SCELIDOSAURUS HARRISONII OWEN, 1861 (DINOSAURIA: ORNITHISCHIA) FROM THE EARLY JURASSIC OF DORSET, ENGLAND: BIOLOGY AND PHYLOGENETIC RELATIONSHIPS

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Abstract:	A layer of keratinous scutes encased the skull of Scelidosaurus. The neurocranium as well as the associated principal sensory systems of this dinosaur are described. The cranial musculature is reconstructed and a subsequent functional analysis suggests that jaw motion was orthal, allowing pulping of vegetation and some high-angle shearing between opposing teeth. Wishboning of the lower jaw was enabled by transverse displacement of the quadrates; and the long-axis mandibular torsion that occurred during the chewing cycle was permitted by flexibility at the dentary symphysis. Limb proportions and pectoral and pelvic musculature reconstructions suggest that Scelidosaurus was a facultative quadruped of ‘average’ locomotor ability; it retains some anatomical features indicative of a bipedal-cursorial ancestry. Hindlimb motion was oblique-to-parasagittal to accommodate the girth of the abdomen. Scelidosaurus used a combination of costal and abdominally driven aspiration. The hypothesis that respiration was an ‘evolutionary driver’ of opisthopuby in all dinosaurs is overly simplistic. A critical assessment of datasets used to analyse the systematics of ornithischians (and thyreophoran subclades) has led to a revised dataset that positions Scelidosaurus as a stem ankylosaur, rather than a stem thyreophoran. The value of phylogenetic definitions is reconsidered in the light of the new thyreophoran cladogram.

Notes for the copy editor:

1. Heading notation used herein:
[A] centred caps
[B] centred itals
[C] lh ital. new line
[D] lh ital. run on

I don't indent the first para after all non-run-on headings (stylistic preference). And, I tend not to indent at the beginning of new sections within body text (and after quotations).

2. I have attempted to use "ize", except where this is completely inappropriate (e.g. exercise, etc.)

3. In-text ref. punct: Author (date); Author, date; Author & Author, date; Author *et al.,* date; Author *et al*. (date). This seems to conform with recent ZJLS style.

4. I prefer not to use the 'Oxford comma' unless it is obvious, in a syntactical sense.

[A] INTRODUCTION

Scelidosaurus harrisonii Owen, 1861 is, paradoxically, the earliest known (1858) substantially complete dinosaur (Norman, 2000, 2001) and yet, at least until recently (Norman, 2020a,b,c) has been among the least well understood of dinosaurs. A combination of historical neglect of dinosaurian studies in Britain, at least until the 1970s, and the formidable difficulties of preparing delicate specimens from their limestone encasement, partly explains why the animal lay scientifically dormant for over a century and is only now being fully described another half century later.

The remains of *Scelidosaurus* have (to date) been collected exclusively from late Sinemurian (Early Jurassic ~193 Ma) cliff exposures on the "Jurassic Coast" (a UNESCO World Heritage Site) near the village of Charmouth in west Dorset, England (Fig. 1). There have been reports of *Scelidosaurus* sp*.* in China (Lucas, 1996) and North America (Padian, 1989). *Tatisaurus oehleri* Simmons, 1965 from the Lower Lufeng Formation (?late Sinemurian) of Yunnan Province in China was referred to *Scelidosaurus* by Lucas (1996) but is a *nomen dubium* (Norman, Butler & Maidment, 2007). Several osteoderms collected in the Kayenta Formation (?Pliensbachian) of Arizona, USA were referred to '*S. harrisoni*' by Padian (1989) on the basis of their greater size than known osteoderms of the coeval taxon *Scutellosaurus lawleri* Colbert, 1981, and general similarity in morphology to those attributed to *Scelidosaurus.* These specimens were not assigned to this taxon on the basis of specific diagnostic characters so they cannot be confirmed as referable to *Scelidosaurus*, or more specifically *S. harrisonii*, until more reliably diagnostic skeletal material has been collected and described.

Two other taxa have been referred to the family Scelidosauridae. *Lusitanosaurus liasicus* Lapparent & Zbyszewski, 1957 (Antunes & Mateus, 2003) was created for the fragmentary remains of a maxilla with some teeth; it is unfortunate that this material is of unknown provenance and age. Originally considered to be stegosaurian, *Lusitanosaurus* was later referred to the family Scelidosauridae because it was clearly ornithischian and thought to be Liassic in age. This taxon cannot be diagnosed and is of uncertain provenance, so it can only be considered a *nomen dubium* (Norman *et al.,* 2004). *Bienosaurus lufengensis* Dong, 2001 was established for some crushed and fragmentary cranial remains approximately contemporary with those of *Tatisaurus oehleri* (above). These remains, referred to as *incertae sedis* (Norman *et al.,* 2004), are now considered undiagnosable (Raven, Barrett & Maidment, 2019).

<Figure 1 near here> Charmouth/Church Bay

The scelidosaur remains collected from the cliffs and foreshore at Charmouth range in quality from isolated fractured and water-rolled bones through to partial or sometimes nearly complete skeletons that range between ~1.5 and ~4.5 metres in length (Norman, 2020a). There has been a slow but relatively steady trickle of specimens emerging from the cliffs of Black Ven (Fig. 1) and these are often associated with local cliff collapses or small landslides that occur after stormy weather. The poorly consolidated nature of the Lias in this area is such that small cliff collapses occur regularly as a consequence of water-lubricated rotational faulting. Identifying the precise bed from which clay-smeared fossils or fossiliferous nodules (found on the scree slopes) emerge can be extremely difficult. There is however a suspicion (based on the long experience of local collectors – David Sole, pers. comm.

2018) that fossils of *Scelidosaurus* are particularly localised on Black Ven; they may only (or very largely) pertain to one specific limestone bed (W.D. Lang's Topstones (Bed 85) – see Norman, 2020a: fig. 7). The limestone bands within the Black Ven Mudstone sequence are diagenetic, reflecting short periods of coarser (higher energy) terrigenous sedimentary input. This coarser sedimentary fabric is more porous than the largely impermeable clay-rich Black Ven Marl sequences, and allows saturated ground water to percolate through these layers and precipitate carbonate. The carbonate tends to crystalise and 'nucleate' on and around skeletal material, leading to the growth and formation of lenticular 'doggers' that surround and eventually enclose these bones. These lenticular bodies may continue to enlarge so that adjacent ones coalesce over time if carbonate precipitation continues. The gradual merging of doggers can ultimately lead to the formation of irregular (lumpy) 'benches' or more laterally continuous hard limestone-rich bands. It is conceivable that many of the dinosaur skeletons that have been recovered from a single limestone band (bed) were victims of a local flooding event and that their carcasses (representing a sample of different aged individuals) were transported by a river, briefly in spate, into the quiet-water near-shore marine setting where they settled and were subsequently buried.

The two original monographs on this dinosaur (Owen, 1861, 1863) focused primarily on osteology insofar as it had been revealed through some associated small bones (Fig. 2) and others of an articulated larger skeleton partly exposed on the surface of a more or less contiguous set of marly limestone (marlstone) slabs (Fig. 3). Three much more recent articles (Norman, 2020a,b,c) summarise what is currently known of the anatomy of *Scelidosaurus*. This article explores some of the palaeobiological, palaeoecological and phylogenetic aspects of this historically important and chronostratigraphically early ornithischian dinosaur.

[B] Historical review of scelidosaur biology and habits

Richard Owen produced a bewildering range of observations and suggestions concerning the morphology as well as the inferred biology and habits of

Scelidosaurus. These have persisted in various guises to the present day in the absence of any detailed follow-up work on this taxon. For example, in relation to its locomotor ability and life habits, Owen observed (somewhat tangentially) that:

> "To whatever extent the Saurian organization has been modified for terrestrial life, that [*sic* = there] has been, in no instance, such as to suggest an inability to swim. On the contrary, the disproportionate shortness of the fore limbs, even in the Iguanodon [*italics*], leads to the suspicion that they might be short in reference to diminishing the obstacles to propelling the body through water by actions of the strong and vertically extended tail; and that, as in the living land lizard of the Gallopagos [= Galápagos] Islands, called *Amblyrhynchus*, the fore limbs might be applied close to the trunk in the Iguanodon [*italics*], when it occasionally sought the water of the neighbouring estuary or sea." (Owen, 1861: 6).

<Figure 2 near here> Owen Tab. 3: 'foetal' bones of a small scelidosaur

Owen became even more speculative in relation to the reproductive biology and habitat preferences of scelidosaurs:

> "One would suppose that the newly born or newly hatched young of a Dinosaur might be safer on shore than at sea, or at least in waters which, like those of the Liassic ocean, seem to have swarmed with carnivorous Enaliosaurs [Owen's plesiosaurs and ichthyosaurs]. If the Dinosauria were ovo-viviparous, and produced but a few young at a birth, the remains from the lower Lias figured in Tab. III [see Fig. 2] might be those of a foetus borne by a gravid Scelidosaur to sea during an occasional excursion, and which by some casualty had there perished, and become imbedded, with her progeny, in the muddy bottom of the old Liassic ocean. I have not, however, been able to obtain precise evidence of the proximity of the small bones above described with any of the larger ones attributed to the *Scelidosaurus*, and bones of more than one small individual might have been expected to occur in juxtaposition if they had perished before birth. The analogy with the crocodile, moreover, would lead us to expect that the newly excluded or newly born Scelidosaur would be of a smaller size than the individual indicated by the bones in Tab. III." (Owen, 1861: 6-7).

In relation to the diet of scelidosaurs, Owen made the following ambiguous observations:

> "The finely and sharply serrated and pointed teeth of the *Scelidosaurus* glided upon each other, the upper on the outerside of the under, like the blade-shaped crowns of the carnassials of feline mammals; and yet the similarity of teeth, in their number and uniformly small size, to those of the modern Iguanas suggests that they may have been put to like uses. The compressed, serrate crowns in those herbivorous lizards worked obliquely upon each other, in a similar scissor-blade way. In *Iguanodon* the dentition is obviously modified more decidedly for mastication of vegetable substances. In *Scelidosaurus* it is adapted for division of such substances, but it would be equally effective in piercing and cutting or tearing through animal textures.
>
> "If this Dinosaur occasionally went to sea in quest of food, it may be expected to present in the fore part of the jaws, wanting in the present specimen, laniariform teeth, as in *Echinodon*, for the prehension and retention of living prey. Should these prove to be absent, and the dental series to begin as it ends, it will incline the balance of probability to the phytophagous nature of the Liassic *Scelidosaurus*." (Owen, 1861: 14).

<Figure 3 near here> assembled bones of the lectotype>

After describing parts of the vertebral column of the lectotype of *Scelidosaurus* (NHMUK R1111) in the second monograph, Owen concluded with the following remark:

> "I infer … especially for *Scelidosaurus*, a greater aptitude for swimming than in the larger *Dinosauria.*" (Owen, 1863: 12).

The functionality that he proposed for the forelimb and pectoral girdle was summarised in the following way:

> "… the functions of the fore limb seem, therefore, to have been less important in regard to locomotion on land than in *Iguanodon*, *Megalosaurus,* and modern Lizards." (Owen, 1863: 14).

The hindlimb and pelvis did not provoke specific interpretation, except that Owen noted that the length of the hindlimb of *Scelidosaurus* was proportionally greater than that seen in crocodiles and that its feet were generally shorter and broader than those of the latter. He regarded the scelidosaur limb proportions as being intermediate between those of crocodilians and lizards.

In Owen's insightful biostratinomic analysis of the lectotype skeleton some interesting (and perhaps revealing) observations are made:

> "The general condition of this almost entire skeleton of a reptile, organized, as seems by the structure and proportions of its hind foot, for terrestrial rather than aquatic life, or at least for amphibious habits on the margins of a river rather than for the pursuit of food in the open sea, I infer that the carcass of the dead animal has been drifted down a river, disemboguing in the Liassic ocean, on the muddy bottom of which it would settle down when the skin had been so far decomposed as to permit the escape of gases engendered by putrefaction."

And a little later …

> "… we may account for the loss of much of the dermo-skeleton and of the two fore *paddles* [my italics]. The larger hind limbs with their stronger muscles and ligaments, would offer better resistance to such predatory attacks …" (Owen, 1863: 26).

What emerges from these discursive passages is that Owen was of the opinion that *Scelidosaurus* was most probably an amphibious, armoured reptile (clearly crocodile-like in habit, if not diet) with a scull-like tail, powerful hindlimbs and shorter (paddle-like?) forelimbs. It may have had a herbivorous diet but, given the marine setting of its remains, piscivory could not be excluded – that could only be clearly decided upon when the teeth at the tip of its snout were discovered. It is obvious, in hindsight, that Owen was influenced in his thinking by the interpretation of the habits of *Hadrosaurus* published a little earlier by Joseph Leidy (1859) – as argued by Norman (2000, 2001). Even more speculatively this species, and perhaps dinosaurs generally, may have been ovoviviparous (capable of retaining fertilized eggs in their oviducts before giving birth to live young).

Since the time of Owen, little fresh work on the anatomy of *Scelidosaurus* has been done. Charig (1972) used some newly prepared pelvic and hindlimb material (NHMUK R6704) as an anatomical reference point in his attempt to model the origin and evolution of the ornithischian and saurischian pelvic structures. Barrett (2001) investigated tooth wear and jaw action in the lectotype (NHMUK R1111) and by doing so removed fish from the diet of *Scelidosaurus*. And Carpenter *et al.* (2013) presented posed photographic reconstructions of the pelvis and sacrum of the lectotype as a basis for resolving the structural evolution of the pelvis in thyreophorans. Norman (2000, 2001) reviewed the original discovery of *Scelidosaurus* and Owen's work on this taxon in a historical context. Apart from these contributions, Coombs *et al.* (1990) and Norman *et al.* (2004) made some general observations about the biology and way of life of *Scelidosaurus*, but neither of these could be regarded as new or original. The description of the osteology of *Scelidosaurus* (Norman, 2020a,b,c) enables a more comprehensive assessment of the biology, functional anatomy and life habits of this animal; it also provides the information necessary for a more informed assessment of its systematic position and phylogenetic relationships.

