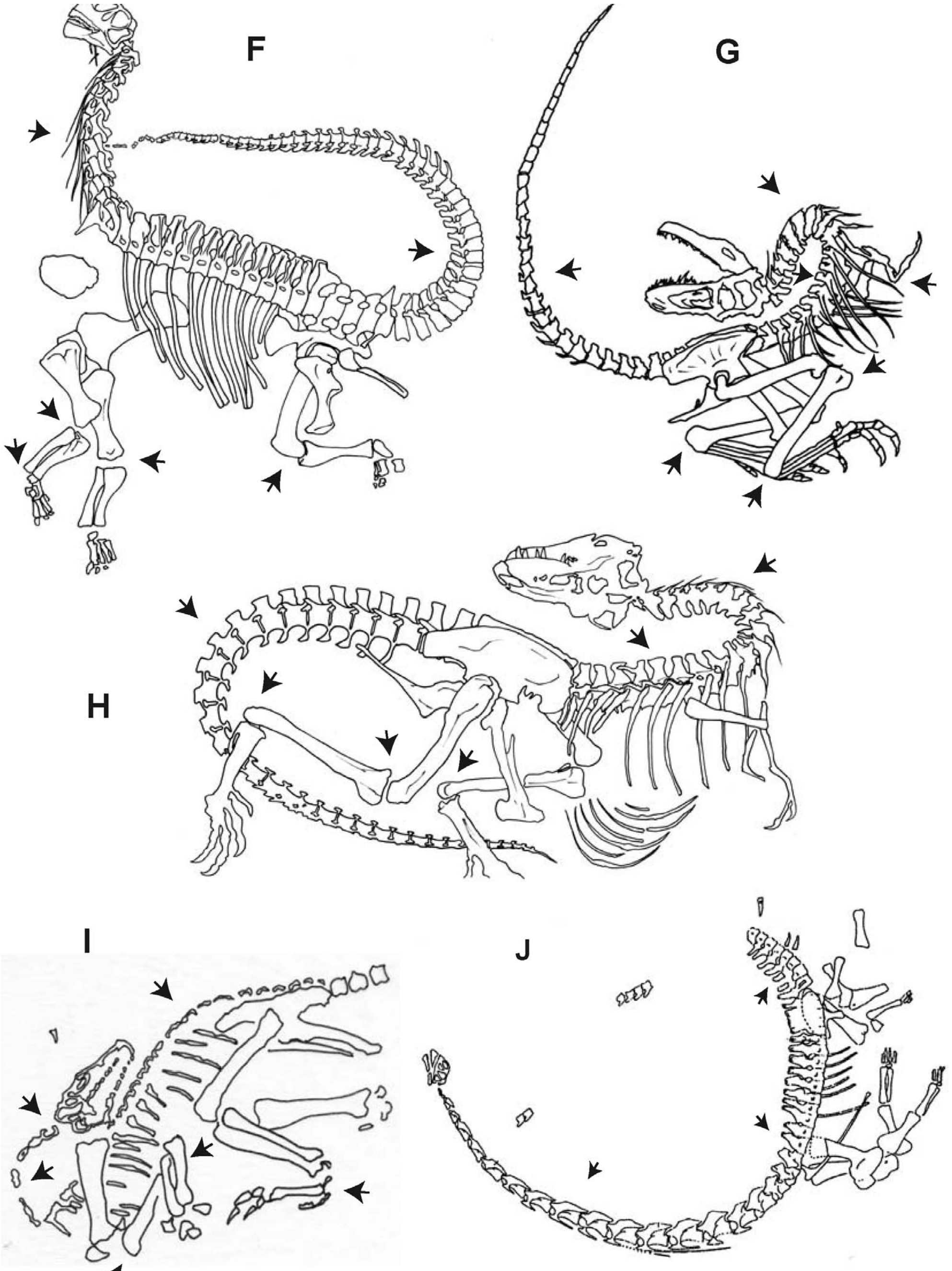


FIGURE 1. The opisthotonic posture in saurischian dinosaurs. A, The basal bird *Archaeopteryx* (plumage not figured); Humboldt Museum, Berlin; skull length 145 mm. Note classic features of opisthotonus: dorsally reflexed neck and back vertebrae, accompanied by commonly seen flexion of elbows, wrists, knees, and ankles (arrows). According to our interpretation of opisthotonic causes, this individual assumed the posture before death, not after, likely as a result of disease of the CNS (for explanation see text). On this view, the individual would have expired in this position on a soft substrate, to which the feathers would have adhered; the carcass was buried relatively quickly in this position, without disturbance by currents or scavengers (see Bickart 1984; Krauss et al. 2005). B, The basal tetanuran theropod *Compsognathus* (after Ostrom 1978); Bayerisches Staatssammlung für Paläontologie BSP 1563; skull length 8.3 cm. C, The ornithomimid *Struthiomimus*; American Museum of Natural History AMNH 5339; skull length approximately 30 cm. D, The basal ornithopod *Jeholosaurus*, drawn from a photograph of a specimen in the Dalian Natural History Museum (2005); specimen number and size unrecorded. E, The feathered manirap-



toran *Protarchaeopteryx* (after Ji et al. 1998); National Geological Museum of China 97–4-A; skull length 11 cm. F, Juvenile *Camarasaurus* (after Gilmore 1925); Carnegie Museum of Natural History CM 11338; skull length 23 cm. The neck and tail are dorsally flexed; the hindlimb is flexed (*decerebrate rigidity*), but the forelimbs are extended (*decerebellate rigidity*), which may occur in the same carcass if different areas of the brain are affected. For explanation see text. G, The tyrannosaur *Albertosaurus* (drawn from a photo supplied by Darren Tanke of a specimen in the Royal Tyrrell Museum of Palaeontology). H, *Gorgosaurus*; National Museum of Natural History USNM 12814. Note that the neck is reflexed dorsally whereas the tail is reflexed ventrally, with no disarticulation. The position of skeletons like this one and the others in this figure cannot be explained by current flow. I, A juvenile specimen of the ornithopod *Tenontosaurus*; Oklahoma Museum of Natural History OMNH 53781; skull length 9 cm, after a sketch in Brinkman et al. 1998 and photographs provided by J. Person. J, The sauropod *Mamenchisaurus* (from Pi et al. 1996); Zigong Dinosaur Museum ZDM 0083; skull length 51 cm.

nearly uniform contraction of all segments resulting from a single cause (a kink in the neck or tail does not qualify as opisthotonus). The posture is well known in the clinical human and veterinary literature (de Lahunta 1983; Ondo and Delong 1996; Bagley 2005; Liu et al. 2005), and appears to be restricted to mammals and birds; it has often been observed in fossil birds and other theropod dinosaurs, pterosaurs, and mammals (Weigelt 1927).

Often associated with opisthotonus, though not necessarily present, are two syndromes that affect the posture of the limbs: *decerebrate rigidity* and *decerebellate rigidity.* In decerebrate rigidity, the individual presents the opisthotonic posture, and all the limbs are stiffly extended. In decerebellate rigidity, opisthotonus is also evident, and the forelimbs are extended while the hindlimbs are flexed. The differences in hindlimb posture reflect damage to separate but proximate areas of the cerebellar cortex (Bagley 2005).

The term ''opisthotonus'' in the clinical literature denotes both the posture and the symptoms that are presented by the affected individual. To avoid circularity, because we cannot observe the symptoms in fossil animals, and so do not want to assume the cause of the position in describing it, we will limit the term ''opisthotonus'' to the symptoms that characterize the opisthotonic posture in living, clinically observable animals, and we will use the term ''opisthotonic posture'' for the hyperextended disposition of the vertebral column that can be observed directly in fossil carcasses.

Numerous explanations have been proposed for the opisthotonic posture:

1. Passive drifting of skeletons that results from current flow operating on a carcass that has sunk and eventually become anchored to the substrate (de Buisonjé 1985; Frey and Martill 1994).
2. Diving into and becoming stuck in mud, for example during pursuit of prey (Deecke 1915).
3. Display of the natural relaxed posture of sleep in which the animal expired (Heinroth 1923).
4. The relaxation of muscles after death, allowing the ligaments to exert an inherent elastic pull, thus drawing the head back (Wellnhofer 1991).
5. A result of the onset of rigor mortis, in which the pull of the stronger antigravity muscles of the dorsal region overcomes the pull of the weaker ventral neck muscles (Gillette 1994; Laws 1996).
6. A consequence of postmortem subaerial desiccation and contraction of the dorsal neck tendons or ligaments (Weigelt 1927).
7. Hypersaline dehydration of tissues, resulting in similar contractions of the dorsal neck tendons or ligaments (Schäfer 1972; Seilacher et al. 1985; Wellnhofer 1991).
8. Perimortem death throes consequent to affliction of the central nervous system (Moodie 1918, 1923).

Each of these hypotheses may be valid for particular cases, but how can we know which, if any, are applicable to a given case? What are the criteria by which such hypotheses could be tested? What independent lines of evidence need to be brought to bear on particular explanations? Moreover, can a common mechanism account for general patterns of the opisthotonic posture in the fossil record?

Most paleontological hypotheses that attempt to explain the death-positions of specimens have proposed essentially postmortem causes (desiccation, rigor mortis, transport, and so on). Whereas these are all valid phenomena, very little experimental evidence has tested these explanations. However, an extensive clinical (human and veterinary) literature that has largely been overlooked in paleontological discussions deals with perimortem causes of the opisthotonic posture. It seems possible to us that the causes of the opisthotonic posture in present-day animals might explain many cases in the fossil record; in fact, living animals would seem to provide the only known clues to the interpretation of the posture in fossils, if its causes are biotic.

In human cases of opisthotonus, presented either at severe risk of death or at the time of death, the head and heels reflex backward and the body bows forward. This condition is also clinically recognized in other mammals (rodents, dogs, cats, ungulates) (O'Reilly et al.

2003; Philbey and Martel 2003; Olby et al. 2004; Uzal et al. 2004) as well as in birds (Liu et al. 2005). In animals with long necks, such as birds, other dinosaurs, and pterosaurs, the neck vertebrae are so extended that the dorsal surface of the skull may even come to rest atop the spines of the anterior dorsal vertebrae. This condition has a number of causes in living tetrapods that are related to dysfunction of the central nervous system (CNS). The causes include hypoxia, poisoning from substances such as strychnine that affect the CNS, infection or injury of the meninges or brain tissue, and congenital diseases; the effects may be reversed, depending on the inciting cause (Davis et al. 1986; Constantini and Beni 1993; Filippich and Cao 1993; Real et al. 1997).