[A] *SCELIDOSAURUS:* CRANIAL BIOLOGY

[B] External features

The surfaces of the skull and mandible (Fig. 4) are coated by widespread exostoses as well as a small number of discrete osteoderms. This suggests that the scelidosaur skull was encased by an array of keratinous epidermal scutes or plates.

<Figure 4 near here> *Scel*. skull in lateral A and dorsal B views.

For comparison, an osteological preparation of the skull of a similarly sized sub-adult Green Turtle (*Chelonia mydas* – Norman, pers. colln – Fig. 5A, B) – a taxon belonging to the clade Testudinata with putative (sister-taxon) archosaur affinities (Crawford *et al.,* 2012) reveals similarly heavily textured skull roofing bones that, in life, are known to anchor a tessellate covering of keratinous scutes (Fig. 5C, D). Unfortunately, this particular specimen does not show the pattern of smooth shallow grooves that mark the edges of some of the principal cranial scutes (Penkalski, pers. comm. March 2020).

> <Figure 5 near here> *Chelonia mydas* skull. Lateral & Dorsal to demonstrate widespread exostoses. Plus tentative restoration of the scute pattern.

[C] The premaxillary beak

In *Scelidosaurus* a rhamphotheca was, without much doubt, an externally smooth casque-like structure referred to as a tomium in *Chelonia* (Fig. 5C, tom) that enveloped the premaxillae (Fig. 6, rsc). The external surface of the premaxilla (not including the narial fossa) is slightly rugose and pitted with small foramina that in combination would have supported, anchored and indicate the presence of a vascular supply that provided nutrients for the growth of an overlying rhamphotheca; closely comparable osteological features are seen underlying the tomium of the turtle. The scelidosaur rhamphotheca formed a short cutting edge along the edentulous margin of the premaxilla (Figs 4, 6). The slightly rugose and vascularized lateral wall to the dentulous portion of the premaxilla is likely to have been similarly encased by a posterior extension of the rhamphotheca, in conformity with the structure seen in *Chelonia.* It is probable that the premaxillary dentition was ensheathed (and supported) by this portion of the keratinous beak; the crowns of the teeth are envisioned projecting from behind the rhamphothecal parapet (Fig. 6A) even though there is no modern analogue for such a composite arrangement. The dorsal portion of the rhamphotheca coated the external surface of the premaxillae and would have extended as far dorsally as the base of the dorsomedian premaxillary process, but would have been cut back so that it skirted the ventrolateral portion of the external naris. Its posterodorsal edge would have merged with the rhamphothecal margin near the posterior end of the premaxilla on either side of the snout (Fig. 6A).

[C] The snout

Anteriorly, the dorsal surface of the nasals (Fig. 4B) is characterized by a radiating pattern of strands of bony tissue that may have anchored a midline scute (Fig. 6A,B, nmsc); this underlying bony pattern corresponds to that which supports similar midline scutes on the chelonian skull (Fig. 5B,D). Farther posteriorly, the surface of these bones develops a thicker knobbly texture that is overprinted by a series of repeated curved ridges. The ridges are oriented (more or less) transversely across the roof of the snout and extend down the sides of the snout where it is walled by the maxilla and prefrontal. The repetition of the curved ridges is suggestive of attachment sites for successive (possibly overlapping) scutes that encased the snout above the buccal emargination and extended posteriorly as far as the naso-frontal suture (Fig. 6, nsc). The lateral wall of the snout formed by the maxilla and premaxilla is reconstructed here covered by a large maxillary scute (Fig. 6, msc); however, there are indications (Fig. 4A) of faint attachment ridges, so it is possible that a series of overlapping scutes were found here as well. Posterior to the reconstructed lateral maxillary scute there is a smooth patch of bone (Fig. 6, ?) behind which the lacrimal bears irregular exostotic growth that would have supported an overlying scute (Fig. 6, lsc).

There is no equivalent patterning of successive curved exostotic ridges on the chelonian skulls that I have examined, so the scute pattern in the scelidosaur skull probably differs from the mosaic-like tessellate pattern of scutes seen in these living, albeit distantly related, diapsid taxa (Fig. 5).

<Figure 6 near here> skull with scutes restored (lateral & dorsal)

[C] The skull roof and occiput

The frontals are dominated by a dense pattern of strand-like superficial bone that radiates from a midline groove (Fig. 4B). As with the anterior portion of the nasal, this morphology is suggestive of the presence of a large shield-like scute (Fig. 6B, fsc) that extended across to the adjacent surfaces of the prefrontal, middle supraorbital and postorbital.

Lateral to the frontal plate, the palpebral (=anterior supraorbital) and posterior supraorbital osteoderms form a shallowly arched bar of bone (=brow ridge) that flanks the dorsal orbital margin of the skull roof. The rugose external surfaces of these bones are structurally distinct from the frontal plate, and are likely to have anchored their own substantial keratinous sheaths (Fig. 6, sosc) that served to shield the orbit and its associated soft tissues. It is possible that these keratinous scutes were subdivided into smaller units than illustrated here, and may have been superficially ornate for behaviourally related reasons; enlarged, sculpted and colourful circumorbital scutes are seen in many living squamates.

A rugose, double-ridged sagittal crest dominates the posterior part of the skull roof. The ridges are flanked by large ovoid supratemporal fenestrae and behind these latter is a divergent pair of prominent curved horn-like occipital osteoderms. The temporal arches and occipital margin show some evidence of irregular exostotic growth that may well reflect the attachment of overlying scutes (Fig. 6, stsc). It is of course possible that this posterior part of the skull table was less extensively scute-covered. The fenestrae themselves would have been spanned by skin that (although scaly) retained a degree of flexibility to allow movement of the underlying temporal musculature. The same consideration should also apply to the adjacent infratemporal fenestrae (itsc). However, there are areas of the skull of *Chelonia mydas* where exostotic bone is absent and the bone surface is, instead smooth-surfaced (Fig. 5A, au); this area (the margins of which are dotted in Figure 5C) is covered in life by several scutes (Fig. 5C, ausc). Therefore, it is possible that in *Scelidosaurus* tessellated scutes enveloped the posterior skull roof as well as its lateral flanks. The restoration (Fig. 6A,B) includes an imaginary array of rather large scutes in these areas.

The occipital osteoderm 'horns' have comparatively smooth, finely grooved surfaces pock-marked by many tiny foramina; these features are interpreted as a combination of points for the connective tissue that tethered an overlying keratinous horn (Fig. 6, hsc), and the vascular supply for its continued growth. Similar textures are visible on the horn-cores of living bovid mammals (e.g. *Ovis aries* – Norman, pers. colln – Fig. 7A, hc). As can be seen in this example, the shape of the horn core may not necessarily have a direct bearing on that of the overlying keratinous sheath (Fig. 7B, kh); the same may be true in the case of the scelidosaur, but in the absence of new discoveries of scelidosaur material in the Lias exhibiting exceptional preservation (e.g.

Brown, 2017; Arbour & Evans, 2017) there is no way of judging on the matter, so a conservative restoration has been illustrated.

<Fig. 7. Ovis near here> to show horn core A and keratinous horn covering B.

[C] Postorbital bar and jugal arch

The lateral surface of the jugal process of the postorbital is covered to a large extent by an externally concave osteoderm. Its dermal origin is betrayed on the internal orbital margin of the postorbital; this latter reveals a row of vascular foramina that appear to mark the interface between the endochondral bone of the postorbital and an overlying dermal bone (Norman 2020a: fig. 19C). Distally (ventrally) along the jugal process the osteoderm structure gradually merges with the surface of the postorbital and more nearly resembles an exostosis, rather than a discrete osteoderm. It may be that in some instances (perhaps the mandible also) these two processes of superficial bone formation become blended – as appears to be the case here. The dorsal part of the postorbital osteoderm thickens and produces a shelf, and an associated hook-shaped structure that lies adjacent to, and encroaches upon, the orbital margin. Together these structures create a sutural surface for the posterior supraorbital osteoderm. It is probable that the postorbital osteoderm anchored a large scute with a depressed centre (Fig. 6A, posc); its dorsal and orbital margins would have been thick and continuous with the keratinous scutes on the supraorbital brow ridge – effectively extending the brow-ridge below as well as behind the eye socket. The postorbital scute would have added to the protection of the eye, and may have augmented a potentially ornate superstructure surrounding the eye. This scute may have thinned ventrally as it approached the jugal – the adjacent postorbital process of the jugal has a completely smooth surface.

The jugal arch is well displayed on the intermediate-sized specimen (BRSMG Ce12785 – Norman, 2020a: fig. 13), but perhaps best shown in the larger referred skull (BRSMG LEGL 0004 – Norman, 2020a: fig. 14); details are a little less clear in the holotype as a consequence of acid-induced degradation of the surface textures. Linear strands of bone overlie the tapering anterior (suborbital) process of the jugal and represent a partial continuation of the line of rugosities that define the dorsal margin of the cheek recess (Fig. 6A, jsc). There also may be some continuity with the strands of exostotic material present on the surface of the lacrimal (Fig. 4A). Farther posteriorly, the body of the jugal deepens and beneath the postorbital process there is a roughly oval patch of granular exostotic bone (jsc); this patch is separated by a smooth trough from a far larger and thicker area of exostotic bone that covers much of the remaining ventrolateral body of the jugal (jsc). The latter patch is rough and granular but has an overlay of irregular strands that are oriented posteroventrally and form narrow troughs that terminate at foramina; the troughs become shallower distally, before fading out or blending into the body of the jugal. The dorsal (postorbital) process of the jugal is completely smooth, and the dorsal (infratemporal) margin as well as the free ventral margin are also smooth surfaced. The external surface of the quadratojugal is not heavily marked by exostoses because it is extensively overlapped by the jugal, except for the exposed surface of the wedge-shaped lateral ridge that interlocks with a notch on the distal edge of the jugal. The jugal may have displayed a moderately complex array of scutes including one that borders the anteroventral margin of the orbit (Fig. 6A, jsc), another that formed a mound-shaped structure at the base of the postorbital process and, separated from the latter, yet another large and probably thick scute that encased the posterior body of the jugal and quadratojugal (qjsc).

Comparisons. In ankylosaurids the main posterior body of the jugal and its associated quadratojugal are capped by a prominent (almost horn-like) osteoderm that has been referred to as the quadratojugal horn (Coombs, 1978a; Arbour & Currie, 2016). Coombs (1978a) noted that nodosaurids lack these quadratojugal horns although some (e.g. *Pawpawsaurus* and *Hungarosaurus*) bear some surface ornamentation. Stegosaurs show no evidence of either exostoses or osteoderms on their jugals or quadratojugals (Gilmore, 1914). *Scelidosaurus* might be interpreted as exhibiting an earlier stage in the ankylosaurian reinforcement of the jugal-quadratojugal region of the skull through the evolution of pronounced exostoses and the implication of their being encased in thick keratinous scutes.

[C] The mandible

The mandible is only adequately represented in the lectotype (NHMUK R1111 – Norman, 2020a: figs 36A, 37A) although both of these rami are damaged near their mandibular tips and have suffered from superficial damage caused by prolonged exposure to mineral acid, which has degraded the bone surface. Layers of consolidant have also smoothed-over the original cortical texture. A predentary (whether mineralized or not) was undoubtedly present and would have been capped by a rhamphotheca (Fig. 6A, pdsc) to match and oppose that present on the tip of the premaxillae (rsc). The dentary ramus in the holotype is bevelled on either side of a curved ridge that marks the ventral margin of the cheek recess. Dorsal to this ridge the external surface of the mandible is smooth and marked only by a series of large fusiform foramina. Ventral to this ridge the external surface of the dentary ramus is generally rugose, rather than smooth, and was coated by a mixture of strands and granules of exostotic bone; this coating may have been denser before it was subjected to prolonged acid immersion. The dentary might have been covered by a mosaic of smaller scutes, but it has been restored in this instance with a single large sheath-like scute (Fig. 6A, dsc).

Posterior to the dentary ramus the external surface of the mandible bears a prominent, discrete exostosis that is centred upon the angular bone. In the lectotype (NHMUK R1111 – Norman, 2020a) this structure has some step-like thickened edges, and this gives the general impression that it represents a discrete osteoderm; however, it is also possible that some damage may have occured during preparation and may account for the appearance of these structures on both mandibles. The slightly smaller referred specimen (BRSMG LEGL 0004 – Norman, 2020a: figs 14, 39) has not been subjected to such corrosive preparation and reveals the natural morphology of the external surface of the angular. The angular exostosis develops a thick central mound of tissue that has a granular texture. Radiating from this mound are strands of bony tissue that extend toward the sutural margins of the angular (and seemingly extend across these margins on to the adjacent surfaces of the surangular and the dentary). The remainder of the external surface of the posterior half of the mandible is smooth and unadorned by exostotic tissue.

The prominence of the angular exostosis suggests that this part of the mandible was covered by a large scute (asc). Whether the overlying scute became mineralized during the later stages of ontogeny, creating a genuinely ankylosaur-like mandibular osteoderm, is considered probable (judged by the appearance of the osteoderm-like structures seen on the mandibles of the holotype – NHMUK R1111 – Norman, 2020a), but this ambiguity remains unresolved at present.