The goals of this paper are (1) to examine the plausibility and testability of competing hypotheses that can explain the opisthotonic posture in tetrapod fossils, (2) to separate the incidence of opisthotonus from other processes (biotic and abiotic) that can cause similar death positions, (3) to test some hypotheses that have been commonly accepted or assumed, and (4) to outline criteria that enable the separation of the influence of one particular cause from another.

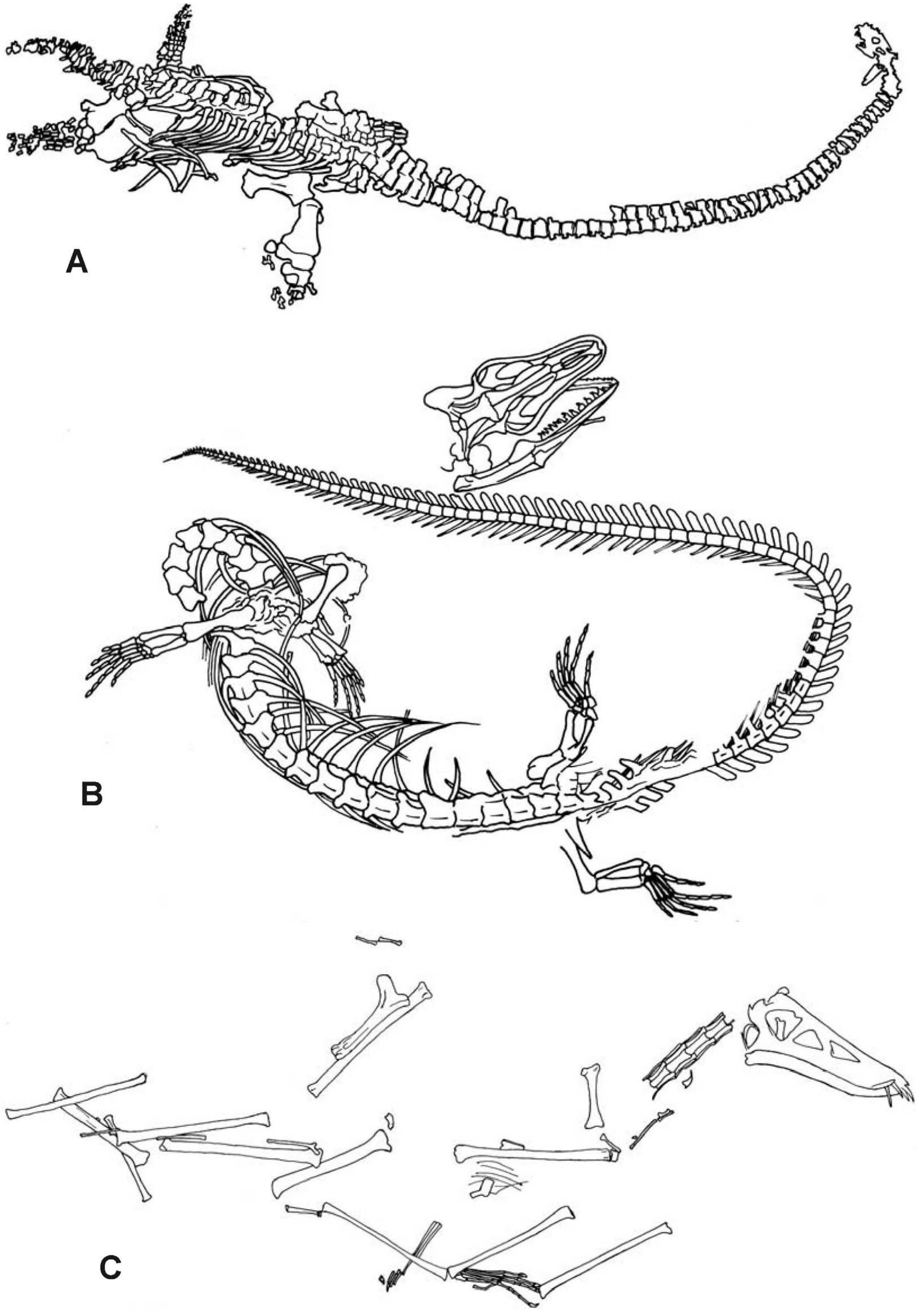
Testing Paleontological Hypotheses

The quality and completeness of fossil preservation depend on several factors, including transport, scavenging, and rate of burial. Most vertebrate skeletons are disarticulated before preservation (Davis and Briggs 1998); large carcasses are rarely transported for some distance without disarticulation, either by water or by scavengers. Rapid burial or other sequestration must be presumed if an articulated skeleton is preserved. These inferences are supported by taphonomic experiments that address patterns and rates of drying, disarticulation, and skeletonization (Bickart 1984; Davis 1996; Sledzik 1990; Davis and Briggs 1998).

Some commonly held assumptions about the opisthotonic position turn out to be surprisingly unsupported. One idea is that after deposition on a beach, a carcass can change its position as it dries out and becomes mummified (Weigelt 1927). But, for example, Bickart (1984) found that the feathers and bones of avian carcasses became stuck to the substrate (whether bare or plant-covered soil) shortly after placement. Carcasses were difficult to remove from the surface of the ground and remained in place even after severe flooding (see also Krauss et al. 2005 for similar findings). These observations indicate that the opisthotonic posture must be established in a carcass during or shortly after death, and before the carcass can stick to the ground or be buried. Another idea is that long-necked taxa will almost automatically be preserved in the opisthotonic position, because the ‘‘nuchal ligament’’ contracts after death and the cervical muscles relax (e.g., Wellnhofer 1970, 1975) But the opisthotonic posture is not an automatic concomitant of having a long neck, because long-necked taxa that are not dinosaurs and pterosaurs, such as plesiosaurs (Fig. 2; cf. Fig. 1), pachypleurosaurs (Young 1958), and hyphalosaurid choristoderes (Chang et al. 2003), are not fossilized in this extreme position. Pterosaurs often were (Fig. 3), but often were not so preserved (Wellnhofer 1970, 1975, 1991; see below), and this is also true for birds and other dinosaurs.

The various hypotheses to explain the opisthotonic posture in fossil organisms are themselves variably testable. We review what has been tested to date, and for each hypothesis we provide evidence, including experimental results of our own, to assess the strength of each hypothesis in turn.

1. Passive drifting of skeletons that results from current flow (de Buisonjé 1985; Frey and Martill 1994) is an important influence on death positions, and its results would be particularly likely to be confounded with those of biological causes when the animal’s spine happens to be flexed. The opisthotonic posture is mimicked, for example, when the body axis comes to lie roughly perpendicular to the current flow, and the flow then moves the head and tail parallel to itself (Fig. 2B). But several criteria can be investigated to tease apart these potential conflations. First, sedimentological evidence, such as ripple marks, heterogeneity of grain size, and alignment of clasts, can often determine direction and degree of current flow (Weigelt 1927). If bones are aligned with prevailing currents, then cur-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rents were probably an important agent, particularly if disarticulation is evident. For example, pterosaurs from the Late Jurassic Solnhofen limestones of Germany (Wellnhofer 1970, 1975) are often preserved with necks and limbs flexed in a typical opisthotonic posture (Fig. 3A–D). But in other cases, such as some pterosaurs from the Early Jurassic Holzmaden Formation (Fig. 2C; but contrast Fig. 3E), the many long bones of the skeleton, as well as the cervical series, have a more parallel alignment and are usually also somewhat disarticulated. These latter instances would support the drift or current flow hypothesis.

A second test of the importance of current flow and drift is redundancy, which we define as the repeated discovery of the same pattern. If several different skeletons are preserved at one site, preferential orientation of their long bones and axes may help to test the role of current flow.

To test the opisthotonic hypothesis in any skeleton, the limbs as well as the vertebral column can provide important evidence. Current flow would not account for the associated limb positions that resemble the clinically observed conditions of decerebrate or decerebellate rigidity (Figs. 1, 3), and that are clearly not in line with current flow.

Finally, in a true opisthotonic posture the successive vertebral segments are flexed to more or less the same degree, so the curvature of the spine is regular (Figs. 1, 3), not discontinuous or kinked (Fig. 2A), and this is another way to distinguish it from the actions of water currents, scavenging, or other disturbance.

We suggest that in most cases the effects of current flow on articulated carcasses can be readily distinguished from the opisthotonic posture. We also think that the two causes are unlikely to affect the same carcass, because individuals that show the effects of opisthotonus will have been buried quickly in relatively undisturbed environments (see below).

2. Diving into or becoming stuck in shallow mud (Deecke 1915) may have occurred in rare instances, and may indeed bear witness to an individual's poor luck or judgment. However, this idea does not plausibly explain the same posture in carcasses of large theropods, cows (Weigelt 1927: Plate 13A), and land birds. It is even a difficult hypothesis to test in particular instances, unless there is evidence of a broken neck or skull and of a shallow water table. We expect that this hypothesis will explain very few cases.

3. Heinroth (1923) suggested that the opisthotonic posture reflects a typical sleeping position in which an animal would naturally come to rest. However, he provided no evidence or examples. Positioning oneself for sleep is an active process, not a default posture. The opisthotonic posture described in the clinical literature is not a typical sleeping position of any known animal. Moreover, birds and related theropods that do appear to have died in a sleeping position (e.g., *Mei long* [Xu and Norell 2004]) do not assume the opisthotonic posture.

4. It is commonly stated that when muscles relax after death the cervical tendons or ligaments exert an inherent elastic pull, thus drawing the head back into the opisthotonic posture (e.g., Wellnhofer 1991 inter alia). We are unable to find any experimental evidence that validates this. Tendons and ligaments occur throughout the musculoskeletal apparatus of all tetrapods, yet when such animals go to sleep or are anaesthetized, and the muscles relax, the tendons and ligaments do not change the animal's position. The dorsal nuchal ligament is not stretched in a normal standing po-

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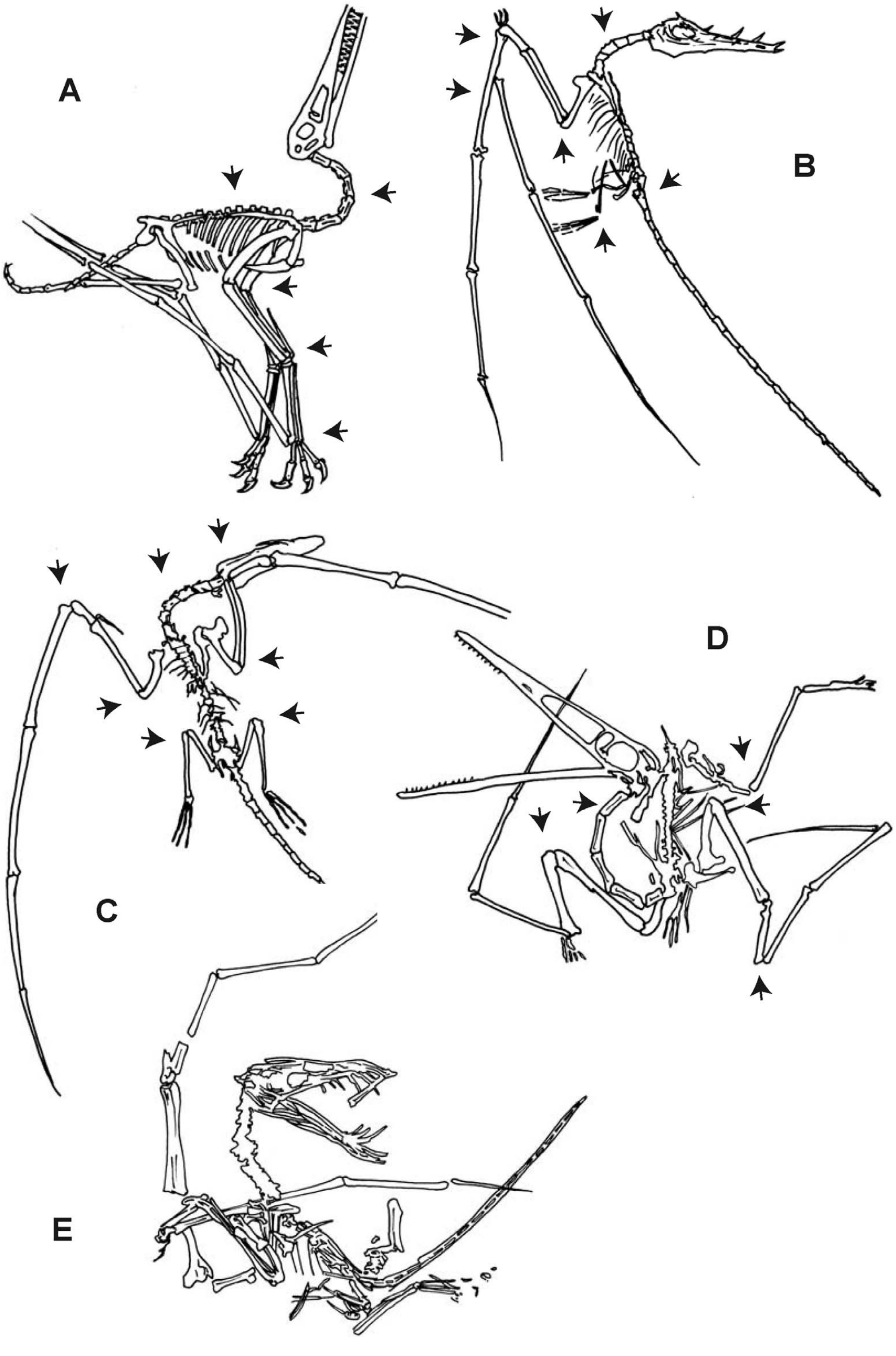
FIGURE 2. Skeletons affected by current flow but not opisthotonus. A, The plesiosaur *Hydrotherosaurus* (after Welles 1943); University of California Museum of Paleontology UCMP 33912; length of specimen 806 cm. This specimen shows that opisthotonus is not an automatic consequence of having a long neck. Here, current flow has drawn the neck and head dorsally. B, The Cretaceous aigialosaur *Opetiosaurus* (after Weigelt 1927: Fig. 24); Natural History Museum, Vienna (unnumbered); skull length 105 mm. Current flow is to the upper left. The skull has separated from the neck and from the lower jaw and drifted to the upper left; the neck has drifted laterally to the left as well. C, The basal pterosaur *Dorygnathus*; Staatliches Museum für Naturkunde Stuttgart SMNS 55886; skull length 8 cm; from the Early Jurassic Holzmaden limestones of Germany; affected by current flow parallel to the direction of the skull and long bones. Compare with Figure 3E.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sition; however, when the animal lowers the head, the ligament stretches and stores elastic energy that helps to return the head to the normal erect position. It also stores energy when the animal is moving, doing up to 60% of the oscillatory work to stabilize the animal's head (the rest is supplied by muscles) (Gellman et al. 2002). Furthermore, when these animals are sleeping or anaesthetized their heads are not pulled caudodorsally. The joints simply move in the direction of gravity, or in whatever direction the skeleton is being otherwise moved.

Therefore, ligaments in their normal position are like unstretched rubber bands. The hypothesis that cervical or any other tendons and ligaments exert a significant inherent elastic pull depends on showing that the tension of the tendons or ligaments at rest is great enough and their elastic properties are sufficiently strong to reflex the neck or other areas of the skeleton. These properties are difficult to assess in extinct animals, and surprisingly the possible elastic effects of tendons and ligaments on carcass position after death have not been extensively tested in extant tetrapods. Camp and Smith (1942) performed experiments on the digital ligaments of the horse, which store elastic energy when the animal walks or runs; however, they found that the stretching was significantly less than 10% of total length, even under extreme loads (until the ligaments failed).

To exert any influence on skeletal position, tendons and ligaments would have to change shape, and that presumes that they would have to dry out in order to shorten. If so, the argument reduces to the desiccation hypothesis, which we show below does not work for these tissues. However, if skeletons are quickly buried, ligaments and tendons would not be able to shrink (even if they could) and thereby flex joints through desiccation, although they might slightly reduce distances between adjacent bones, such as vertebrae, with the disintegration of intervertebral cartilage disks, for example. This possibility remains to be tested, but we suppose that it will not account for very many cases of fossil preservation, and in any case would not account for more than about 10% of contraction.

5. Rigor mortis, or cadaveric rigidity, has often been invoked to account for the opisthotonic position of fossil birds, other reptiles, and mammals (Gillette 1994; Laws 1996). Numerous factors are known clinically to affect the onset, intensity, and duration of rigor mortis. These include the cause of death (asphyxiation, intoxication, trauma, etc.), ambient temperature, exertion immediately before death, and physical condition of the individual (Krompecher and Fryc 1978; Krompecher 1981, 1994; Krompecher et al. 1983; Hullard 1985). A lack of ATP in the cells causes the muscle proteins actin and myosin to become chemically ''locked,'' and this lack results in stiffness (not contraction) of the muscle (Krompecher 1995; Kobayashi et al. 1996). This distinction is critical: rigor mortis does not cause muscle contraction, only stiffness. It therefore cannot produce the opisthotonic posture; it can only preserve it temporarily if the carcass is already in that position.

Immediately after death, vertebrate skeletal muscles are relaxed and movable, and one can position a carcass in a variety of attitudes at

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FIGURE 3. The opisthotonic posture in pterosaurs. Typically, in addition to the opisthotonic hyperextension of the spinal column, the hindlimbs are drawn up toward the body; the metacarpo-phalangeal joints of the wings are strongly flexed, as are the joints between the forearm bones and wrist (which allow very little motion). A, *Pterodactylus* (after Wellnhofer 1970: Plate 8, Fig. 3); Paleontological Institute and Museum of the University of Zurich A/III 100, skull length 39 mm. B, *Rhamphorhynchus* (after Wellnhofer 1975: Plate 20, Fig. 1); E. Schöpfel collection; skull length 98.5 mm. C, *Rhamphorhynchus* (after Wellnhofer 1975: Plate 21, Fig. 1); Carnegie Museum of Natural History CM 11427; skull length 99 mm. D, *Pterodactylus* (after Wellnhofer 1970: Plate 1, Fig. 1); Bayerisches Staatssammlung für Paläontologie BSP AS I 739; the preservation in anterodorsal view is unusual, but most of the typical flexions are present. A–D are from the Late Jurassic Solnhofen limestones of Bavaria, Germany. E, In contrast, the *Dorygnathus*, from the Early Jurassic of Holzmaden, Germany, shows ambiguous evidence at best of opisthotonic flexure. Rather, the disposition of the wing-fingers and tail and particularly the partial disarticulation of the hindlimbs suggest current flow, possibly toward the upper right. Institute and Museum of the University of Uppsala R 156; skull length 128 mm.

this point. Postmortem rigidity sets in within hours of death, stiffening the muscles and immobilizing joints in the death position; it can remain in effect for 24–48 hours, at which point stiffness resolves and muscles are once again flaccid (Henssge et al. 1995; Krompecher 1995). Postmortem rigidity has been observed in a wide variety of animal clades, including insects, fishes, birds, non-avian reptiles, frogs, and mammals (Miller and Tregear 1972; Bergman 1983; Krompecher 1995; Skjervold et al. 2001).

Experimental Results.—We tested the effects of rigor mortis on recently deceased birds. The postmortem body positions of numerous raptors, including great horned owls (*Bubo virginianus*), red-tailed hawks (*Buteo jamaicensis*), and falcons (*Falco sparverius* and *Falco columbarius*) euthanized for humane reasons were observed at the Montana Raptor Conservation Center (MRCC) in Bozeman, Montana. Immediately upon death by injection with a sodium pentobarbital solution, all muscles were relaxed and flaccid. *Rigor mortis* was generally established within two hours, as determined by stiffening of the muscles and immobilization of joints. All carcasses simply became stiff in the position in which they were placed; the head and neck did not change position. After resolution of rigor, the carcass was again flexible and its position was easily changed. The head was never drawn back, either through the onset of cadaveric rigidity or the elastic pull of tendons. At no time did rigor mortis produce the opisthotonic position in these birds.

From these observations and the description of the etiology of rigor mortis given above, it is difficult to see how it could be responsible for the opisthotonic posture.

6. Weigelt (1927), in his classic work, was of the opinion that postmortem, subaerial desiccation accounted for the opisthotonic position in a wide variety of tetrapods, including mammals (cow, *Palaeotherium*, *Diceroceras*, guanaco, camel), reptiles (theropod, stegosaurian, and sauropod dinosaurs, and a soft-shelled turtle), and birds (*Archaeopteryx*, rhea, magpie, pheasant cucal). However, there are two critical problems with this hypothesis. First, it has never been observed, and second, it has not been simulated experimentally.

Original Observations?—In none of Weigelt's examples was the actual death of the animal observed. All were carcasses, and had been decomposing for quite some time. He provided no actual first-hand examples of desiccation resulting in the opisthotonic posture at the Smithers Lake catastrophe. He discussed a single cow carcass (Weigelt 1927: p. 103), which he assumed was transported and beached by the receding river, but it was already defleshed when he saw it. Its position was determined primarily by current flow, as he acknowledged, but he attributed its posture to desiccation of muscles and tendons. He did not remark that its left horn was mired in the sand, which may have affected its disposition, but rather inferred that the shoulder anchored the carcass upon deposition. In fact, although many of the carcasses that Weigelt (1927) mentioned suffered desiccation at some point, it is surprising that he reported almost none of them in the opisthotonic position, because if desiccation was an important cause of the opisthotonic posture, one would expect the condition to be almost default in accumulations of such carcasses.