Comparisons. It is notable that among ankylosaurs both ankylosaurids and nodosaurids (among examples for which there is sufficient osteological evidence) have a large, rugose bony ossification referred to as a mandibular osteoderm (Coombs, 1978a). The osteoderm overlies the position occupied by the well-developed angular exostosis in *Scelidosaurus,* but is also considerably larger in proportion to the length of the mandible. In contrast stegosaurs do not possess an equivalent structure (Gilmore, 1914 – Carrano, pers. comm. 2018).

[B] Sensory systems

In the absence of good quality soft tissue preservation it is only possible to infer a few aspects of the sensory biology of *Scelidosaurus* from hard-part evidence.

[C] Vision

The orbit of *Scelidosaurus* is large and circular and the depth of the orbital cavity suggests that the eyeball may have been close to spherical (even though many living diapsids are known to have non-spherical eyeballs). Sight was evidently well developed in this taxon. There is no osteological evidence of additional soft tissue encroaching upon the orbital cavity (e.g. large vascular sinuses or orbital salt-glands) that might reflect physiological adaptations to specific environments.

The discovery of a few ossified segments from the sclerotic ring is not unexpected; representatives of all three principal clades of Dinosauria

(Ornithischia, Theropoda and Sauropodomorpha) have been reported with sclerotic bones. These bones articulate and form a ring that is embedded in the sclera that immediately surrounds the iris in living diapsids (excluding crocodilians and snakes). Because sclerotic ossicles form an articulated ring that is embedded in the sclera, a role associated with structural support of the eye cannot be doubted (Hall, 2008), but how this may have translated into the functionality of the visual system is a matter of continuing debate (Martin, 1982). Muscles associated with altering the shape and positioning of the lens (and thus the focusing of visual images on the retina) are known to be attached to the sclerotic ring; and, because the individual ossicles imbricate, the anchorage for these muscles is stable and there would be less tendency for distortion of the eyeball during accommodation than would be the case if the compliant tissues of the sclera alone were relied upon (as is the case in extant mammals and crocodiles). Pressure-related (hydrostatically-induced) distortion of the eyeball may be a factor that accounts for the exaggerated evolution of sclerotic rings in extant diving birds and extinct aquatic reptiles such as ichthyosaurs and marine crocodiles (metriorhynchids and teleosaurs – Romer, 1956); this may also account for the pronounced thickening of the peri-iris sclera reported in deep-diving mammals (cetaceans). In non-aquatic taxa, extreme lens distortion (linked to accommodation) is also known to occur in some birds (notably Strigidae – owls [Martin, 1982]) and this is likely to have been facilitated by the sclerotic ring-based muscles as well as the almost tubular structure of the sclerotic ring.

There has been some discussion concerning the aperture of the sclerotic ring and whether its size might be a predictor of habitat preference. Schmitz & Motani (2011) proposed, after surveying a range of living and extinct taxa, that the diameter of scleral aperture and the diameter of the orbital cavity provided a proxy that allowed them to predict the preferred light level of the animal. Large apertures signify a preference for scotopic (primarily nocturnal) conditions, small diameters indicate photopic (primarily diurnal) habits, and intermediate diameters suggest a preference for mesopic (twilight) conditions. Hall *et al.* (2011) examined the data presented by Schmitz & Motani and identified a range of reasons (statistical, sampling and metrical) why the claimed correlations could not be justified.

<Figure 8 near here> sclerotic ossicles and stapes

The few sclerotic ossicles known in *Scelidosaurus,* either as isolated elements or attached to the cultriform process and medial surface of the left jugal (Fig. 8A, sc.os) are facetted, showing that individual ossicles overlap one another and formed an articulating ring in the living animal (Fig. 6A, sc.os – aperture diameter unknown). The individual ossicles are flattened so they would have lain roughly parallel to the surface of a spherical eyeball, as is the case in many birds and squamates. The role of the sclerotic ring in the visual acuity, habits and physiology of this dinosaur remains frustratingly unclear.

[C] Hearing

The preservation of an ossified proximal portion of the stapes (*columella auris*) in its original location on the skull of the lectotype (NHMUK R1111 – Charig, pers. comm. *c.*1980: Fig. 8B,C) confirms the existence of auditory sensitivity in *Scelidosaurus* (Romer, 1956; Dooling *et al.,* 2000). The distal truncation of the bony stapes (Fig. 8B, C, est) marks the point of attachment for an extrastapedial cartilage. The latter is expected to contact the tympanic membrane (assuming there was one) and may have had the remnants of dorsal and ventral processes that branched off the extrastapes; the extrastapes would have maintained a rudimentary connection with the hyoid arch, at least during the early stages of the animal’s development. There are no clear osteological markers of the rim (*annulus*) of the eardrum (*tympanum*), but if this membrane was present it would likely have been located in the vicinity of the notch between the embayed posterior margin of the dorsal end of the quadrate and the adjacent paroccipital process (Figs 6A, 9, tym). The location of the oval window (*fenestra ovalis*) on the braincase wall and length of the ossified portion of the columella (~3 cms – Fig. 9, st) implies a modest span for the extrastapes (Fig. 9, est). A pressure equilibrating round window (*fenestra rotunda* – Fig. 9, rw) is present immediately beneath the fenestra ovalis and separated from the latter by an oblique bony partition.

<Figure 9 near here> Sc. reconstructed extrastapes, tympanum and middle ear cav?

For the effective transmission of pressure waves from the low-impedance medium of air to the high-impedance fluid medium of the inner ear, it is essential that the pressure waves in air are collected by a large-diameter tympanum that is acoustically matched to the impedance of air, and therefore focuses the majority of this energy on the attached extrastapedial cartilage, rather than acting as a reflective surface. The stapes and its extrastapedial cartilage are suspended within an air-filled middle ear chamber that facilitates energy transfer to the fluids of the inner ear. There will, of course, be some inertial energy loss associated with the mass of the stapes. Nevertheless, the areal differential between the tympanum and the footplate that impinges upon the membrane spanning the oval window magnifies energy transfer between the tympanum and the stapedial footplate-oval window interface. It is therefore reasonable to suppose that the tympanum of *Scelidosaurus* was large (Fig. 9, tym), and that the acoustic sensitivity range of such ears was likely to have been limited to the higher energy and larger air displacement levels associated with comparatively low frequency sounds (~2-20kHz). Details concerning the structure of the scelidosaur inner ear and whether this has some bearing on its potential sensitivity range are not at present available but may be visualized after MicroCT scanning (Norman & Porro, in preparation).

<Figure 10 near here> Scel – recon nasal passages, soft palate and olfactory lobes?? sagittal.

[C] Taste, smell and nasal passage function

There are no osteological markers that can be used to determine the gustatory and olfactory senses in this taxon. In the case of its olfactory capabilities, the impression of the passages for the olfactory lobes can be seen on the interior roof of the frontals of the lectotype skull (Fig. 11) and are reconstructed diagrammatically (Fig. 10, ol.b), but the distribution of the olfactory epithelium associated with the nasal passages is unknown. The nasal passages are dorsally positioned in the snout and, judged by the structure of the anterior palatal complex (vomers, epivomers and pterygoids), consist of shallowly arched channels (Fig. 10, np). There is no bony secondary palate (as there is in ankylosaurs – Coombs, 1978a), but the presence of a short premaxillary palate beneath the external nares, the partial internal shelving on the medial walls of the maxillae and the proximity of the ventral edge of the vomers suggests that connective tissue spanned the gap between the maxillae and was tethered to the ventral edge of the vomers. This would have created a soft secondary palate that separated the oral and nasal cavities (Fig. 10, sp). The presence of thin epivomers (Epi) that may have reinforced the soft tissues forming the roof of each nasal passage is unexpected.

From a physiological perspective it is improbable that the nasal passages of scelidosaurs would have been simple tubular passages; they are likely to have accommodated the structural equivalent of turbinates, necessary for filtering inspired air, providing surfaces for the location of the sensory epithelium associated with olfaction, and to serve as energy/moisture exchangers during respiration. The ossified portions of the vomers and pterygoids that form the internal walls of the nasal passages show no clear evidence of anchorage points for turbinates. It is however possible that the plate-like epivomers, with their bevelled anterolateral margins (Norman, 2020a: fig. 26), added not only rigidity to the roof of each nasal passage but served to anchor turbinate-like structures that projected ventrally, across the nasal passages in *Scelidosaurus.*

<Figure 11 near here> Skull-Braincase as preserved in the lectotype.

[C] Neural anatomy

The neurocranium of the lectotype is suspended from the bones of the skull roof. This portion of the skull has been well-exposed following acid-mediated preparation (Fig. 11) and subsequent accidental damage to what was originally a fully articulated skull. The latter event resulted in the left side of the snout, suspensorium and entire palate being broken away so that the left, ventral and posterior sides of the neurocranium can be examined with comparative ease, although the remaining portions of the skull roof and adjacent structures are extremely fragile. The exposed surfaces of the neurocranium reveal an array of fossae and foramina that can be identified, comparatively, as being associated with many of the principal cranial nerves and vessels that passed through the walls of the neurocranium as they either enter or leave the endocranial cavity.

The brain itself would have been smaller than the endocranial cavity, judged by the fact that the neurocranial walls are smoothly contoured. This suggests (as noted by Romer, 1956; Jirak & Janacek, 2017; Watanabe *et al*., 2019) that the brain was centrally located, not in direct contact with the walls of the braincase, and enveloped by thick meninges; it would also have been cushioned dorsally and laterally by large vascular and lymphatic sinuses. The ventral portion of the neurocranium anterior to the dorsum sellae (posterior wall of the pituitary fossa) is not preserved and was presumably cartilaginous in life. The foramina for the cranial nerves provide important and reasonably consistent landmarks on the archosaur neurocranium; several of these are present on the scelidosaur neurocranium (Figs 12, 13).

<**Figure 12** near here> Lateral view reconstructed neurocranium with cranial nerve foramina id.

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<**Figure 13** near here> transparent reconstruction of the brain and its associated vessels and nerves in the endocranial cavity.

[D] Cranial nerve I (cn.I - olfactory) can be reconstructed only speculatively (Fig. 13) and would be represented by nerve fibres running from the sensory area of the nasal mucosa to the olfactory bulbs (Fig. 10, ol.b). There is a central channel on the ventral surface of the skull roof on either side of the suture between the conjoined frontals; this is interpreted as the roof of the passage for the olfactory tracts leading to the anteriorly placed olfactory bulbs.

[D] Cranial nerve II (cn.II – optic). There is no osteological indicator for the presence of this nerve because it would have entered the neurocranium through the presumably cartilaginous wall of the braincase immediately

anterior to the pituitary fossa (Fig. 13 – this interpretation is confirmed by the osteology of this region described by Norman, 2020a).

[D] Cranial nerve III (cn.III – oculomotor). This small nerve leaves the neurocranium just posterior to the optic nerve and therefore leaves no trace in this specimen (Fig. 13).

[D] Cranial nerve IV (cn.IV – trochlear). This is a small nerve associated with one of the eye-moving muscles. It has a complex route from the brain, emerging through the neurocranium high on the anterolateral surface of the neurocranium. It may be the case that the nerve pathway includes the foramen preserved on the 'blade' of the orbitosphenoid. The position of this foramen correlates reasonably closely with that expected of the route taken by cn.IV (Figs 12, 13).

[D] Cranial nerve V (cn.V – trigeminal). This large and important nerve emerges from the neurocranium via the proötic fossa/fenestra anterior to the otic capsule; it is readily identified in many dinosaur neurocrania, as is the case in *Scelidosaurus* (Figs 12, 13). This nerve tract produces three rami that emerge from the large ganglion that fills the proötic fossa; of these the ophthalmic branch (cn.V(oph)) is the only one that is clearly discernible in the lectotype and is represented by a channel extending anteriorly and roofed partly by the laterosphenoid. Typically, the other two rami (maxillary and mandibular – cn.V(m,m)) loop behind the epipterygoid (still present in *Scelidosaurus* – Norman, 2020a: fig. 28, Ep) before passing into their respective skull bones (Fig. 12).

[D] Cranial nerve VI (cn.VI – abducens). Another small cranial nerve supplying a single eye muscle; this arises in the floor of the medulla and typically pierces the lateral wall of the dorsum sellae (Fig. 13). This is the only part of the pituitary fossa that is well preserved in the lectotype (Norman, 2020a: fig. 33) and shows two small foramina on either side of the midline. The passages from these foramina run obliquely posterodorsally to emerge on the floor of the neurocranium, exactly as predicted.

[D] Cranial nerve VII (cn.VII – facial). This nerve emerges from the medulla posterior to the trigeminal and typically runs through the anterior wall of the otic capsule and emerges just behind the much larger proötic fossa (Fig. 12).

One ramus runs down toward the palate via the vidian (=carotid) canal (Figs 12, vid; 13) and pituitary fossa, while another ramus (Fig. 13, cn.VII(h)) runs posteriorly near the lateral head vein and above the fenestra ovalis and ossified portion of the stapes.

[D] Cranial nerve VIII (cn. VIII – vestibulocochlear). The nerve cannot be traced externally because it never emerges from the side of the medulla directly into the otic capsule.

[D] Cranial nerve IX (cn. IX – glossopharyngeal). A comparatively small nerve that often accompanies cn.X (vagus) as it leaves the medulla and more often than not uses the same foramen as the latter; this route may be the situation in *Scelidosaurus* (Fig. 13).

[D] Cranial nerve X & XI (cn.X+XI – vagus and spinal accessory nerve). A large and more important nerve emerges from the lateral surface of the medulla through a large vagus/jugular foramen that forms at the junction between the opisthotic and exoccipital bones (a remnant of the metotic fissure (see Figs 12, vag-jug; 13).

[D] Cranial nerve XII (cn.XII – hypoglossal). There may be as many as three roots that emerge from the neurocranium via two or three foramina all of which exit through the lateral wall of the exoccipital. There are two separate foramina in the wall of the opisthotic-exoccipital (Figs 12, 13). In some taxa an anterior root may also leave via the vagus/jugular foramen and there is room for such a possibility in *Scelidosaurus*.