Weigelt's (1927: pp. 103–106) second-hand examples were also long-dead carcasses: the camel skeleton in the desert noted by Dienst; the guanaco and rhea noted by Huene; and Heinroth's magpie and cucal. All the rest were fossils, and no human saw them die. Note further that the necks of some large ungulates and hadrosaurs, for example, have a natural curve; the long thoracic dorsal spines can accentuate the curve of the neck relative to the body when the skeleton is observed in death-pose. Without considering the original relative position of the spinal column elements, as Weigelt himself noted, observations such as he reported cannot be taken as evidence of movement of the carcass. On the other hand, given that the Smithers Lake and some other skeletons were not quickly buried, scavengers could have had an important effect on the positions of many bones (Hill 1979; Hill and Behrensmeyer 1984), notably the jaws and pelvis. (Weigelt [1927: Plate 6C] shows the effect of scavenging crabs on the position of the jawbone of a calf.)

Experimental Results.—There is some question about the validity of experiments that support traditional wisdom about the connection between desiccation and opisthotonus. In Heinroth's (1923) experiments, desiccation did not intensify the opisthotonic posture: the birds were already dead, and he carefully placed them in the positions shown in the Berlin specimen of *Archaeopteryx*, then watched the bones disarticulate as the skeletons dried out. Given these conditions, it is difficult to conceive of other explanations that Heinroth (or Weigelt) would have expected or reported. On the other hand, it seems significant that his specimens did not contract further out of the classic *Archaeopteryx* position, if desiccation plays a role of any importance in the opisthotonic posture. The heads simply fell backward, as one would expect as connective tissues deteriorate.

Davis (1996) repeated Heinroth's experiment, removing muscles from a pigeon and drying the carcass for three days in a fume cabinet. Davis stated that ''the neck curved backwards and the legs assumed the 'bicycling pose' [i.e., opisthotonic posture] evident in *Archaeopteryx*.'' Davis did not describe the original position in which he placed the carcass, nor did he provide measurements of any changes in position or analyze what specifically caused them. He concluded that it is most likely that the muscles in the Solnhofen specimens decayed away, and that hypersaline conditions in the lagoon desiccated tendons to bring about the ''bicycling'' pose. (We show below [item 7] that hypersalinity does not account for these changes.) If the carcass dried subaerially (i.e., exposed to the air) and then was transported into water before finally sinking, it is unlikely to have avoided disarticulation and perhaps scavenging.

Davis (1996) inferred that the defleshed skeleton achieved the posture observed in *Archaeopteryx* ''because, without the muscles to act as antagonist force to the desiccating and shortening tendons, the skeleton contorts'' into the posture. This general explanation appears to be widely received among paleontologists, but it requires further analysis. Tendons connect muscle to bone, whereas ligaments connect two or more bones, cartilages, or other structures (Stedman 1982). As noted above, muscles exert their pull on bones through the tendon, but the tendon is passive. If the muscle is experimentally removed, the tendon is effectively free where it attaches to the muscle. No pull on the skeleton, inherent or otherwise, is possible. So Davis's procedure of defleshing the bones would not appear to simulate natural conditions of desiccation. In *Archaeopteryx*, in particular, there are feather impressions, and therefore the skin was intact. The selective loss of muscles, while leaving the skin and ligaments intact, would seem to reflect preservation under truly extraordinary circumstances. At the least, a detailed argument, integrating independent evidence from sedimentological and biochemical studies, would have to be made to support this scenario.

Ligaments, in contrast to tendons, attach bone to bone directly. Ligaments are not necessarily deployed in the skeleton in strictly anti-gravity positions. For example, the collateral ligaments and the patellar ligament in the knee restrict lateral and ventral motion of joints. In ligaments and tendons, type I collagen is the principal structural element of the extracellular matrix, which directly transmits force between bones or between bone and muscle, respectively (Provenzano and Vanderby 2006). Therefore, the fibrous structure of tendons and ligaments should produce comparable force upon desiccation, if any. Does the desiccation of tendons produce the opisthotonic posture?

We tested the hypotheses that drying of muscles, tendons, or ligaments caused the extreme opisthotonic posture by allowing carcasses of two red-tailed hawks (*Buteo jamaicensis*) to dry for a minimum of three months. The hawks were post-rigor, fresh, unskinned carcasses (again euthanized for humane reasons at the MRCC). One hawk was placed on waxed paper to prevent the head and neck from sticking to the tray as the body fluids dried, and the other was placed in a box with foam packing ''peanuts'' beneath it to prevent any possible adherent effects of the substrate. Neither carcass changed from its initial posi-

TABLE 1. Change in length and weight of beef tendons through time under different experimental conditions of salinity and desiccation. Tendons A and B under salinity 1.105 ppt; tendons C and D under salinity 1.060 ppt; tendons E and F in desiccant. For explanation see text.

	Weight (g)	Length (mm)	Width (mm)	Change (%) after 50 days
Salinity 1.105	Tendon A			
Day 1	47	179	n/a	
Day 9	47	178	n/a	
Day 50	51	176	n/a	length: −1.7%, weight: +8%
Salinity 1.105	Tendon B			
Day 1	3	90	9	
Day 9	7	90	10	
Day 50	8	91	13	length: +1%, weight: +34%
Salinity 1.060	Tendon C			
Day 1	6	105	7.5	
Day 9	11	108	10	
Day 50	12	105	10	length: 0, weight: +100%
Salinity 1.060	Tendon D			
Day 1	6	100	11.8	
Day 9	9	101	11.8	
Day 50	15	99	15.9	length: −1%, weight: +150%
Dessicant	Tendon E			
Day 1	13	105	15	
Day 9	2	100	11	
Day 50	2	98.4	n/a	length: −6%, weight: −84.6%
Dessicant	Tendon F			
Day 1	46	180	13.6	
Day 9	18	161	10.5	
Day 50	16	159	n/a	length: −11.6%, weight: −65.2%

tion throughout desiccation. Both carcasses were dry, solid, and stiff when the experiment ended after three months. These laboratory experiments provide no evidence that desiccation of muscles, ligaments, and tendons is a general cause of the opisthotonic posture, whether or not the muscles are left intact.

To measure the possible kinetic effect of drying tendons, we obtained fresh beef tendons from a commercial grocery. These were relatively large tendons, and, from the bifurcation of the distal end could be identified as the superficial and deep digital flexor tendons of the lower limb. The tendons were dissected free from other surrounding connective tissue, measured in length and width, and weighed to the nearest gram. The straight superficial digital flexor (*sdf*) tendon was pinned with dissecting pins near each end to a piece of styrofoam 15 × 10 × 1 cm and covered with silica gel pellets, a nontoxic commercial desiccant. Measurements were taken at both ends of the tendon and across its mid-length. The deep digital flexor (*ddf*) tendon is a bifurcated tendon, so measurements were taken of the ends instead of the middle of the tendon. This tendon was buried in silica gel ''sand,'' but it was not pinned.

After nine days, both tendons had shrunk only slightly in width and length, but had lost 60–85% of their original weight (Table 1). The pins at either end of the *sdf* were not dislodged, or even inclined slightly from their original position, demonstrating that the extensive desiccation produced no measurable force at all. The pins were then removed and more silica gel was added. After a total of 50 days, the *ddf* tendon had lost 67% of its original weight but had shrunk in length by only 11%. The *sdf* tendon was still 85% of original weight, but only 6% of its length was lost. (These numbers are commensurate with the degree of stretching that Camp and Smith [1942] obtained for the interosseus tendon of the horse.) Both tendons twisted; the *sdf* tendon twisted more than the larger *ddf* tendon did.

This experiment tests the hypothesis that the desiccation of tendons produces force that could be responsible for substantial postmortem movements of bones across joints. The digital flexor tendons in cattle are comparatively large tendons and bear a considerable load. But if the superficial digital flexor tendon did not dislodge the small pins at either end as it dried, it is difficult to infer that the shrinkage of tendons could ''pull'' large portions of a desiccating carcass over a plane surface. Our drying experiments of whole, fresh animals and of individual tendons do not support desiccation as a cause of the opisthotonic posture.

7. The opisthotonic posture has been attributed to hypersaline dehydration of tissues (Schäfer 1972; Seilacher et al. 1985; Wellnhofer 1991; Davis 1996). This condition of ''salt-shrinking'' specifically refers not to normal (isotonic) marine waters but to environments of concentrated salts, as has been hypothesized for the Late Jurassic Solnhofen limestones (Barthel 1970; Seilacher et al. 1985; Viohl 1985, 1994). Cases in which fossilized specimens were dehydrated under such conditions are probably comparatively rare, and can be tested by independent analyses of isotopic compositions of the sediments (Palmqvist and Arribas 2001). (Hypersalinity is an improbable cause of the opisthotonic posture in most fossilized specimens that are preserved in terrestrial sediments, because hypersaline conditions are rare in terrestrial environments.)

Experimental Results.—We tested whether hypersaline conditions applied to postmortem soft tissues (tendons and muscles) produced significant contraction in their lengths, which would be necessary in order to move the positions of attached hard parts. As in the previous experiments, fresh beef tendons were purchased from a commercial grocery for submersion in hypersaline solutions. These were relatively large tendons, identifiable as the superficial and deep digital flexor tendons of the lower limb. The tendons were dissected free of other surrounding connective tissue, measured in length and width, and weighed to the nearest gram. Hypersaline conditions were simulated by using scientific grade marine salt (Coralife Salt, Energy Savers Unlimited, Inc., Carson, California, a commercial preparation used in the saltwater aquarium hobby trade) at specific gravities of 1.060 and 1.105. (''Normal'' seawater salinity for saltwater aquaria is between 1.021–1.023.) From the lack of evaporite beds, the salinity of the Solnhofen lagoon is estimated to have been no greater than 117 ppt (Barthel et al. 1990). If the Solnhofen lagoon were to act as an ideal liquid, the maximum specific gravity would be estimated at approximately 1.117. Therefore, the salinity levels for this experiment were comparable to the highest estimated concentration for the Solnhofen lagoon.

Two tendons were placed in each solution. The containers were refrigerated at 4–7°C for the duration of the experiment to minimize microbial activity. After two weeks in the hypersaline solutions, far from contracting, the tendons had ''plumped up,'' increasing in weight by up to 150% (Table 1). All tendons increased in width. The longest tendon (in the 1.060 solution) decreased in length by 1 mm, but the second tendon remained at the same length. Both tendons in the 1.105 solution increased in length by 1–3 mm. Fresh tendons have a turgid, firm feel; but after two weeks in the solutions, these tendons were soft and flexible. There was minimal change in length but a large increase in weight, attributed to imbibition of water.

We conducted an additional experiment to assess the effect of hypersaline conditions on whole carcasses. Three frozen adult *Coturnix* quail were purchased from a commercial quail farm. Again, two hypersaline solutions were prepared using the aquarium ocean simulant (at specific gravities of 1.060 and 1.090). The carcasses were thawed. One intact quail carcass was placed in the 1.090 solution, and one intact and one skinned and gutted quail carcass were placed in the 1.060 solution. The containers were large enough to allow complete movement and submersion of the carcasses. The containers were subjected to late spring temperature fluctuations of approximately 4–18°C.

Neither intact quail sank or changed posture during the experiment. The body of the skinned quail sank after one day, but the head remained attached and continued to float until nine days later, when the 1.060 solution accumulated excessive bacterial overgrowth and was discarded. The body was fully flexible and had not changed position from its initial immersion. The quail in the 1.090 solution did not sink, even after two weeks. These results are consistent with those reported by Krauss et al. (2005), who found that it took up to three to four weeks for bird carcasses to decompose and sink (see also Davis and Briggs 1998).

From these experiments it is apparent that (a) tendons do not shrink enough, if at all, in hypersaline solutions to account for the posture observed in these sediments; and (b) fully feathered birds can take a long time to sink (30–40 days [Schäfer 1962, 1972; Krauss et al. 2005]). Under these circumstances, the opisthotonic posture would have to be achieved through desiccation of tissues while the body was floating on the surface. This possibility would have to eliminate all action of scavenging, currents, and bacterial rotting that would cause disarticulation and other random changes in posture, which seems unlikely. (Simple, subaerial drying as a cause of the opisthotonic posture has been discounted above.)

Finally, a further test can be drawn from the death-positions of the most common tetrapods of the Solnhofen limestones themselves, the pterosaurs, which number in the hundreds in collections worldwide (Wellnhofer 1970, 1975, 1991; K. Padian, unpublished notes). Wellnhofer (1975) illustrated 67 different, nearly complete skeletons of *Rhamphorhynchus*, plus two of *Scaphognathus* and one of *Anurognathus*, and 25 nearly complete skeletons of *Pterodactylus* (Wellnhofer 1970), as well as many more partial specimens of the two most common genera. We first assessed the degree of articulation of each specimen by scoring a point for each preserved articulation: jaw to skull, skull to neck, neck to trunk, wings to trunk, legs to trunk, tail to trunk (for pterodactyloids, pelvis to trunk), wing bones to each other, and leg bones to each other. Slight disarticulation or unnatural articulation of joints was duly noted. The non-pterodactyloids had an average articulation score of 5.25 of a possible 8; 19 specimens of 67 (28%) scored 8 points, 6 others scored 7 points, 11 scored 6, 9 scored 5. *Pterodactylus* specimens were generally more highly articulated: they scored a mean of 7 points; 17 specimens of 25 (68%) scored 8 points. *Rhamphorhynchus* specimens are generally one-third to one-half larger in wing span than *Pterodactylus* (Wellnhofer 1970, 1975, 1991), and as our results show, they are generally more disarticulated.

We then assessed the frequency and degree of the opisthotonic posture in these pterosaurs. A qualitative value of 0–5 was given to the degree of backward curvature of the neck and the dorsal flexure of the skull (0 for no flexure, 5 for strong intervertebral flexure plus flexure of skull on cervical series); a value of 0–5 was given to the degree of flexure of the limb joints (measured by relative acuteness of the joint angles, as well as the number of joints flexed versus relatively unflexed). (Some authors have postulated that an interfemoral membrane in pterosaurs would have affected hindlimb posture in death; if so, this would have been no less true for the effect of the wings on the much longer forelimbs, and we made no assumptions about these possibilities.)

Our results show a strong disparity. Only four of the 67 Solnhofen non-pterodactyloids that Wellnhofer figured (of which 25 to 35 are reasonably articulated) show the strong possibility of opisthotonus (Wellnhofer 1975: Plates 20:1, 21:1, 27:1, and 28:1). In contrast, the vast majority of the 17 fully articulated, figured specimens of *Pterodactylus* (Wellnhofer 1970) display opisthotonic features. Ten show very high neck curvature, 15 show very high limb flexure; nine of these (over half) show both features. Six show low neck curvature but high limb flexure. Only one specimen shows both low neck curvature and low limb flexure. And one shows high neck curvature but low limb flexure (we interpret this as an artifact, because the limbs are so much more frequently flexed than the neck is).

These results cast doubt on the hypersalinity hypothesis, because if hypersalinity were dehydrating the soft tissues of carcasses, one would expect all or virtually all specimens to attain the same opisthotonic position. Why should *Pterodactylus* be affected whereas *Rhamphorhynchus* is not? One possibility is Wellnhofer's (1970) hypothesis that opisthotonus is correlated with size; could this be generalized? Apparently not: the four *Rhamphorhynchus* specimens that show opisthotonic features are relatively large (small specimens have skull lengths of 35–40 mm; these four are in the range of 90–100 mm). (Wellnhofer [1970] noted that larger *Pterodactylus* had a greater tendency to disarticulate.) *Archaeopteryx* specimens are generally larger than most *Pterodactylus* and closer to most *Rhamporhynchus* in size, and every articulated specimen of *Archaeopteryx* shows opisthotonus, as do the two known specimens of the small theropod *Compsognathus* (Ostrom 1978; Peyer 2004), which are also larger than *Pterodactylus* and *Archaeopteryx*. Therefore, we can reject the hypotheses that opisthotonus is caused by hypersaline conditions and that it is correlated with size.

8. Moodie (1918, 1923) proposed that the opisthotonic posture in fossil vertebrates reflected a pathological condition that followed from terminal malfunction of the central nervous system (CNS). This hypothesis was discounted by Huene (see Weigelt 1927), who asserted that the position was assumed after death, not before, and therefore could have nothing to do with disease. But Huene was incorrect, as other authors have been. Opisthotonus occurs with tetanic contraction of the dorsal muscles of the spine, as much clinical evidence has shown (Bagley 2005). Various malfunctions of the CNS, which we discuss below, release normal nervous inhibitions of muscular control, resulting in hypercontraction of these muscles (Moodie 1918, 1923). For reasons that we will explain, clinical evidence strongly supports Moodie's hypothesis.

What Explains Opisthotonus in Living Amniotes?

Opisthotonus is a clinical sign of neurological or muscular dysfunction; the posture is not a disease, nor does it in itself cause death (Sullivan 1970; Sukoff and Ragatz 1980; Klein et al. 1994; Palmer 2002; Olby et al. 2004). Opisthotonic posturing is not diagnostic of a specific cause, but it is clinically observed in a variety of conditions that affect the central nervous system. These conditions can be broadly classified under the following categories: infectious (including bacterial, viral, fungal, parasitic and protozoal), congenital, and acquired conditions (including neoplasia), traumatic injury, toxic insults, and nutritional deficiencies (Swank 1940; Wyatt et al. 1975; Filippich and Cao 1993; Klein et al. 1994; Van der Lugt et al. 1994; Ondo and Delong 1996; Park et al. 2000; Palmer 2002; Austin et al. 2004; Olby et al. 2004). Opisthotonus is observed after hypoxic damage in a variety of conditions: in bacterial and viral meningitis, secondary to administration of certain drugs including some anesthetics, secondary to poisoning with strychnine, thiamine deficiency, edema of the brain, and cerebellar swelling or atrophy (Swank 1940; Sullivan 1970; Sukoff and Ragatz 1980; Saunders and Harris 1990; Ersahin et al. 1992; Filippich and Cao 1993; Klein et al. 1994; Palmer 2002; Olby et al. 2004). Opisthotonus is not in itself fatal; it is a symptom of malfunction of the CNS, albeit a serious malfunction. The lesion (underlying cause) that incites the posture may or may not be reversible: for example, anesthetically induced opisthotonus (Saunders and Harris 1990) or thiamine deficiency (Swank 1940) can be reversed. Not all cases of strychnine poisoning or tetanus are fatal, although they can incite opisthotonus. Bacterial meningitis often causes human babies to present the opisthotonic condition (Ondo and Delong 1996). In short, a constellation of causes can bring on opisthotonus, but in the clinical community there is no doubt that its onset occurs during life or near death, not after death. Opisthotonus is observed in many recent cases of avian influenza, for example, in decidedly perimortem conditions (Liu et al. 2005).

Opisthotonus is different from pleurothotonus, a condition in which the vertebral column flexes to one side or the other, rather than dorsoventrally (Cossu et al. 2004). (In humans this occurs in the neck and upper back and is called the ''Pisa Syndrome,'' after the leaning tower in Italy.) The pleurothotonic position is often observed in fishes, amphibians, and reptiles, and is especially obvious in taxa with long necks and tails (Moodie 1918), such as the unusual choristodere *Hyphalosaurus* (Chang 2003; Dalian Natural History Museum 2005). In cases of pleurothotonus, as in opisthotonus, the successive vertebral segments are flexed to more or less the same degree, so the curvature of the spine is regular, not discontinuous or kinked (Fig. 2A), and so it also can be distinguished from the actions of water currents, scavenging, or other disturbance. The pathophysiology varies and is poorly understood: in dogs the posture can result from forebrain damage (Holland et al. 2000), including tumors, and it has been experimentally induced in salamanders by ablation of the ear region (Greene and Laurens 1923). Weigelt (1927) and others have hypothesized that in carcasses it results from asymmetrical distension of the abdomen after death. In any case, there is no established relationship between the causes of opisthotonus and those of pleurothotonus.

Because various conditions may manifest themselves in opisthotonus, and because there is no single unifying lesion that causes it, relatively little has been written about the specific pathophysiology of opisthotonic posturing (Ondo and Delong 1996). However, lesions in specific portions of the brain, particularly the cerebellum, more or less reliably lead to dorsal extensor rigidity. Opisthotonus has been experimentally induced in birds by destroying certain regulatory regions of the cerebellum (Ariens Kappers et al. 1960) and observed in turkeys in which nutritional thiamine deficiency led to swelling of the cerebellum (Swank 1940; Klein et al. 1994). Opisthotonus secondary to asphyxia has been produced experimentally in rabbits (Saunders and Harris 1990).