[C] Associated vascular anatomy of the neurocranium

A large fissure can be seen on the dorsolateral surface of the neurocranium, at the junction of the parietal, laterosphenoid and proötic (Fig. 12, vcd). This marks the entry point for venous blood draining from the adductor chamber and the occiput (via the remnant of the post-temporal fenestra) into the transverse sinuses that lie on the endocranial wall flanking the dorsolateral regions of the brain. The lateral sinus vents from the endocranial cavity through the neurocranial wall into the ventral part of the adductor chamber and from there into the lateral head vein. There is no clear indication of the ventral drainage of this system; however, it may be the case that the transverse sinuses drained into the lateral head vein via the large jugular-vagus foramen (Fig. 12) farther posteriorly on the braincase wall (as shown in Fig. 13, jug.v).

A large carotid (vidian) canal foramen is present on either side of the basisphenoid. It marks the entrance of a canal that enters the ventrolateral corner of the dorsum sellae; this represents the passage for the carotid artery (Fig. 13, c.art) that supplies blood to the pituitary (p), the floor of the brain itself and the more anteriorly positioned organ systems.

Apart from these few fenestrae and foramina, no other indicators of the cranial circulatory system of *Scelidosaurus* are visible.

[B] Musculature, jaw motion and feeding

[C] Musculature

Little attention has been paid to the jaw musculature of thyreophoran ornithischian dinosaurs for a combination of reasons. Stegosaurs rarely preserve skull material and those known in some detail are not particularly informative osteologically, so jaw muscle reconstructions have been comparatively simple (Holliday, 2009; Nabavizadeh, 2016). In contrast, the skulls of ankylosaurs are robust, highly consolidated and many more are known; however, the degree of development of exostoses and osteodermal shielding obscures much of their anatomy that is relevant to the description of their jaw musculature, which is treated either fleetingly or not at all (Holliday, 2009). Haas (1969) attempted to identify and reconstruct parts of the jaw musculature in ankylosaurs by reference to two well-preserved skulls of cf. *Euoplocephalus* (but it should be noted that the taxonomy of these specimens, and of others formerly assigned to the genus *Euoplocephalus* is in a state of flux [Penkalski, 2018 – and pers. comm. March 2020]). Most of Haas' observations focused upon the unadorned posterior, medial and dorsal portions of the mandible, and limited areas of the adductor chamber that were enveloped by what he referred to (appropriately) as a 'carapace' of osteoderms. Components of the adductor mandibulae complex were cautiously identified by reference to their insertion points, represented by muscle scars on the mandible and rather vague indications of their origins within the skull roof. Ösi *et al.* (2017) attempted a slightly more detailed reconstruction of the jaw musculature in ankylosaurid and nodosaurid ankylosaurs and, although it provides a little more information concerning the internal architecture of the skull and likely areas of muscle origin, the general anatomical pattern conforms closely in the inferred lines of muscle action (Ösi *et al.,* 2017: fig. 13) to the original interpretation of Haas – although the muscle identification and figure annotations are slightly contradictory.

Unlike more derived thyreophorans, the skull of *Scelidosaurus* has the advantage of being comparatively little modified from that of a more generalized early ornithischian such as *Lesothosaurus* (Sereno, 1991). Although the skull of *Scelidosaurus* bears a patina of exostotic bone and a few osteoderms, it lacks the carapace-like plating of osteodermal tissue seen in ankylosaurs. However, the evidence for the presence of individual muscles on the skull and mandibular bones is fraught with difficulty in fossil taxa. Areas of muscle attachment vary greatly in appearance between the various muscles in a single individual and this is compounded by differentiation that occurs during ontogeny (as well as through evolutionary time) that may alter muscle size, orientation and function. Therefore similar anatomical locations cannot be used to establish unequivocal muscle homology and the use of such approaches as phylogenetic bracketing (Bryant & Russell, 1992) to constrain the interpretation of muscle locations is either of limited utility or may be totally inadequate (*viz.* Holliday, 2009). Extant squamate skulls ('typical sauropsids' – Fig. 14) provide a generalized template for comparison and interpretation of scelidosaur jaw muscle distribution; this helps to avoid some of the problems of identification that arise because of the evolutionary history of profound skull modification and muscle reorganisation seen in the more closely related (archosaur-line) crocodilians or birds.

<Figure 14 near here> *Varanus* muscle origins and insertions

In the instance of *Scelidosaurus,* cranial and mandibular construction is not too dissimilar to that seen in the generalized sauropsid (Figs 14, 15). As a consequence a simple (comparatively uncontroversial) reconstruction of its jaw musculature is possible; this has also been informed by interpretations that have been generated through the study of other ornithischians (Ostrom, 1961; Galton, 1974; Norman, 1977; Norman & Weishampel, 1990; Holliday, 2009; Norman *et al.,* 2011). Luther (1914) established the fundamentals of our current recognition of mandibular musculature, and this was augmented by the work of many others in subsequent years (notably Lakjer [1926] for sauropsids). Luther established the fundamental separation of the trigeminal musculature into the three functional groupings seen in non-mammalian tetrapods: adductor mandibulae, constrictor dorsalis and intermandibularis. The first two muscle groups and a small part of the branchial musculature are described below.

<Figure 15 near here> Jaw muscles of *Scelidosaurus*

[D] M. levator anguli oris (AN.OR). There are few osteological correlates associated with this superficial slip of muscle, but the thick and rugose ventral edge of the jugal is a perfectly acceptable area for origin of this muscle, which would have run forward to insert on a ligament near the 'angle of the jaw' [corner of the mouth] (Haas, 1969). The possibility exists that an anterodorsal expansion of this muscle (following the rugose edge of the jugal on to the adjacent lateral surface of the maxilla) and an equivalent expansion along the rugose ridge on the lateral surface of the mandible produced a sheet of muscle (a physical cheek) that enclosed the buccal emargination. This hypothetical cheek muscle is indicated in Figure 15B (AN.OR).

[D] M. adductor mandibulae externus superficialis (MAMES)*.* In the squamate (Fig. 14) this muscle originates along the entire lateroventral surface of the narrow postorbital-squamosal bar. Birds show a highly modified skull that entirely lacks an upper temporal bar and this muscle originates on the squamosal. Crocodiles also have a much-altered adductor chamber and this muscle originates on the medial surface of the quadratojugal. In *Scelidosaurus* the external surface of the squamosal, anterior to the articular cotylus for the quadrate, forms a recess above which there is an overhanging ledge; this would have provided an area of origin for this muscle. It is unclear how far along the postorbital-squamosal bar the origin of MAMES extended. In squamates this muscle inserts on the dorsolateral surface of the surangular. In *Scelidosaurus*, the dorsolateral surface of the surangular is marked by a

clearly defined horizontal ridge and it is likely that this muscle inserted here. Given the horizontal extent of the surangular ridge it is probable that the origin of MAMES extended along the entire length of the postorbital-squamosal bar and anchored a broad (curtain-like) sheet of muscle that spanned most of the infratemporal fenestra (Fig. 15B, MAMES).

[D] M. adductor mandibulae externus medialis (MAMEM). In squamates this is a substantial muscle that originates along the dorsal and posterior margin of the supratemporal fenestra (Fig. 14). In birds and crocodiles this muscle is considerably more varied in form and attachment areas on the skull (Holliday, 2009); there is however a little more consistency of its attachment to the coronoid region of the mandible (generally via a shared aponeurosis). In *Scelidosaurus* there is a large recess in an equivalent area formed by the lateral lamina of the parietal and a medial lamina of the squamosal, so it is likely that this was the area for origin of this muscle (Fig. 15A, MAMEM). Its insertion site is unclear osteologically in a range of sauropsids because this muscle combines with other adductor muscles to insert via a common attachment (the bodenaponeurosis) that projects from the dorsal surface of the surangular. A similar arrangement probably pertains in *Scelidosaurus* (Fig. 15C, bod).

[D] M. adductor mandibulae external profundus (MAMEP). In squamates this muscle originates on the lateral surface of the braincase immediately beneath the MAMEM (Fig. 14). In crocodiles this muscle originates in the posteromedial corner of the supratemporal fenestra and runs forward across the oblique quadrate-quadratojugal partition before abruptly descending to insert on the surangular of the mandible. In birds the huge expansion of the cranial vault obviates a temporal fenestra origin and this muscle attaches to the temporal fossa or postorbital process although a discrete insertion is found on the coronoid portion of the mandible. A broadly similar pattern to that seen in the squamate probably pertains in *Scelidosaurus*: the dorsolateral surface of the braincase (proötic-opisthotic) forms a broad, concave passageway for this muscle that was tethered to the sagittal crest (Fig. 15A, MAMEP). A mandibular insertion on the surangular via a bodenaponeurosis is likely.

[D] M. pseudotemporalis (MPST). In the squamate this muscle typically occupies an anterodorsal position within the temporal cavity (Fig. 14). In crocodiles the muscle is constrained by the structure of the adductor chamber, being confined to the laterosphenoid; it inserts via a tendon in the adductor fossa. In birds this muscle is reduced to a slip that originates on the laterosphenoid buttress of the temporal region and inserts on the medial side of the coronoid area of the mandible. In *Scelidosaurus* the area of origin may have been along the anterolateral margins of the parietal and the main body of this muscle would have been guided by the shape of the laterosphenoid in its passage toward the mandible. An attachment toward the anterior end of the surangular (possibly distinct from the bodenaponeurosis) might be expected, and in *Scelidosaurus* may be reflected in the pattern of striations seen on, and around, the coronoid and surangular where they project dorsally at the anterior end of the coronoid eminence (Fig. 15C).

[D] M. pterygoideus (MPT). In squamates, crocodiles and birds this muscle (undivided into dorsal and ventral components in squamates) originates along the lateral surface of the main body of the pterygoid and extends posteroventrally toward the posterior end of the mandible, wrapping around its ventral surface and forming an extensive insertion area beneath the jaw articulation (Fig. 14). In crocodiles (and birds) the *M. pterygoideus* is subdivided and originates dorsally and ventrally on a deeper and more complex pterygoid than seen in squamates (Iordansky, 1964).

Overall, this muscle acts as an adductor (massive and very important in crocodiles) and also stabilizes the jaw joint; it also imparts a torsional force (lateral rotation at the level of the dentition) on the mandible. In *Scelidosaurus* the details of muscular origin are not clear; it is probable that the ectopterygoid, pterygoid and palatine, where they form the pterygoid flange or its supporting framework, provide areas for attachment a dorsal component of this muscle. Additional slips of this muscle may also have extended on to more medioventral surfaces of the pterygoid (in the manner suggested by Ostrom, 1961: fig. 42). Insertion on the mandible, in the area beneath the jaw articulation on the angular and laterally on the surangular, is probable and the surangular displays a patina of ridges on its lateral surface in just this area that are indicative of muscle attachment (Fig. 15D).

Casey Holliday proposed that a ventral slip of this muscle wrapped around the ventral margin of the mandible before extending anterodorsally up the lateral side of the mandible and inserted along the ventral edge of the jugal in both ornithopodan hadrosaurs and theropodan tyrannosaurs (Holliday, 2009: fig. 7). This reconstruction was partly informed by the fact that this muscle “even attaches to the jugal in some parrots (Hofer, 1950)” (Holliday, 2009: 1259). It was claimed that there was no clear demarcation between the points of insertion of the MAMES and MPT on the lateral surface of the mandible of the taxa in question, and that striae along the ventrolateral edge of the jugal could be best interpreted as indicating an area of insertion of MPT in hadrosaurs and tyrannosaurs.

In *Scelidosaurus* there is a clear ridge on the surangular available for insertion of MAMES, and there is a muscle scar on the lateral surface of the surangular below the glenoid for the MPT. On these bases the extraordinary layout suggested for this muscle in hadrosaurids and tyrannosaurids is considered improbable in the case of *Scelidosaurus*.

[D] M. adductor mandibulae posterior (MAMP)*.* This muscle originates on the anteromedial surface of the quadrate (pterygoid wing) and inserts on the medial surface of the surangular and adductor fossa (Fig. 14). In *Scelidosaurus* the anteromedial surface of the quadrate forms a deep plate that overlaps the pterygoid and was available for muscle attachment; the medial surface of the surangular and adjacent adductor fossa on the mandible would also have been available for muscle insertion even though there are no clear osteological correlates for attachment (Fig. 15D, MAMP).

[D] Mm constrictor dorsalis complex. In squamates *M. levator pterygoideus* (MLPt) originates on the lateral surfaces of the parietal and proötic and inserts on the epipterygoid (Fig. 14). An origin on the proötic (Fig. 15D, MLPt) is plausible in *Scelidosaurus* (the side walls of the braincase are much higher than squamates, which probably excludes an origin on the parietal). The retention of an epipterygoid in this taxon may betray the existence of a remnant of this muscle, but its function (it is thought to have some influence on palate/pterygoid motion in kinetic taxa) is unclear because the skull of

Scelidosaurus is structurally akinetic. Interestingly, a discrete flange ("saddle-like groove" – Heaton, 1972: 190) is present on the central dorsal margin of the pterygoid (topographically equivalent to the position of the epipterygoid in *Scelidosaurus*) in the hadrosaur *Edmontosaurus*. This structure represents the basal articulation (Lambe, 1920; Ostrom, 1961; Heaton, 1972; Weishampel, pers. comm. October 2019) – rather than an area for the insertion of the *M. levator pterygoideus* (or its ligamentous remnant) as claimed by Holliday (2009: fig. 3I: 1256).