The physiological mechanism that produces the onset of opisthotonus is also understood medically. The cerebellum is critical for control of the dorsal extensor muscles. This part of the brain is not involved in conscious control of movement; rather, it refines and coordinates postural signals. The cerebellum actually works much like a damper on nervous excitation of the extensor muscles. In other words, if cerebellar control is removed, the neurons that signal extensor muscles to contract are uninhibited, resulting in an overcontraction of the extensor muscles, particularly of the neck and back. A cerebellar lesion may produce either flexor or extensor contraction in the forelimbs, depending on the area of the cerebellum that is affected, and will generally produce flexor contraction in the hindlimbs (Holliday 1980; Bagley 2005; Lorenz and Kornegay 2004).

In wild animals, terminal hypoxia (lack of oxygen) from circulatory collapse secondary to trauma, disease (such as meningitis), viral agents, and toxins are the most likely primary triggers of opisthotonus (as opposed to anesthetics or other unnatural agents). Events that result in asphyxiation or respiratory failure and lead to brain injury—such as traumatic injury, drowning, dehydration, or poisoning—can result in opisthotonic posturing. In such cases, opisthotonus is occurring *perimortem,* during the death throes of the animal, not postmortem, and it reflects the release of the dorsal musculature from central nervous system control (Holliday 1980; de Lahunta 1983; Bagley 2005).

Discussion

What Explains the Opisthotonic Posture in Fossil Skeletons?

Among the plethora of explanations proposed for the opisthotonic posture, most can be eliminated by circumstantial or experimental evidence, including the abiotic effects of postmortem transport and disarticulation by currents and scavengers, and the biotic hypotheses of diving into shallow mud and death in a natural sleeping posture. *Rigor mortis*, ligamental or tendinous contraction, drying, and hypersalinity, like postmortem repositioning by currents, do not adequately explain the frequency or patterns of distribution of the hyperextended posture of the spinal column found in the fossil record, particularly in terrestrial sediments that are not heavy-flood or fluvial deposits.

The available evidence shows that, instead of being a postmortem artifact, the true opisthotonic posture is a consequence of the spasmodic response of the animal's CNS and musculoskeletal systems to hypoxia and other CNS diseases experienced in the final moments of life. The subsequent onset of rigor mortis would (temporarily) fix the carcass in this position, if it is not previously disturbed, and burial would provide ultimate preservation. So it could be concluded that, in general, vertebrate skeletons preserved in the opisthotonic position were buried soon after death, generally without substantial transport, and did not suffer extensive deterioration from currents or scavengers.

We conclude that Moodie's (1918, 1923) long-discounted explanation of the opisthotonic posture in articulated fossil vertebrate skeletons is correct, and that the explanations predominantly accepted by paleontologists (*rigor mortis,* desiccation, contraction of muscles, ligaments, or tendons) fail to explain most if any cases. Our experiments are of course not exhaustive, and need further testing; but we could not reproduce results inferred by hypotheses other than the one demonstrated repeatedly by clinical observations of living animals.

Does Opisthotonus Have a Phylogenetic Signal?

One test of the validity of the redundant pattern of the occurrence of the opisthotonic posture is its phylogenetic distribution (Fig. 4). A true opisthotonic posture appears most redundantly (i.e., repeatedly, providing a reliable pattern) and almost exclusively in certain groups of amniotes: pterosaurs, birds and other non-avian dinosaurs, and in crown-group placental mammals (Weigelt 1927). Examples of these clades are provided in Figures 1 and 3–5. The opisthotonic posture is especially common in dinosaurs (including birds) and pterosaurs. Theropod dinosaurs so affected include *Coelophysis*, *Allosaurus*, *Compsognathus*, many ornithomimids and tyrannosaurids, and the vast majority of *Archaeopteryx* specimens as well as the ''feathered dinosaurs'' from the Liaoning Province of China. Examples occur in sauropod dinosaurs from *Mussaurus* (Bonaparte and Vince 1979) to *Mamenchisaurus* (Fig. 1J). Ornithischian dinosaurs do show the opisthotonic posture in a somewhat less pronounced way than saurischian dinosaurs do, but they have shorter necks than saurischians; furthermore, euornithopods have ossified tendons along most of the vertebral column (including the tail) and high spines, both of which would limit spinal flexion. The most commonly preserved ornithischians either have very large skulls (e.g., ceratopsians) that would be expected to be difficult to raise very far, or heavy carapaces (ankylosaurs) or paravertebral spikes and plates (stegosaurs) that would inhibit hyperextension of the vertebral column. Nevertheless, a Dalian Museum specimen of *Jeholosaurus*, a basal ornithopod from the Jehol Biota (Fig. 1D), clearly shows the condition, as does an undescribed juvenile specimen of *Tenontosaurus* in the Oklahoma Museum of Natural History (Fig. 1I) (Brinkman et al. 1998).

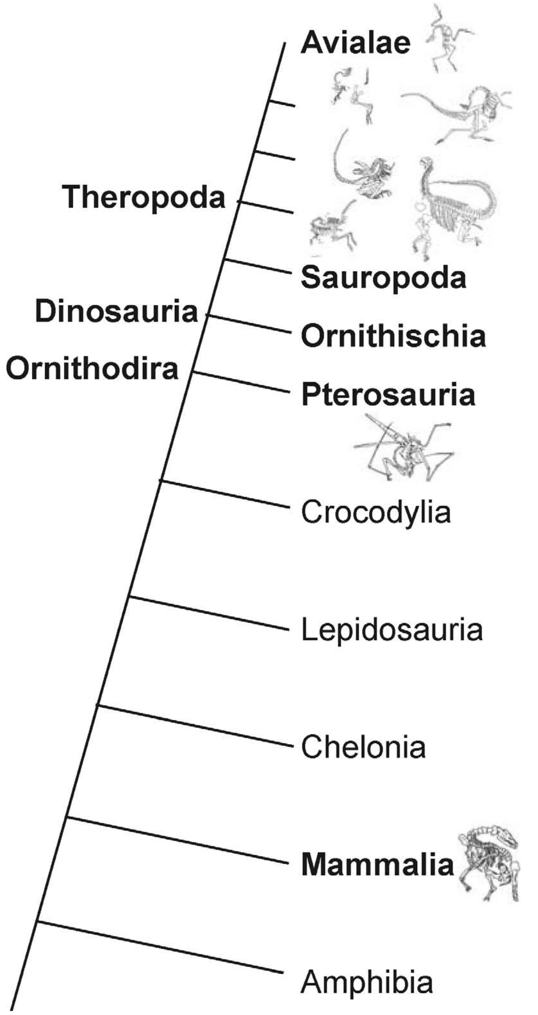

FIGURE 4. Cladogram showing distribution of the living and fossil amniote groups in which the opisthotonic posture has been identified (bold type). Opisthotonus appears to have evolved as a syndrome twice: once in mammals and once in ornithodiran archosaurs.

Almost unexceptionally, when the spinal column is curved in non-ornithodiran reptiles the curvature is pleurothotonic (side to side),

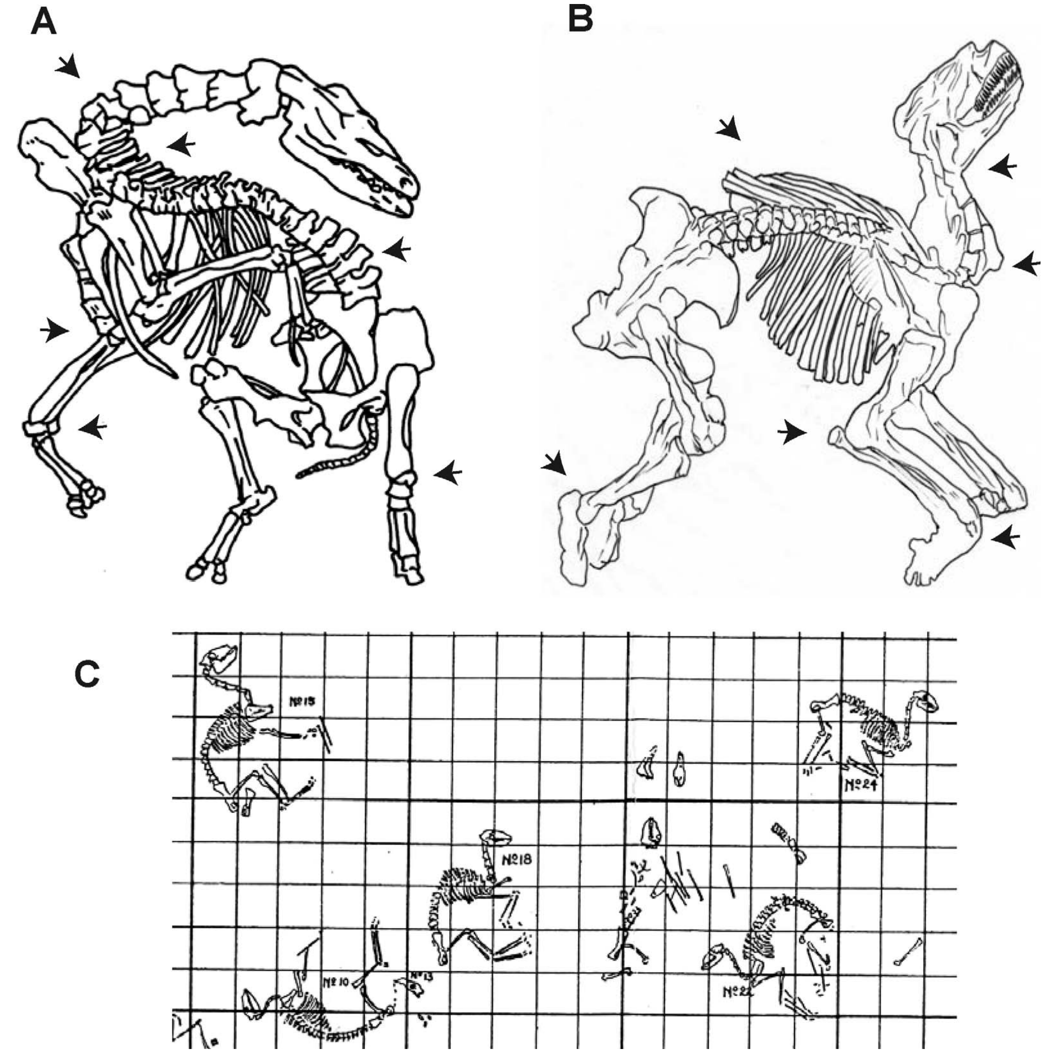

FIGURE 5. The opisthotonic posture in fossil placental mammals. A, The Eocene perissodactyl *Palaeotherium*, from the Paris Basin of France, after a sketch by Weigelt (1927); specimen mounted in the National Museum of Natural History, Paris; skull length approximately 68 cm. B, The Oligocene notoungulate *Scarrittia*, after a photograph in Chaffee (1952); AMNH 29571; skull length 48 cm. C, Detail of the Stenomylus Quarry map (Oligocene), from Peterson (1911); grid squares are 30 cm on a side.

not opisthotonic (dorsoventral). Moodie (1918) suggests four exceptions, all crocodile skeletons, from the Jurassic of Cerin, France, described by Lortet (1892). However, we have reservations about his diagnoses. In three of the four *Alligatorellus* (atoposaurid) skeletons, the neck is indeed flexed dorsally but neither the back nor tail is, and the limbs are extended flaccidly. The fourth case is clearly pleurothotonic, as are many examples of Lortet's sphenodontids (*Homoeosaurus*, *Sauranodon*, and *Pleurosaurus*). A different, possibly valid crocodile example is a beautifully preserved *Diplocynodon* from the Eocene Messel shales near Darmstadt, Germany (Schaal and Ziegler 1988: p. 109, Fig. 167); but other Messel crocodiles do not seem to show opisthotonic features (nor do atoposaurids from the Solnhofen [Wellnhofer 1971]).