In squamates *M. protractor pterygoideus* (MPPt) originates from a discrete area on the ventrolateral wall of the basisphenoid and inserts along the dorsal margin of the rod-shaped pterygoid; this muscle is involved in palinal displacement of the push-rod-like pterygoid during snout elevation and depression in these kinetic taxa (Fig. 14). In *Scelidosaurus* the anterior portion of the basisphenoid is unossified so no osteological correlates for the origin of this muscle can be identified. The fact that *Scelidosaurus* has an akinetic skull suggests that this muscle, if it was present, would have been little more than a remnant muscle slip (or residual ligament sheet) serving to counter torsional strain in the pterygoid and maintain position the pterygoid adjacent to the braincase.

[D] Branchial muscles. As in all extant taxa (Fig. 14; see also Ostrom, 1961: fig. 52) *M. depressor mandibulae* (MDM) links the occipital region of the skull to the retroarticular process of the mandible. The paroccipital process of *Scelidosaurus* is robust and its distal end bears a discrete vertical facet that probably provided an origin for this muscle. MDM would have spanned the shallow embayment created by the bowed posterior edge of the quadrate shaft (Fig. 15B, MDM). The dorsal portion of this embayment accommodated the tympanum (Fig. 9, tym) and the latter was physically protected from deformation by the overhang of the paroccipital process. The retroarticular process of the mandible, although relatively short, would have provided an area for the attachment of the tendon of MDM and sufficient leverage for muscle-assisted mandibular abduction.

[C] Jaw motion

The principal anatomical features of the dentition, jaws and their supporting skeletal framework in *Scelidosaurus* have been summarised earlier (Norman, 2020a). Assembling the evidence from the original dental and osteological observations and the more interpretative work on the myology of the skull, it is possible to gain a more detailed understanding of the jaw action and food processing capabilities of *Scelidosaurus*.

<Figure 16 near here> – curvature of dentitions

[D] Dentition. The maxillary and mandibular tooth rows are inset relative to the external surface of the cranium, creating substantial recesses (buccal emarginations) that were covered by fleshy-muscular cheeks that may have derived muscle fibres from *M. levator anguli oris* – Fig. 15B. Individual tooth crowns are triangular in profile with coarsely cuspidate edges; their bases overlap their neighbours and sit obliquely in their alveoli creating an *en echelon* array (Figs 16, 17). Abrasion facets, where present, are high-angle and mostly localized on the crowns of individual teeth, and those on dentary crowns, when well-developed, extend on to the swollen base of the crown. A lip (a small, oblique shelf – Norman, 2020a: figs 42, 43) is sometimes present along the basal edge of this facet, creating an imperfect crushing structure (Barrett, 2001). The discontinuous distribution of abrasion facets along the dentition (*contra* Ösi *et al.,* 2017: fig. 15) reinforces the impression gained from tooth macro- and micro-wear features that jaw motion was primarily orthal (Barrett, 2001) and combined orthal pulping of vegetation and irregular high-angle shearing resulting from crown-crown occlusion (Fig. 17D,ii). Dentitions that show little development of abrasion facets on crowns (*viz*. BRSMG LEGL 0004 – Norman, 2020a: figs 14, 39) indicate that some individuals used orthal pulping alone (Fig. 17, Di); these latter individuals conform more closely to the expectation generated in the theoretical model of the basal style of ankylosaur jaw action suggested by Ösi *et al.* (2017).

<Figure 17 near here> Occlusion of dentitions

The complementary bowing/curvature of the opposing dentitions (Figs 16, 17A,B) supports the view that jaw action in *Scelidosaurus* was orthal because aligned occlusion could only occur when the two dentitions matched one another positionally (Fig. 17B). Palinal displacement would misalign the dentitions and create malocclusions and irregular damage to tooth crowns (Fig. 17C). The medial inset of both maxillary and mandibular dentitions imposes asymmetrical forces on the jaw bones. During jaw closure some (but not all) teeth occlude – judged by the distribution of abrasion facets of the crowns of teeth along the dentitions. Occluding teeth in the mandible encounter orthal (vertical) and medial force vectors: a combination of adductor muscle vectors and the reaction forces generated by the pressure on the occlusal surfaces of the crowns if the teeth are to achieve an effective power-stroke and shearing action (Fig. 17, Dii). In equal measure, the body of the maxilla would experience a combination of vertical and lateral force vectors because there is overbite.

[D] Jaws and skull form. The skull roof is akinetic. However, slight pivoting of the quadrate head against the squamosal cotylus permitted minor lateromedial translation of the distal end of the quadrate (Fig. 18A,B, q-sq.j - arrows). Combined with the modified trochlear structure of the mandibular joint (Fig. 18B), the jaw rotates around a transverse axis (ensuring orthal occlusion).

The mandibular joint is slightly offset ventrally, relative to the occlusal plane of the posterior portion of the mandibular dentition (Fig. 4A). The longitudinal (ventral) arching of the mandibular dentition causes the anterior dentition (and beak margins) to occlude in-line with the mandibular joint.

<Figure 18 near here> skull mechs diagrammatic

The suturing between the bones of the skull roof (and secondary reinforcement created by the exostoses and their overlying scutes) anchored and strengthened the maxillary bones to counter the lateral forces induced in these bones during jaw closure and tooth-tooth shearing occlusion. In contrast, the mandibles articulate freely against the quadrates and are more susceptible to force vectors generated by the adductor mandibulae complex that tend to induce medial long-axis rotation (Fig. 18C, AM). The structure of the mandibular joint, which is expanded transversely, abutting the surangular

(Fig. 18B, Sa), is adapted to resist induced torsion. However, the mandibular symphysis, in the single juvenile example that displays this structure (Norman, 2020a: fig. 40), is incapable of resisting torsion; and the predentary (insofar as its structure may be inferred) is equally unlikely to have prevented mandibular torsion at the symphysis.

[D] Muscular effects during jaw closure. The principal jaw adductor muscles (MAMES, MAMEM, MAMEP, MAMP, MPST) have their origins on the lateral walls of the braincase, temporal arches and quadrate (Fig. 15). The muscles run obliquely (ventrolaterally) from their areas of origin to insert principally upon the coronoid eminence either directly (Fig. 15B, C, MAMES, MPST), or via a common bodenaponeurosis (Fig. 15C, bod). While such muscles exerted force vectors that result in orthogonal (vertical) closure of the jaws, the posterior portion of the mandibles where the musculature inserted would also be subjected to medially directed forces: reflecting the sum of the predominantly mediodorsal lines of action of these jaw muscles, combined with the dorsolateral location upon the mandible of many of the points of muscle insertion (Fig. 18, AM). Occlusion (with overbite) that occurred between some of the teeth within the dentition would also impose medial force vectors on the mandibles. The combination of the muscular and occlusion-induced medial forces would induce medial torsion on both mandibles during isognathic (Norman & Weishampel, 1985) jaw closure.

Some degree of torsional ‘balance’ would have been generated by the action of the pterygoideus group that forms a sling-like arrangement in which muscles arising on the pterygoid (dorsomedially) wrap around the posteroventral end of the mandibles and insert on the lateral surfaces of the surangular-retroarticular processes. These muscles help to stabilize the jaw joint during jaw closure and induce a modest (clockwise) torsional couple (Fig. 18C, MPT) that counteracts the (anticlockwise) medial couple (Fig. 18C, AM) experienced by the mandibles.

The presence of the epipterygoid, a comparatively rare and unusual feature among dinosaurs generally, can be associated with the presence of components of the constrictor dorsalis musculature in extant squamates (Fig.

15D). In the context of a consideration of the stress (and potential strain) induced in the skull roofing bones when subjected to lateral forces experienced by teeth involved in occlusion in the maxillae, the constrictor dorsalis musculature (perhaps even as ligamentous remnants) may have been retained to act as the equivalent of 'tensioners' linking the maxilla to the braincase via the physical bridge formed by the palate bones (pterygoid and palatine). A complementary role (stabilizing the maxillae) may also have been played by the connective tissues that appear to have spanned the gap between the maxillae to form a soft secondary palate (Fig. 10, sp).

[C] Jaw motion summarised

Anteroposterior pivoting of the quadrate (conventional streptostyly) did not occur. Slight movement of the quadrate head within the squamosal cotylus was possible and would have allowed subtle mediolateral displacement (wishboning) of the mandibles. Such motion facilitated passive re-positioning of the mandibles during the chewing cycle. The structure of the mandibular joint indicates that each mandible hinged uni-axially against the quadrate condyle. The lateral expansion of the quadrate condylar surface (to contact and form an articular facet with the surangular) as well as the ventromedial angulation of the quadrate condyle may have helped resist medial rotation (torsion) induced in the mandible during jaw closure.

The orientation of the principal mandibular adductor muscles and their insertion on the coronoid eminence promoted principally orthal motion of the mandible. The positioning of the teeth (medially offset, relative to the longitudinal axis of the tooth-bearing bones) as well as the shape of the opposing dentitions had several predictable effects. The overbite of the maxillary dentition induced medially directed forces (a torsional couple) on each mandible and laterally directed forces on the maxillae. The bowing seen along the length of both dentitions in occlusal views created large-scale 'guides' that ensured accurate positioning of mandibular and maxillary dentitions during biting to ensure that opposing dentitions engaged correctly (Fig. 17B). The sinuous profile of each dentition altered the mechanics of occlusion along the length of the dentition because the anterior dentition is at the level of the jaw articulation (facilitating a scissors-like action), whereas the posterior dentition is dorsally displaced and would have occluded simultaneously (*en bloc*). Displacement of the latter type is seen in specialist herbivores (Norman & Weishampel, 1985; Greaves, 1995). This mechanical variation in configuration along the length of the mandible is suggestive of a partial differentiation of function: the beak and anterior dentition provided a cutting and pulping apparatus, whereas the posterior dentition was more involved in orthal pulping (non-occluding crowns) and shearing-crushing (occluding crowns) prior to swallowing. Repeated jaw closure, particularly at the rear of the mouth would have required cheeks to enclose the buccal cavities and limit food loss from the sides of the mouth during each cycle of occlusion (Lull & Wright, 1942; Ostrom, 1961; Galton, 1973; Norman, 1984a; Weishampel, 1984; Norman & Weishampel, 1985).

The symphyseal region of the mandible was unfused in ontogenetically immature specimens and it is considered unlikely that fusion occurred in adults because the inferred dynamics associated with jaw closure imply a combination of active and passively induced mandibular torsion. Torsion that occurred during biting would also generate elastic strain energy in the ligaments binding the mandibles at the symphysis that would be released during abduction. This elastic recoil would contribute to the restoration of the mandibles to their pre-closure configuration. The undulatory pattern seen on the surface of the bones that form the symphysis in the immature specimen (BRSMG Ce12785 – Norman, 2020a: fig. 40) lends support to the hypothesized mobility of this joint. The predentary may well have played a role in the symphysial stabilization and recoil system proposed here, but until this bone (or its soft tissue equivalent) is discovered this suggestion remains speculative.

[C] Oral food processing (and potential diet)

On the basis of the interpretations above, oral food processing in *Scelidosaurus* may be considered to have been ‘imperfect’ judged by the irregular and discontinuous occlusal surfaces found along the dentition. The beak and anterior dentition formed a relatively narrow but sharp-edged cropping structure. A narrow beak is commonly interpreted as being associated with selective feeding that equates to specialized food preferences (Jarman, 1974; Carrano *et al.,* 1999; Ösi *et al.,* 2017).

Posterior to the beak region the upper and lower dentitions are inset medially, creating a prominent embayment that was spanned by a (muscular) cheek. The longitudinal curvature of the dentitions creates guides that impose precision on (orthal) jaw motion because the dentitions can only effectively engage in one position. The surfaces of the teeth in the dentition are not uniformly abraded: some develop high-angle abrasion facets indicating a close occlusal relationship with an opposing tooth, whereas others show little or no wear. As a consequence, the non-beak dentition combined orthal pulping with a degree of power-stroke shearing, and a minor component of crushing where a few abrasion facets form oblique ledges near the base of dentary crown facets (Norman, 2020a: figs 42, 43).

The duration of oral processing prior to swallowing cannot be determined but it is inevitable that vegetation was pulped and partly chewed (hence the need for cheeks to retain food as it was repeatedly cut) before it was swallowed. This probably represents an adaptation to the type of vegetation consumed by, or available to, this animal; or more subjectively the position occupied by *Scelidosaurus* on an functional-evolutionary trajectory associated with dinosaurian feeding efficiency. The remains of the terrestrial flora associated with the marine Lias of Charmouth are limited to comparatively rare (usually pyritized) chunks of coniferous wood and extremely rare leaf fragments. Roughly contemporaneous deposits reveal that the Early Jurassic flora associated with the tropical summer/wet environment of the Lias was dominated by microphyllous cycads, bennettitaleans, conifers, abundant ferns and sphenopsids (Rees, Ziegler & Valdes, 2000; Willis & McElwain, 2014). Most of these plants are low-growing potential browse for scelidosaurs. The narrowness of the cropping beak of *Scelidosaurus* suggests some selectivity of food items: fleshier leaves might have been susceptible to non-occlusal pulping and comparatively less cutting and crushing (see below: *Digestion*)

[B] Osteological anomalies

[C] Epistyloid bones

Long, blade-ended bones are seen projecting obliquely from the posterior surface of the skull in the articulated skeleton (BRMSM LEGL 0004: Fig. 19A) and a partially ossified epistyloid is preserved with the skeleton of the smaller individual (CAMSM X39256 – Fig. 19B). The structure of the bone in the juvenile individual differs from that seen in the larger (sub-adult) individual because its shaft is narrow rather than rod-shaped and the bladed distal portion is more asymmetrical and is not as fully developed as in the larger individual.

<Figure 19 near here> epistyloids

Norman (2020a) suggested that these bones represent a calcified tendinous portion of the *m. cucullaris cervicis* complex (Theis, 2010) that in diapsids runs from the pectoral girdle to the floor of the braincase and controls head movement and positioning (see Fig. 20). If these bony structures in these two individuals are correctly interpreted, they grew during the life of the dinosaur and, as they did so, developed from a tendinous origin into a narrow, flattened shaft that finally 'matured' into more cylindrical form, whereas the distal blade deepens and develops additional vanes that anchored tendon sheets. This sparse and tentative morphological ontogeny implies that these bones are metaplasticly remodelled from the tendinous portion of the cucullaris musculature. The tendons that develop in the calf muscles of extant domestically bred turkeys first form as laterally compressed sheaths (Norman, pers. obs) and this may echo the initial stages of development of the epistyloids recovered in *Scelidosaurus*.

<Figure 20 near here> reconstructed cucullaris musculature

Remarkably, given the range and variety of dinosaur skull material discovered and described to date, this is the first report of these anatomical structures in the skull of any dinosaur. These bones were not observed or recorded in the articulated lectotype skeleton but this may be because the skull nodule was detached from the original skeleton and then eroded by water-rolling before it was discovered. If remnants of these bones were preserved during the process of acid-mediated preparation they may have been mistaken for fragments of cervical rib or perhaps ossified tendons displaced from the spine.

[C] Epivomer bones

These shallowly arched, thin, roughly triangular bones have only been recorded in the acid-prepared skull of the lectotype (NHMUK R1111 – Norman, 2020a: fig. 26; and diagrammatically in Figure 10). Evidence suggests that they are associated with the vomers in the dorsal region of the nasal cavity of *Scelidosaurus*. These bones are as enigmatic as the epistyloids described above. They are paired structures, and each displays a bevelled sutural edge (Norman, 2020a: fig. 26, sut) that corresponds in shape and surface topography to an equivalent bevelled edge on the dorsolateral margin of each vomer. There is another bevelled margin on each anterolateral edge (Norman, 2020a: fig. 26, bev). If correctly identified, these bones represent ossifications within the connective tissue that formed the roof of each nasal passage. It has been suggested above (see *Taste, smell and nasal passage function*) that they might have anchored respiratory/olfactory turbinates.

[C] Epipterygoid bones

Among dinosaurs epipterygoid bones are comparatively rare (Holliday, 2009). The preservation of an epipterygoid adhering to the dorsolateral edge of the central portion of the pterygoid in *Scelidosaurus* Norman, 2020a: fig. 28) is not entirely unexpected because epipterygoids have been reported in some ankylosaurids (Maryańska, 1977). The retention of an epipterygoid (more commonly associated with kinetic skulls) may be associated with a remnant of the constrictor dorsalis musculature that connects the lateral wall of the braincase and the dorsomedial edge of the pterygoid (Fig. 15D, MLPt). This muscle, or a ligamentous remnant thereof, counteracted strain induced in the skull roof during chewing by tensioning the pterygoids medially.

The structure of the epipterygoid shows that it was not part of an articular linkage between the palate and braincase (traditionally associated with cranial kinesis). It either represents an atavism linked to its theropod and dinosauromorph ancestry (Baron *et al.,* 2017b), or its presence reflects some other, so far unexplained, role associated with the functionality of the skull.

[C] Pterygoid 'pocket'

A narrow pocket-like structure is preserved near the ventral edge of the medial wall of the left pterygoid of the holotype skull (Norman, 2020a: fig. 28B). Its medial wall is partially split away from the body of the pterygoid and resembles a rectangular flake of bone attached to the medial wall of the pterygoid. Nevertheless, it appears to have had a good dorsal edge and creates a narrow, pocket-like structure of unknown function. This feature is not preserved on the right pterygoid, so it seems more likely to be a preservational artefact created by physical damage.

[C] Antorbital fossa

The antorbital fossa is small and has a bean-shaped outline. Its edges and extent are demarcated clearly because its internal (medial) wall is smooth (in marked contrast to the exostotic bone that corrugates the surface of most of the bones surrounding it on the side of the snout). The role of the antorbital fossa in archosaurs and dinosaurs has been much discussed in the past. Explanations have focused mainly upon its housing a glandular structure, usually interpreted to be an extra-renal salt gland (Broom, 1913) – a view supported by Ewer (1965), a muscle (Dollo, 1884; Ewer, 1965; Schumacher, 1973), or a diverticulum of the nasal/pneumatic system (Osmólska, 1985; Witmer, 1997).

The glandular hypothesis is negated by the fact that in extant taxa such glands are located within the orbital cavity, along the dorsal margin of the orbit or the more medial portion of the nasal cavity (rather than the lateral surface of the snout). Equally, the muscular origin hypothesis, most often linked to providing an enlarged origin for the anterior pterygoid muscle, has been refuted on several occasions because this muscle invariably originates on the pterygoid and palatine bones. And in forms such as extant crocodiles, in which this muscle inserts on the maxilla, there is no antorbital fossa (this latter argument fails when Mesozoic crocodiles are considered because they retained an antorbital fossa). In contrast, the proposal that the fossa represents a cavity to accommodate a diverticulum of the paranasal pneumatic sinus system is preferred because osteological correlates exist in living archosaurs (including birds) and these can be traced back through the dinosaur fossil record to pseudosuchian archosaurs (Witmer, 1997).

<Figure 21 near here> Facial region of 0004.

In *Scelidosaurus* the posterior portion of the antorbital fossa marks the position of the anterior edge of a more deeply positioned (posterior) antorbital fenestra. The anterior margin of this latter fenestra is a pillar formed by the maxilla that swings acutely anteromedially into the floor of the nasal cavity, medioventral to the lacrimal (Norman, 2020a: fig. 12A,B, af). This structure can reasonably be interpreted as the passageway for a paranasal sinus that lined the antorbital fossa. The function of such a sinus is unclear and it may represent no more than a dwindling attempt by the pneumatic system to invade the fabric of the snout in an otherwise robust skull, as argued by Witmer (1997). However, in the skull associated with the large referred skeleton (BRSMG LEGL 0004 – Fig. 21) there is a discrete smooth patch of bone and an adjacent groove directly above the antorbital fossa. This bony surface is particularly noticeable because all the surrounding bone surfaces are adorned by roughly textured exostotic tissue. The absence of exostotic bone just in this one place suggests that the tissues associated with the paranasal sinus and its associated tissues may have extended between the keratinous scutes immediately dorsal to the antorbital fossa (see Fig. 6, ?). A sinus extension of this sort might have formed an inflatable pouch adjacent to the orbital region, perhaps associated with some aspect of the behavioural repertoire of this animal.

[A] *SCELIDOSAURUS*: POSTCRANIAL BIOLOGY

[B] Digestive system

A diet of terrestrial plants requires a variety of modifications to be made to the digestive system (King, 1996; Sues, 2000). Land plants have a skeletal scaffold formed by a combination of structural polymers: lignin, hemicellulose and cellulose, none of which can be hydrolysed by vertebrate gut enzymes. To release the soluble contents of plant cells their lignin/cellulose fabric needs to be broken down. This process is started in the mouth using teeth and jaw muscles. There is structural evidence in *Scelidosaurus* for a small, sharp keratinous beak that was narrow so that the animal was capable of cropping plant material (perhaps more succulent items) selectively. Once in the oral cavity a modest amount of pulping and shearing of plant tissue occurred prior to swallowing, judged by the morphology of the dentition. The structure of the gut into which the browse was passed is unknown in *Scelidosaurus* but the wide span of the ribcage (Norman, 2020b) indicates that the torso was broad. In its proportions and general body shape *Scelidosaurus* more closely resembles those seen in ankylosaurs (Fig. 22A) than the vertically extended (narrow and deep) torso morphology exhibited by stegosaurs (Fig. 22B).

<Figure 22 near here> comparison on body shapes.

It is reasonable to assume that a modest amount of chewing of ingested plant material occurred in the mouth; however, the residence time in the gut to allow for the enzymatic breakdown of lignin and digestion of cellulose would be expected to be long, prior to absorption and assimilation of the plant breakdown products. There are additional factors to be considered, such as the presence of anti-predation chemical defences produced by the plants such as alkaloids, terpenoids, condensed and hydrolysable tannins (Swain, 1976), as well as the relative succulence and physical texture of the browse. A crop can be inferred (because it is present in living archosaurs) as a specialized sac-like compartment at the base of the oesophagus, adjacent to the stomach. The crop can store and chemically prepare the browse for subsequent digestion by softening and enzymatically detoxifying plant tissue. Herbivorous reptiles and birds have a far greater tolerance of alkaloids than, for example, crop-less herbivorous mammals (King, 1996); this may in part be attributed to the ability of the former groups to chemically neutralize these poisons in the crop before they enter the absorptive part of the digestive system.

The stomach of living birds and crocodiles is also modified by the presence of a muscular gizzard whose walls are abrasive and used to physically pulverise the plant tissues (or large bones in the case of crocodiles) in preparation for digestion. Birds and crocodiles are known to swallow grit or stones (gastroliths) that become lodged in the walls of the gizzard and assist in the physical breakdown of food in the stomach (gastroliths are also known to serve as ballast in crocodiles – Taylor, 1987). Beyond the stomach and gizzard, the intestine has an absorptive section (small intestine) that can remove soluble plant cell contents released by the crushing of their tissues. In herbivorous birds this region of the gut contains a series of blind-ended pouches (caecae). The caecae are diverticulae in the gut (sometimes spirally coiled) into which the partly digested and crushed plant material passes for further digestion mediated by symbiotic microbes (prokaryotes and protistans). Unlike their vertebrate hosts these microbes are capable of producing enzymes that hydrolyse plant cell walls by converting them to breakdown products such as sugars and volatile fatty acids (McBee, 1977). Enzymatic breakdown of the plant cell walls releases sugars, proteins, minerals and vitamins that can be absorbed through the lining of the caecum and small intestine. The process of providing nutrition to the population of symbiotic microbes boosts their population, which in turn allows the host to absorb amino acids and other breakdown products derived from cell death among symbionts. In living herbivorous lizards (and mammals) the more distal region of the gut accommodates a voluminous caecum that arises at the junction of the small and large intestines (Romer & Parsons, 1980).

The size of the abdominal cavity simply reflects the storage capacity of the gut and its ability to cater for the lengthier phases of digestion and absorption inherent in a vegetarian diet. Only in exceptional circumstances are traces of the soft tissues of the gut (cololites) preserved (Dal Sasso & Signore, 1998; Ji *et al.,* 1998), but in the case of *Scelidosaurus* there is, to date, no known preservation of gut tissues or gastroliths in association with the abdominal cavity that might illuminate gut structure and function.

[B] Respiratory system

The respiratory systems of dinosaurs are not preserved but they are so central to the development of an understanding of the physiology and metabolic status of these animals that they have become a persistent subject of investigation. Carrier & Farmer (2000a,b), Perry (2001) and Perry & Sander (2004) did much to promote debate on this topic by focusing on the respiratory *potential* in dinosaurs, given what was then known about the skeletal mechanics and respiratory physiology of extant squamates, crocodiles and birds. The close relationship between theropod dinosaurs and birds (Huxley, 1868; Ostrom, 1976; Xu *et al.,* 2014) focused much of the subsequent discussion about dinosaur lung structure on the osteological correlates identifiable in theropods: pneumatized bones, uncinate ribs and gastralia (Claessens, 2004; O'Connor & Claessens, 2005; Codd *et al.,* 2008; Benson *et al.,* 2012) and to a lesser extent sauropods (Britt, 1997; Perry & Reuter, 1999). Benson *et al.* (2012: 188), in an article that focused solely upon skeletal pneumaticity and its implications for dinosaurian (including bird) physiology, noted that Ornithischia is a clade of diverse and abundant dinosaurs that is deeply nested within ornithodiran archosaurs and yet lacks a pneumatic postcranium, implying that this factor needed to be reconciled in any model of dinosaurian biology.

Aspiratory respiration became established in amniotes ancestral to Archosauria, resulting in the potential to increase the overall efficiency of gas exchange among these animals (Perry & Sander, 2004). Most models of amniote respiration were understood to be driven by muscle-induced repositioning of the ribs to change the volume of the thoracic cavity (costal aspiration). However, it has become clear that respiration can be augmented by cuirassal aspiration (indicated by the presence of an abdominal skeleton of gastralia – belly ribs), and pelvic aspiration (dependent upon an ability to flex either the entire pelvis against the dorsal vertebral column, or specialized parts of a fixed pelvis – Carrier & Farmer, 2000a, b).

In living birds, highly compliant air sacs evolved in association with a unidirectional ('flow-through') lung structure. A strictly comparable respiratory system was hypothesized for theropods ancestral to birds (O'Connor & Claessens, 2005; Benson *et al.,* 2012). Abdominal wall compliance probably increased in birds with the loss of gastralia. However, cross-current (unidirectional) gas exchange systems were then identified by Farmer & Sanders (2010) in the lungs of alligators. The strong similarity in air-flow patterns in the lungs of birds and crocodilians suggests that these features are plesiomorphic for Archosauria (Schachner *et al.,* 2013a). Flow-through lungs are also now recognized more widely among diapsid amniotes including squamates (Schachner *et al.,* 2013b; Cieri & Farmer, 2016) so the inference of the existence of this type of lung in dinosaurs cannot seriously be doubted.

[D] Crocodiles. The combination of a non-pneumatic postcranium and an absence of air sacs in association with flow-through lungs in crocodiles and varanid squamates is of importance in relation to any interpretation of the biology of ornithischian dinosaurs because, as Schachner *et al.* (2013a) argued, it breaks what had become over time an embedded stack of inductive reasoning: pneumatic bones = an air sac system = unidirectional ('flow-through') bird-like respiratory system = bird-like physiology. However, crocodiles also exhibit two other osteological correlates linked to interpretations of respiratory physiology: uncinate plates or flanges (Hofstetter & Gasc, 1969) reminiscent of – but not necessarily homologues of – the slender, ossified uncinate processes seen on the ribs of avian theropods and birds (Codd *et al*., 2008); and gastralia (an indicator of cuirassal aspiration).