(Moodie [1918] also suggested that several examples of fossil fishes may show opisthotonus [see also Viohl 1985, 1994], but we suspect that these are either pleurothotonic and laterally compressed or otherwise distorted.

When fish carcasses bloat the abdomen distends and the anterior skeleton may be flexed dorsally as well as laterally [Weigelt 1927; Grande 1984].)

Among mammals the condition is more difficult to delineate phylogenetically. We provide figures of crown-group placentals that display the opisthotonic posture, but we have been unable to find reliable examples in monotremes and marsupials. Surveys of Permo-Triassic faunas and consultations with experts (K. Angielczyk, B. Rubidge, C. Sidor, R. Smith, personal communications 2006) have not turned up examples of the opisthotonic posture in non-mammaliamorph synapsids, although lateral flexion and ''curling up'' (pleurothotonus) of skeletons is common. We were also unable to confirm the condition in the various mammaliaforms found in the Jehol Biota (see below). This absence of evidence is significant, because virtually every dinosaur (including birds) and pterosaur shows the opisthotonic posture, which testifies to some kind of environmental poisoning that we hypothesize should have affected the mammals in the same way. There are clear examples of the opisthotonic posture in fossil placentals, including palaeotheres, notoungulates, and camelids (Fig. 5), but the phylogenetic limits of this syndrome in more basal mammaliamorphs need further testing.

It is indeed difficult sometimes to detect opisthotonic conditions in mammals that have relatively short necks and tails. However, even humans who are affected by strychnine or other tetanic-producing poisons, meningitis, some anesthetics, and certain diseases show this posture (Moodie 1923; Sullivan 1970; Sukoff and Ragatz 1980; Ondo and Delong 1996).

What features, if any, does this pattern suggest? Each of the clades that shows the opisthotonic posture is known (in living forms) or inferred (in fossil forms on the basis of independent lines of evidence [de Ricqlès 1980; de Ricqlès et al. 2000; Schweitzer and Marshall 2001; Padian et al. 2001; Padian and Horner 2004]) to comprise animals that have elevated basal metabolic rates and a thermal physiology that would best be described by the term *endothermy.* This posture is not reliably identified in amphibians or other reptiles, such as lizards and crocodiles (Weigelt 1927). This does not mean that in the former clades the death posture will always be opisthotonic, as living birds and mammals attest; so we need draw no conclusions simply because *Rhamphorhynchus* shows a lower frequency of the opisthotonic posture than *Pterodactylus* and other Solnhofen ornithodirans do. The point is that only ornithodirans and mammals are reliably reported to show it at all.

What specific mechanism could account for why a malfunction of the CNS would so radically affect animals with apparently high basal metabolic (and hence respiratory) rates, but not those with lower metabolic rates? As noted above, when cerebellar control is removed, as for example during hypoxia, the neurons that signal extensor muscles to contract are uninhibited, resulting in an overcontraction of the spinal extensors. Because endothermic vertebrates have metabolic rates up to 17 times higher than ectothermic vertebrates (Nagy 1987), the opisthotonic posture might be expected to occur in animals that normally operate at higher levels of oxygen consumption. Animals with low basal metabolic rates, on the other hand, are more accustomed to operating at relatively low levels of oxygenation, and would not be expected to be so strongly affected.

Opisthotonus: A Faunal Test of a Phylogenetic Signal

One way to test the hypothesized phylogenetic pattern is in fossil Lagerstätten where a diversity of fossil vertebrates is preserved. When some taxa appear consistently to show diagnostic criteria of the opisthotonic posture, whereas others do not, the consistent pattern allows a unified explanation of cause of death and a validation of the phylogenetic signal.

One example is the now-famous Jehol Biota from the Early Cretaceous Liaoning exposures of northeastern China (e.g., Chang 2003; Zhou et al. 2003). Although these specimens come from a variety of geographic locales and stratigraphic horizons, most share the same general features of preservation, suggesting that their environments and even conditions of death may have had much in common from one locality to another. In this case, volcanic

TABLE 2. Jehol Biota tetrapod specimens illustrated in a CD-image catalog of the Dalian Natural History Museum (2005), with taxonomic distribution of specimens showing opisthotonic and non-opisthotonic posture. Identifications as in catalog. Specimen numbers (when more than 1) in parentheses; disarticulated or poorly preserved specimens not considered. Catalog numbers were not provided in the reference. All complete, articulated specimens of ornithodiran reptiles (including birds) showed the opisthotonic posture.

NON-OPISTHOTONIC SPECIMENS

Amphibians: *Jeholotriton* (4), indeterminate newt; *Dalianbatrachus*, indeterminate Anura
Non-ornithodiran reptiles: *Ikechosaurus*, *Monjurosuchus*, *Hyphalosaurus* (3), indeterminate Choristodera [all choristoderans]; *Yabeinosaurus*, *Liaoningosaurus*, indeterminate lizard (2)[all lepidosaurs]; *Manchurochelys*, indeterminate Testudines [both Chelonia]
Omithodiran reptiles (Ornithischia): *Psittacosaurus* (2)
Mammalia: *Eomaia*; *Repenomamus*

OPISTHOTONIC SPECIMENS (ALL ORNITHODIRAN REPTILES)

Pterosauria: Pterodactyloidea (2)
Ornithischia: *Jeholosaurus* (2)
Non-avian theropods: *Sinovenator*, *Mei*, *Sinosauropteryx*, *Sinornithosaurus*, indeterminate maniraptoran, *Microraptor* (3), *Caudipteryx*, *Shanzhouraptor* (2), indeterminate dromaeosaur (2)
Birds (avian theropods): *Confuciusornis* (12,+2 indeterminate), *Protopteryx*, Enantiornithes (9), *Eoenantiornis*, *Sapeornis* (2), *Longipteryx*, indeterminate Aves (2)

activity associated with the fossiliferous beds (Zhou et al. 2003) permits the inference that atmospheric poisoning and asphyxiation, consistent with CNS damage, may have contributed to the mass mortality. A recent catalog from the Dalian Natural History Museum (2005) in Dalian, China, displayed 86 Liaoning specimens from all major tetrapod groups. Of these, 56 (65%) were of ornithodirans (pterosaurs, birds, and other dinosaurs). All the ornithodirans except two of the four ornithischian dinosaurs were preserved showing virtually all diagnostic criteria of the opisthotonic posture (i.e., a 4 or 5 on our scale), whereas none of the other tetrapods showed opisthotonic features (Table 2). The two *Psittacosaurus* specimens, with large skulls and relatively short tails, did not obviously display the opisthotonic posture, although the two specimens of the basal ornithopod *Jeholosaurus* (Xu et al. 2000) did. The four mammaliamorphs showed no clear signal, although most were incomplete or disarticulated. It could be that by coincidence virtually all the ornithodirans died under circumstances that the other vertebrates escaped; however, we suspect it is more likely that most or all of the affected vertebrates died from the same cause, but that only the ornithodirans were able, for whatever anatomical or physiological reasons, to express the opisthotonic posture. (The Jehol mammaliamorphs require further study: see below.)

An independent compendium of Jehol vertebrates edited by Chang (2003) shows a similar pattern (Table 3). Of 58 figured skeletal specimens, 36 (62%) did not show the opisthotonic posture and 22 (38%) did. Only pterosaurs and dinosaurs (including birds) were in the latter group; other reptiles and amphibians never were, nor were the five mammaliamorph specimens.

In the Early Jurassic Holzmaden black shales of Germany, there are no known articulated dinosaurs, but there are pterosaurs and non-ornithodiran reptiles (Hauff 1960). The pterosaurs (*Dorygnathus* and *Campylognathoides*) sometimes show the opisthotonic posture (Padian unpublished notes), but other reptiles never do (Hauff 1960). In the Late Jurassic Solnhofen limestones of Germany, as already noted, the crocodiles and squamates are not known to show the opisthotonic posture. Among pterosaurs, some rhamphorhynchids do, and most pterodactyloids do. Among dinosaurs, the two specimens of *Compsognathus* do, and all the articulated specimens of *Archaeopteryx* do.

A further test comes from the Eocene fauna of the Messel oil shales near Darmstadt, Germany (Schaal and Ziegler 1988). Among the figured specimens, none of the known non-avian specimens (8 amphibians, 6 turtles, 4 crocodiles, 11 lizards, and 4 snakes) show signs of the opisthotonic posture; all 13 birds do. However, the mammals are difficult to interpret in this regard. The skulls are almost

TABLE 3. Jehol Biota tetrapod specimens illustrated in Chang et al. 2003, with taxonomic distribution of specimens showing opisthotonic and non-opisthotonic posture. Identifications as in catalog. Specimen numbers (when more than 1) in parentheses; disarticulated or poorly preserved specimens not considered. Catalog numbers were not provided in the reference. All complete, articulated specimens of ornithodiran reptiles (including birds) showed the opisthotonic posture.

NON-OPISTHOTONIC SPECIMENS

Amphibians: *Callobatrachus*, *Mesophryne*, *Sinerpeton*, *Lacotriton*, *Jeholotriton* (2), *Chanerpeton*, *Liaoxitriton*
Non-ornithodiran reptiles: *Monjurosuchus* (3), *Hyphalosaurus* (5) [both choristoderans]; *Yabeinosaurus* (2), *Dalinghosaurus*, *Jeholacerta*, [all lepidosaurs]; *Manchurochelys*, indeterminate Testudines [both Chelonia]
Mammalia: Specimens of *Zhangeotherium* (2), *Jeholodens*, and *Sinobaatar* were preserved in dorsoventral view and showed no obvious signs of opisthotonus; nor did *Eomaia*, in lateral view

OPISTHOTONIC SPECIMENS (ALL ORNITHODIRAN REPTILES)

Pterosauria: *Jeholopterus*, *Sinopterus*
Non-avian theropods: *Sinosauropteryx*, *Microraptor*, *Caudipteryx* (2)
Birds (avian theropods): *Confuciusornis* (5), *Jeholornis*, *Cathayornis*, *Liaoxiornis*, *Protopteryx*, *Eoenantiornis*, *Sapeornis*, *Longipteryx*, *Liaoningornis*, *Yanornis*, *Yixianornis*

never thrown over the back, even if the (relatively short) necks are (somewhat naturally) curved; and the tails, when long, are almost always curved ventrally, not reflected dorsally. Nor are the spinal columns bowed ventrally. The limbs are frequently flexed to a greater degree than in life. The signals are not as clear as in some mammalian specimens from other horizons (Fig. 5). Koenigswald et al. (2004) noted that five out of about 50 skeletons of the Messel ungulate *Propalaeotherium* are of pregnant females, and inferred from this that the deaths may have occurred in late Spring, when it is possible that toxic cyanobacterial blooms polluted the lake and poisoned animals that drank or lived in its waters. This may explain the opisthotonic posture of the birds and perhaps some mammals (such as the bats); however, the *Propalaeotherium* specimens that Koenigswald et al. figured do not show strong evidence of the opisthotonic posture (see also Braun and Pfeiffer 2002).

Opisthotonus and Paleoecology

If opisthotonus is a result of hypoxia, poisoning, or other CNS damage, what does its occurrence tell us about the circumstances of an individual's death? It may have contracted an infection, a respiratory illness, a deficiency of a necessary nutrient; or it could have ingested a toxin. Supporting biochemical evidence for such causes is difficult to find in fossils that lack preserved soft tissues, but they remain possible causes.

Another set of explanations involves lack of oxygen (hypoxia). This condition could be brought about by choking, blood loss, atmospheric poisoning, suffocation by burial or other cause, or drowning (in freshwater). At least the last three of these factors may have supporting evidence available in the surrounding sediments. Less obvious would be factors related to dehydration or starvation, which could also result in malfunction of the CNS; they might be discernible from evidence of desert conditions.

For terrestrial carcasses, the opisthotonic posture can be manifested only in individuals that did not experience transport, scavenging, or other disturbance after death. We have detailed above many of the clinical causes of opisthotonus in living animals. Drought has frequently been invoked as an explanation of the opisthotonic condition in animals that have died on land, but it has often been assumed that desiccation produced it. Although drought would be a valid cause of CNS damage leading to the opisthotonic posture, desiccation after death appears not to be a valid explanation. Rather, the skeleton assumed the posture at the time of death, which implies a perimortem rather than a postmortem cause.

One possible cause of death, during which the opisthotonic condition may be manifested, is infection of the CNS pursuant to an injury, and this may show up in the skeleton. For example, the opisthotonic specimen of *Allosaurus* that Hanna (2002) described presented numerous bony lesions that suggest a blood-borne spread of bacteria to bones and joints.

Bacterial infection is a common cause of meningitis, which in turn is a common cause of opisthotonus (Ondo and Delong 1996). Although it is nearly impossible to demonstrate directly that a particular fossilized specimen died from any particular lesion or infectious disease, the point is that such lesions and diseases, and not postmortem causes, are correlated with the opisthotonic posture.

In some cases, it may be possible to test such a diagnosis from independent lines of evidence. For example, a toxin in an animal's environment of preservation—if that is where the animal died—might have been the cause of death. This hypothesis can be tested by geochemical means if the toxin has been preserved, but this is less likely in the case of biotic toxins or any others that deteriorate with time. An unusual case of opisthotonic posture in connection with apparently toxic environmental conditions may have obtained in the preservation of a bird carcass as a mold in the Quaternary sediments of the hot springs of Yellowstone National Park (Channing et al. 2005). The head and neck were reflexed over the back, as in characteristic opisthotonus; as the authors noted, the hot springs may have at once attracted and poisoned the bird. It seems most plausible that asphyxiation resulted in opisthotonus, and that after death the carcass was swiftly entombed in that position (perhaps in a state of rigor mortis). The rapid burial and immobilization of the carcass would force us to reject hypotheses of desiccation, rigor mortis, contraction of muscles, ligaments, or tendons, or hypersalinity as explanations of opisthotonus. In these ways, individual cases of the opisthotonic posture may be explained by more or less substantiated hypotheses, even if none is necessarily conclusive.

But we may also move beyond the individual to the general in some cases. The ''hypoxic'' hypothesis of opisthotonus, if generalized as we suggest, should substantially change the interpretation of some paleoenvironmental deposits and of the circumstances of death of individual specimens. It would be testable by examining whether a significant number of skeletons from the same deposits exhibited the opisthotonic posture. In the Jehol Biota, as noted above, ash deposits indicate volcanic activity, which in addition to entombing the carcasses may have contributed to the asphyxiation of the animals. This is also the prevailing explanation for the mass deaths of notoungulates and other mammals in the Scarritt Pocket (Lower Oligocene: Deseadan) of Patagonia (Chaffee 1952), many of which are preserved in the opisthotonic posture. The locality is the site of a pond within a caldera from which it is presumed that volcanic gases were periodically escaping, accompanied by ashfalls, which together would have asphyxiated and then quickly buried the animals to prevent further disturbance.

A well-known example of mass death (which surprisingly has not been restudied for nearly a century) is the *Stenomylus* Quarry, a camelid fossil site from the Miocene of Nebraska (Loomis 1910; Peterson 1911; see Fig. 5C). The taphonomic interpretation traditionally has been that a herd met with a catastrophe upstream and floated down to be lodged ''in the backwater of some large cove in which sands were accumulating behind a barrier of considerable elevation'' (Peterson 1911: p. 268). But these skeletons are not preferentially oriented in any direction, nor are their long necks and limbs aligned with current flow, and there is little evidence of disarticulation or scavenging (as, for example, in the *Centrosaurus* bone beds described by Ryan et al. [2001]); in fact, most skeletons are preserved down to their cartilaginous ribs (Loomis 1910). Rather, the carcasses are preserved overwhelmingly in the opisthotonic posture (Fig. 5C), suggesting little or no postmortem disturbance or transport, but rather one of the biotic causes of death that damage the CNS.

In a different example, the prevalence of opisthotonic posture in carcasses from the Solnhofen deposits indicates not only quiet waters, rapid burial, and the absence of pervasive scavenging (as many authors have established), but also the possibility that the environment itself was sometimes toxic (e.g., from algal blooms or ''red tide'' [Barthel 1970]). If toxicity, and not hypersalinity, was a principal cause of the preserved positions of so many skeletons, then the focus of explanation should not be postmortem but perimortem. It raises anew the question whether the pterosaurs, birds, and terrestrial dinosaurs (who obviously did not live in the lagoon waters) died in the lagoon for some reason, or died very near it and were rapidly immersed and buried in it. A similar pattern seen in the Messel Eocene biota has been attributed to cyanobacterial blooms, as noted above (Koenigswald et al. 2004).

Without attempting a Jurassic version of the detective shows *CSI* or *Cold Case,* we suggest that some further inferences about circumstances of death may be possible for some fossil specimens. For example, the juvenile *Camarasaurus* specimen shown in Figure 1F clearly displays the opisthotonic posture, and associated with it are clear symptoms of decerebellate rigidity: the forelimbs are rigidly extended, and the left hindlimb is flexed (the right is not visible). If this posture can be taken at face value, and if the causes that present these symptoms are the same as in mammals and birds, a primary indication is damage to the caudal cerebellum (Bagley 2005). (This assumes that sauropods, like mammals and birds, had high basal metabolic rates, which has been inferred from their bone growth rates [Sander 2000; Curry 1999]. Although the animals in question differ in cerebellar anatomy, it cannot be presumed that cerebellar function differs accordingly.) The damage could have resulted from various forms of hypoxia, including blood loss due to trauma (internal or external), meningitis, neurotoxins, drowning, or choking, among other causes.

These and other examples suggest that reevaluation may be in order for an untold number of paleoenvironments whose story has been at least partly explained on the basis of the death positions of many of their fossil vertebrates. We might suggest a tentative further step. It has often been said that microbial diseases must have been important in shaping the history of life by contributing to extinction of species that could not mount sufficient resistance to them. Whereas individual localities, even with mass deaths, can at best point only to extirpation of a population and not extinction of a species, at least a correct interpretation of the opisthotonic posture may provide some basis for the further assessment of microbial influence on populations, given additional independent lines of evidence.

Conclusions

As far as we can determine, the overwhelming evidence supports a single general explanation for the opisthotonic posture seen in many fossil amniotes: it is the consequence of ‘‘death throes’’ and not of postmortem processes. That is, the individual was already in this position at the time of death. Certainly not every apparent case of the opisthotonic position is the result of perimortem contractions. However, most traditional interpretations and explanations of the ‘‘dead bird’’ posture explain few or no cases. Physiological (biotic) rather than taphonomic (abiotic) processes provide a better explanation of the opisthotonic posture, and among physiological explanations, only perimortem contraction of muscles has been validated experimentally, whereas other hypotheses can be rejected or are generally unsubstantiated. Opisthotonus reflects a malfunction of the CNS in certain groups of amniotes, and paleoecologists and taphonomists may gain substantial insights about the conditions of death of their subjects, and the environments in which they lived, by taking into account the timing as well as the biotic cause of the opisthotonic posture. A single individual preserved in this position may say little about environmental conditions, and more about its own health at the time of death. Conversely, if many cases of the opisthotonic posture are found in fossil specimens from the same deposit, an environmental cause may well be suspected. Finally, the phylogenetic pattern that we induce from the variety of fossil and extant cases of the opisthotonic posture suggests a correlation with high basal metabolic rates, but this hypothesis requires further investigation and testing.

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Note added in proof:

Liz Reed (University of Flinders, Australia) reports witnessing the adoption of the opisthotonic posture in kangaroos, just prior to death, for example after having been poached by hunters (personal communication 2007). This confirms that the phenomenon is not postmortem, but perimortem, and would appear to extend its phylogenetic distribution among synapsids to marsupials as well as placentals. Its possible occurrence in monotremes and other groups of extinct mammals is as yet unknown. Because marsupials are warm blooded, the inference of association of opisthotonus with elevated metabolic rates that we suggest here is reinforced. We are grateful to Dr. Reed for her help.