The respiratory physiology of living crocodiles is multifaceted and linked inextricably to secondary skeletal modifications for a life spent both in water and on land. Such animals are unlikely to be reliable analogues from which to infer respiration in ornithischian dinosaurs because of their secondarily evolved aquatic adaptations (e.g. Crush, 1984). Nevertheless, they possess anatomical features that may offer tangential insights into scelidosaur breathing. On land, there are two distinct modes of respiration. Adult crocodiles spend considerable amounts of time lying motionless and thermoregulating (basking); when doing so they lie sprawled on the ground with their bodies unsupported by limbs. Gravitational compression of the body results in the ribcage becoming anchored against the substrate and forming a self-supporting arch (the individual strut-like ribs may be reinforced by the presence of the uncinate plates). The lungs can thus hang comparatively freely within the thoracic cavity without becoming compressed by anterior displacement of the abdominal organs (the gastralia may also strengthen and tension the abdominal wall in this regard). In this sprawled posture pelvic aspiration dominates and is mediated by musculature attached to a movable pubis and body wall that facilitates the slow piston-like motion of the liver (the hepatic piston pump) that alternately compresses and decompresses the thoracic cavity (Gans, 1970). It should be noted that experimentation on *juvenile* crocodiles (e.g. Munns *et al*., 2012, Brocklehurst *et al.,* 2017) demonstrates that costal ventilation is a component of resting terrestrial ventilation, but these animals are far more agile and considerably less gravitationally challenged than adult crocodilians and can be more adaptively flexible in their recruitment of aspiratory musculature.

When walking terrestrially, the hindlimbs support a high percentage of the body weight, and the vertebral column (particularly in large crocodiles) bows downward anterior and posterior to the pelvic region. The dermal skeleton controls the degree of bowing of the vertebral column by tensioning the vertebral column and ribcage via sheets of ligament that connect the overlying osteoderms to the neural spines and dorsal surfaces of the ribs (Frey, 1984, 1989). As a consequence, during the 'high walk' the back of the animal is stiffened and the mobility of the ribs is reduced: thus cuirassal and diaphragmatic aspiration become of greater importance. Abdominal musculature (ischiopubis-ischiotruncus) anchored to the ischium, and a kinetic pubis attached to the gastralia draw the gastralia posteriorly and ventrally, decompressing the abdominothoracic chamber (inspiration). The rectus abdominus musculature linking the gastralia to the sternum draws the gastralia forward and dorsally, reducing the abdominothoracic volume during expiration (Carrier & Farmer, 2000a,b). In water, the vertebral column and ribcage are freed from the gravitationally imposed tensile restriction imposed by the dermal skeleton. The ribs can also be moved by intercostal musculature and the iliocostalis system to alter the volume of the thoracic cavity (Brocklehurst *et al.,* 2017; Codd *et al.,* 2019). Whether the diaphragmatic (hepatic-piston pump) and cuirassal systems operate during swimming is unknown; but as Gans (1970) pointed out, crocodiles, when hunting prey could avoid the tendency to 'bob' in the water by adjusting their mode of breathing to minimize unwanted buoyancy-related side-effects (see also Uriona & Farmer, 2008).

[D] Ornithischians in general. Osteologically, this clade exhibits neither postcranial pneumatism nor gastralia. However, some thyreophoran ornithischians (including *Scelidosaurus* – Norman, 2020b) possess crocodile-like mineralized uncinate plates; these have also been identified in ankylosaurs (Brown, 1908), a basal stegosaur (Zhou, 1984) and several ornithopods (Butler & Galton, 2008).

Carrier & Farmer (2000a) reviewed the occurrence of pelvic respiratory mechanisms in archosaurs and considered the enigma of ornithischian aspiratory mechanics. The absence of gastralia removes the possibility of cuirassal aspiration, and it was argued that the large herbivore gut would have made cuirassal breathing “uneconomical” because of the energy expenditure needed to raise the heavy viscera for each expiration. Three possibilities remain: costal aspiration alone, costal and diaphragmatic aspiration in combination, or costal and some “unique form of pelvic aspiration” (Carrier & Farmer, 2000a: 282). Costal aspiration alone was considered unlikely and there was no osteological evidence for a crocodile-like diaphragmatic system, so attention was focused on the distinctive pelvic morphology displayed by this clade.

The anteroposterior elongation of the iliac blade for the attachment of limb protractor and retractor muscles, the large number of sacral vertebrae, the sagittal expansion of the blades of tall neural spines that were flanked by bundles of ossified tendons clustered around the pelvic region, indicated “strength and limited ilio-sacral mobility” in ornithischians. It was also noted that the pubis and ischium did not support the femoral articulation and were “loosely” attached to the ilium judged by their unfused articular joints. The latter has led to ambiguity in pelvic reconstructions (as noted in Norman, 2020b). In such (generally) large-bodied animals the pubis and ischium would have had to respond to increasing support-related and locomotor muscle-induced forces, but this was evidently not reflected in the strengthening of their sutural relationships. However, instead of diminishing in size and importance (because their support and anchoring roles were of secondary importance), these bones became enlarged through the development of large "paddle-shaped" prepubic processes, and ischia that became strong, elongated bones.

A pelvic aspiration model was proposed for the lower pelvic bones. Using the example of derived ceratopsians, it was proposed that the pubo-ischium (as a unit) was capable of parasagittal rotation against the ilium: in effect rocking backwards and forwards to expand and contract the abdominal cavity and pressurize-depressurize the thorax. This system was suggested to have been driven by antagonism between the *rectus abdominis* and *ischiotruncus* musculature (Carrier & Farmer, 2000a: fig. 10A). Alternatively, using the example provided by stegosaurs and ornithopods, it was suggested that the pubis acquired a kinetic relationship with respect to the adjacent pelvic bones: the joints between the pubes and the ilia became mobile and the (posteriorly-directed) pubic shaft was considered to be capable of rotating about its long axis where it lay parallel to the ischium. As a consequence, the "paddle-shaped" prepubic blades could be abducted, thereby expanding the abdomen. A new iliopubic muscle was proposed (Fig. 23) that ran between the dorsal margin of the iliac blade and lateral surface of the prepubic blade (although an antagonist to this muscle was not considered). It was also noted that the pumping action of the prepubic blades would have been more effective if there were lung diverticula (or air sacs) in the abdominal cavity – for which there is no evidence.

<Figure 23 near here> Carr & Farm model of pelvic asp. in ornithischians

It can be noted that in stegosaurs the pubic shaft rests snugly against the entire length of the shaft of the ischium and would have been bound to the latter by ligaments that may have permitted some axial twisting of the pubis and consequential abduction-adduction of the prepubic blade. In ornithopods, a characteristic feature of the ischium is the presence of the tab-shaped obturator process; this latter had the potential to provide an appropriate anchoring point and attachment site for ligaments that controlled the movement of the pubic shaft.

It is perhaps understandable why Carrier and Farmer did not expand their idea to reconcile their theoretical model with aspiratory mechanisms in ankylosaurs: the construction of the ankylosaur pubis (reduced and fused to the ilium) is not compatible with their line of reasoning. Equally, the fusion between dorsal ribs and dorsal vertebrae of ankylosaurs has the potential to compromise a costal aspiratory mechanism. Ankylosaur aspiratory mechanisms are enigmatic and may well have been diaphragmatic given the mechanical restrictions that seem to have applied to their costal and pelvic regions. However, one consistent feature among ankylosaurs is the extremely broad, laterally overhanging preacetabular process of the ilium. This structure has the potential to anchor a sling of musculature surrounding the abdomen and capable of alternately compressing and decompressing the abdominal region in these animals to achieve ventilation of the lungs.

[C] Scelidosaurus

Contrary to Richard Owen's interpretation that "In different parts of the matrix of blocks (Tabs. II and IV) are portions of long and slender bones, which are, most probably, abdominal ribs" (Owen, 1863: 6), there is no convincing evidence of gastralia in *Scelidosaurus*; and there is no evidence of postcranial pneumatism (Norman, 2020b). If Carrier & Farmer (2000a) are correct in their general thesis concerning archosaur aspiratory mechanisms then the dinosauromorph ancestors of this lineage (represented by *Herrerasaurus* – see Fig. 27A) are likely to have used a combination of costal and cuirassal aspiration. The additional presence of osteoderms (retention of an archosaur symplesiomorphy?), or even their secondary development in thyreophorans, may have influenced rib mobility and the extent to which the costal system could contribute to volume/pressure changes within the thoracic cavity (*cf*. crocodiles). Such constraints might have required thyreophorans (including *Scelidosaurus*) to use additional (but so far unknown) mechanisms for ventilation.

[D] Costal aspiration. Brocklehurst *et al.* (2017) examined rib mobility in juvenile alligators. One particular consideration was the arrangement of the para- and diapophyseal articular facets along the dorsal series and the degree

to which the positioning of the facets affected rib motion. Archosaurs (and alligators are no exception; Brocklehurst *et al.,* 2017: fig. 1; see also Norman, 1980: figs 34, 37) display migration of these facets along the dorsal vertebral series: the parapophysis rises from the lateral surface of the centrum to the transverse process and then migrates toward the distal end of the latter before finally merging with the diapophysis. In *Scelidosaurus,* the parapophyses of the first three dorsals rise sequentially to occupy a position on the anteroventral edge at the base of the transverse process. However, once this position is attained no further migration takes place until the last two dorsals in the series (Norman, 2020b: figs 20, 21). The parapophyseal facets are all dimple-shaped and smoothly concave, indicating a normal synovial joint. The diapophyseal facets are more complex having a ventral half that is synovial and a dorsal half that is pockmarked by ligament pits (Norman, 2020b: fig. 16, pits), suggesting that the upper half of the suture between the diapophysis and tuberculum formed a firmer, fibrous joint.

The ribs are notable for their span when placed in articulation (Norman, 2020b: fig. 34): the back of the animal was broad rather than narrow and deep. The distal ends of the thoracic ribs are bluntly truncated, indicating that their ends articulated with sternal rib cartilages (none of the latter are preserved). The presence of facets on the trailing edges of some of the longer anterior dorsal ribs, as well as what appears to be a partly mineralized plate (Norman, 2020b: fig. 35A) shows that uncinate plates were present – but may have been localized to the middle of the shafts of the longer thoracic ribs – and similar indications of uncinate plates have been reported in other ankylosaurs (e.g. Brown, 1908 – see also Gilmore, 1930) as well as the basal stegosaur *Huayangosaurus* (Zhou, 1984: fig. 19). The more specialized slender uncinate processes reported in some avialians have been linked to the mechanics of the respiratory system (Codd *et al.,* 2008). Recent work (Codd *et al*., 2019) has also shown that in alligators the *iliocostalis* musculature is attached to the uncinate plates on the ribs and was capable of facilitating rib movement, augmenting thoracic compression (exhalation) under terrestrial conditions. Slender uncinate processes are present on all the dorsal ribs of the extant lepidosaurian *Sphenodon*, but these have muscular connections to the gastralia and may be associated with cuirassal aspiration (Codd *et al.,* 2019).

In *Scelidosaurus*, the uncinate plates are mineralized sheets of tissue (probably cartilage) that are in their structure more similar to the flap or flange-like uncinate plates seen in crocodiles. These are here interpreted primarily as rib stabilisers or ‘spacers’, but there is the possibility that they also anchored *iliocostalis* musculature that facilitated exhalation, as described in alligators.

Ribs may also play a role in supporting the osteoderms that form conspicuous rows running the length of the torso. The most prominent osteoderms are found along the flanks of the animal and lie adjacent to the distal ends of the rib shafts. There is superficial similarity between the osteoderms covering the back of *Scelidosaurus* and those seen in crocodiles; however, crocodilian osteoderms are more closely packed and articulate, creating a flexible dermal carapace, whereas those of this dinosaur do not articulate (apart from in the cervical region), being more widely spaced. The area between individual torso osteoderms comprises a semi-flexible dermis formed by a mosaic of much smaller osteoderms (Norman, 2020c: fig. 36). Individual large osteoderms are lightly constructed, with a thin cortex and a cancellous medulla (Norman, 2020c: fig. 43), so the weight of the dermal armour was unlikely to have been excessive. The extent to which osteoderms were anchored by ligaments to the ribcage and formed part of a tension system similar to that seen in extant crocodilians is unclear, but is considered to be unlikely given their widely spaced and non-articular arrangement in the thoracic region. The ossified tendon bundles that flanked the neural spines of the dorsal vertebrae would have tensioned the backbone in an analogous manner to the osteoderm-based tension system of crocodilians. However, the larger osteoderms were likely to have been capped by keratinous sheaths (Brown, 2017) and formed rows of defensive spikes. Firm anchorage in the dermis and to the underlying skeleton (ribs) might be expected – and this anchoring is perhaps reflected in the preservation of semi-natural arrays of these osteoderms in some articulated skeletons (e.g. BRSMG LEGL 0004 – Norman, 2020c: fig. 8).

Overall, the ribcage of *Scelidosaurus* has a broad span and there was a conspicuous uniformity in the articular relationships (and range of possible movements) of the thoracic ribcage. Rib motion is likely to have been of the bucket-handle type (Brocklehurst *et al.,* 2017) which would have permitted modest volumetric change in the thoracic cavity; this may have been augmented by the *iliocostalis* musculature that, in alligators, inserted on the uncinate plates (Codd *et al*., 2019). The longer thoracic ribs were stabilized proximally by fibrous connections running across the diapophyseal-tubercular joints, and their shafts were 'spaced' distally by the presence of cartilaginous uncinate plates (that became mineralized in more mature individuals) so that the thoracic ribs moved as a parallelogram-like unit. The ribs supported and helped to anchor the larger osteoderms. There is, however, no convincing evidence that the ribs and osteoderms formed a tensioning system that stiffened the backbone as in crocodiles. Modest uniform flexure of the thoracic ribs provided a mechanism for costal aspiration.

[D] Cuirassal aspiration. In the absence of gastralia there is no osteological evidence for cuirassal aspiration and this aspiratory mode is considered improbable by Carrier & Farmer (2000a).

[D] Diaphragmatic aspiratory mechanisms akin to those seen in extant crocodilians cannot be entirely discounted because diaphragmatic muscles might have been anchored to the prepubic blades, although their lateral positioning counts against this possibility, provided that the crocodilian model of hepatic pistoning is an applicable comparator.

[D] Pelvic aspiration. The observations of Carrier & Farmer (2000a) prompt brief consideration in relation to the respiratory capacity/potential in *Scelidosaurus*. Pelvic flexure (between the dorsal vertebrae and sacrum) can be excluded given the presence of bundles of ossified tendons that run along the entire dorsal series and are anchored to the sacrum; these would inhibit flexure between the dorsal series and sacrum. The pubis and ischium are not fused to the ilium but rather articulate with the latter via thick connective tissue pads. The pubic shaft and ischium are equal in length, whereas the prepubic process forms a laterally-directed blade. In basal ornithischians (*Lesothosaurus* – Baron *et al.,* 2017a; *Heterodontosaurus* – Santa Luca, 1980; Galton, 2014) the prepubic process forms a rectangular plate that projects anteriorly beneath the preacetabular process of the ilium to a greater extent than indicated in the reconstruction of Carrier & Farmer (2000a: fig. 11A). In *Scelidosaurus*, the prepubic process is short in juvenile individuals (NHMUK

R6704: Norman, 2020b: fig. 73) but becomes a more substantial rectangular plate in larger (sub-adult) individuals (Norman, 2020b: fig. 74).

The pubic shaft is a long rod, coterminous with the distal end of the ischium and lies against the shaft of the ischium. The Carrier-Farmer model of rotation of the pubic shaft permits the prepubic blade, if adducted, to compress the broadly expanded posterior abdominal wall. If diverticula or air sacs were present (unknowable), respiration would have been augmented. A model involving a combination of costal (possibly diaphragmatic?) and pelvic aspiration (achieved by pubic mobility) is at least plausible for *Scelidosaurus*.

[A] OPISTHOPUBIC PELVIC STRUCTURE: A REFLECTOR OF HERBIVORY OR RESPIRATORY BIOLOGY?

Macaluso & Tschopp (2018) argued that it was necessary to demonstrate that respiration was more likely to be an “evolutionary driver” of opisthopuby in dinosaurs than was herbivory. The basis for this proposition was a false premise: that opisthopuby in *all* dinosaurs had previously been causally linked to the adoption of an herbivorous diet. Furthermore, they claimed that this idea had been proposed by Weishampel & Norman (1989). However, Weishampel & Norman never made such a claim in that article. Rather opisthopuby, which characterizes Ornithischia, was proposed as a biomechanical adaptation that permitted *small ornithischian herbivores* to retain a bipedal posture and limb proportions indicative of cursoriality in the face of predation by coeval bipedal and cursorial theropods (Norman & Weishampel, 1991). This latter proposition was *never* expanded by these authors to encompass all dinosaurian sub-clades. The evolution of an analogous form of opisthopuby among some avian-theropods, although interesting *per se* from an evolutionary perspective – particularly in light of the work of Baron *et al*., (2017b,c) – has always been considered (certainly by Norman and Weishampel) to be a functionally and physiologically unrelated matter.

An awareness of cranial adaptations that can be interpreted as indicators of a herbivorous or omnivorous diet among theropods (traditionally considered exclusively carnivorous) was highlighted in a general review by Barrett & Rayfield (2006). Their general thesis was further developed by Zanno *et al.,* (2009) in which a wider range of cranial as well as postcranial morphologies, and their distribution among taxa, were mapped phylogenetically across a range of coelurosaurian theropods (Zanno *et al.,* 2009). They concluded that coelurosaurian theropods were not primitively 'hypercarnivorous' but were dietarily flexible, ranging from herbivory through omnivory to carnivory, and that strict carnivory was a secondary specialization found in one group of paravian theropods (dromaeosaurids). The recognition of dietary flexibility among coelurosaurians was posited as an evolutionary benefit because it allowed them to be dietary opportunists.

Returning to the issue of respiration vs herbivory as a driver of opisthopuby, Gatesy & Dial (1996a,b) demonstrated that the evolution of opisthopuby is coupled with a reconfiguration of body proportions and limb function among Avialae; this alteration presaged the 'modularized' bodies of extant birds. In short, the tail undergoes progressive reduction in its skeletal and muscle mass; as a consequence, the tail's cantilevering effect is reduced and it simultaneously reduces its capacity to anchor the principal hindlimb retractor muscles (*m. caudifemoralis longus*). An anatomical marker reflecting the reduction of the femoral retractor musculature is the size and prominence of the femoral 4th trochanter, which progressively reduces before disappearing completely in 'paravian' theropods (see Fig. 28). To maintain a bipedal pose a number of sub-clades of shorter- or slender-tailed avian-theropods evolved degrees of pubic retroversion, ranging from intermediate (mesopuby) to full opisthopuby – followed by eventual separation of the pubes and ischia in the midline so that the abdomen can extend posteriorly beneath and behind the sacroiliac vault (see Figs 27, 28). These changes reflect a re-balancing of the body to compensate for the loss of the cantilevering effect of the tail. There is also a consequential re-purposing of the hindlimb. The femur becomes an exclusively anteriorly-directed suspension member of the hindlimb, and the knee-joint adopts the role of a 'neoacetabulum'. The anteriorly displaced knee-joint becomes the centre of balance and the locomotor stride of the hindlimb is achieved by swinging the elongated tibiotarsus and tarsometatarsus, pendulum-like, from the knee (as is the case in extant birds).

In this general context, gross expansion of the gut cavity and retroversion of the pubis (linked to a shortening of the tail), and the maintenance of a bipedal stance, can be correlated with herbivory in the highly modified opisthopubic condition described in therizinosaurs such as *Nothronychus* (Zanno *et al.,* 2009) but these are truly exceptional theropodans – see Figure 27D.

[C] Observations

Macaluso & Tschopp (2018) undertook a study that was purposely restricted in scope: they limited the biological 'drivers' considered to just two. In terms of logic, the study is internally consistent in that they consider whether dinosaurs exhibit carnivory, omnivory or herbivory, assign these traits to the taxa under consideration, and then plot their assignments on a general phylogeny (Macaluso & Tschopp, 2018: fig. 2). They indicate, on that phylogeny, the presence or absence of gastralia and whether pelvic anatomy was 'propubic', 'mesopubic' or 'opisthopubic' – employing the terminology adopted by Rasskin-Gutman & Buscalioni (2001). Dinosaur taxa (representative of selected dinosaurian sub-clades) are then scored according to the authors' interpretation of pelvic morphology, diet and respiratory capacity. An analytical protocol was applied to their scores which promotes the view that opisthopuby is more strongly correlated with respiratory mechanics than with herbivory in these dinosaurs.

Their approach conflates an objective analytical protocol with a set of subjective decisions concerning diet and respiratory capacity, and uses simplified two-dimensional images of hip structure. They admit in the discussion section "that a change in the ventilatory system was [not] the only evolutionary force acting on the structure of the archosaurian pelvis. For instance, egg morphology, locomotion, nesting behaviour and reproductive organs could all have been equally influential." (Macaluso & Tschopp, 2018: 714). There was no mention of herbivory, but these other factors were not explored because they were considered by the authors to be "more difficult to recognise in the skeleton" (p. 714).

On the basis of the published literature and available descriptions, it can be stated objectively that ornithischians and sauropods are the only dinosaur groups that show no evidence of gastralia. Representatives of all the theropod clades considered by Macaluso & Tschopp are known to possess gastralia (*contra* Macaluso & Tschopp, 2018: fig. 2 – note that node 4 in this figure implies that all 'Pennaraptoran' taxa [oviraptorosaurs, dromaeosaurs + *Sinovenator*] possess gastralia and yet, paradoxically, were designated as non-cuirassal breathers. Taken in total, the approach adopted in their article establishes a false premise and subsequently fails to account for the range and variety of anatomy, inferred biology and functional organisation of these animals – all of which have a material bearing on our understanding. It has always been understood (certainly by Norman & Weishampel) that the unique evolution of the opisthopubic pelvis in ornithischians, and also seen to have arisen *iteratively* among some avian-theropod sub-clades, were independent, anatomically distinct and functionally-unrelated events.

To provide an overview of the biological and functional issues associated with respiratory capacity and its linkage to the evolution of pelvic structure in dinosaurs (and their extant descendants birds) a set of summary comments is offered.

<Figure 24 near here> Dinosaur phylogeny crude

[C] Summary

Irrespective of basal dinosaur systematics (Baron *et al.,* 2017b,c; Langer *et al.,* 2017) it can be agreed (following the work of Carrier & Farmer, 2000b) that stem-lineage taxa (dinosauromorph archosaurs) had mobile bicipital dorsal ribs and gastralia. This indicates that they were capable of using to varying degrees a combination of costal and cuirassal modes of aspiration. Gastralia, and by implication cuirassal-style aspiration, are retained (symplesiomorphically) in Late Triassic dinosaurian taxa belonging to Sauropodomorpha and Theropoda (Fig. 24), but this anatomical character and the inferred aspiratory mechanism is absent (synapomorphically) in the Early Jurassic clade that has a sister-taxon relationship with Theropoda: the Ornithischia (Fig. 24) – although it does not matter from which basal dinosaurian clade the Ornithischia are derived in this regard. It is established that the iterative evolution of degrees of opisthopuby among sub-clades of Theropoda can be linked functionally to the re-organisation of the bodies of these animals (Gatesy & Dial, 1996a,b). It is only among Aves (flight-adapted birds) that gastralia are lost and the structural adaptations associated with the avian flow-through respiratory system can plausibly be inferred (see Fig. 27).

<Figure 25 near here> repr ornithischian skeletons

1. Ornithischia. The earliest known (Jurassic) ornithischians were small, bipedal cursors with long, muscular cantilever tails and a herbivorous diet (Fig. 25A). They processed food orally using a combination of orthal pulping and irregular occlusal shearing; they were also narrow-snouted (selective) feeders capable of utilising more readily digested succulent plant material. Their enlarged plant-adapted gut could hang beneath the pelvis and between the legs because of the retroversion of the pubis; this arrangement did not compromise either their bipedal pose or locomotor ability. A large gut is a *sine qua non* for ornithischians even if some were occasional omnivores (as argued by Barrett, 2000) because all living herbivorous-omnivorous lizards are characterized by their possession of comparatively large guts. Costal aspiration was likely to have been their primary respiratory mechanism, but might have been supplemented by some form of pelvic kinesis (Carrier & Farmer, 2000a). The energetic losses incurred by actively raising and lowering the gut, if cuirassal aspiration had been an important component of their respiratory strategy, were thereby avoided.

The subsequent evolutionary history of the ornithischian clade demonstrates that opisthopuby was maintained, albeit with elaboration of the pelvic bones in particular sub-clades, and several sub-clades independently acquired a secondarily quadrupedal style of locomotion (Barrett & Maidment, 2017 – Figure 25B,C).

<Figure 26 near here> repr prosauropod-sauropod skeletons

2. Sauropodomorpha. Triassic sauropodomorphs (prosauropods) are generally small-headed, large-bodied facultative bipeds with large muscular cantilevering tails and an essentially herbivorous diet (Fig. 26A) although, as

pointed out by Barrett (2000), omnivory cannot be excluded. Cropped vegetation was orally pulped after which food was swallowed and then further processed in a gastrolith-laden gizzard (Attridge *et al*., 1985). The enlarged herbivore-adapted gut was positioned anterior to the propubic pubes; these latter bones meet in the midline and form a curtain-like wall at the back of the abdominal cavity (Norman & Weishampel, 1991). The gut and gastrolith-laden gizzard, and its forward position relative to the centre of balance at the acetabulum, was counterbalanced by the massive tail. The abdominal floor was lined by well-developed gastralia (Fig. 26A), implying that cuirassal aspiration supplemented costal ventilation and, furthermore, that the raising and lowering of the mass of the gut during cuirassal aspiration could not have been at an overwhelming energetic cost.

Jurassic and Cretaceous sauropodomorphs (sauropods) are extremely large, pillar-limbed quadrupeds with long tails and necks (Fig. 26B). They were microcephalous herbivores that raked and/or cropped food into the mouth before swallowing after minimal oral treatment (Barrett & Upchurch, 1994). The pelvis was mesopubic and the pubes formed a bony wall at the rear of an abdominal cavity that lay in front of the acetabulum. Quadrupedality, an arched dorsal vertebral column and pillar-like limbs created bridge-like support for a massive gut. Food passed into a stomach that included a substantial gastrolith-filled gizzard and, judged by the space available in the torso, a voluminous (probably multi-chambered) gut. No gastralia are preserved in sauropods (Claessens, 2004 – Fig. 24) and cuirassal aspiration is considered unlikely because it would have involved the raising and lowering of an exceptionally massive gut (Carrier & Farmer, 2000a). The aspiratory mechanics of sauropods are not well understood, although it has been inferred (because of the presence of postcranial pneumatism) that sauropods had an avian-style flow-through respiratory system (e.g. Sander *et al*., 2011). Dorsal vertebrae have conventional synovial articulations for their ribs, suggesting that costal aspiration was possible.

<Figure 27 near here> repr theropod skeletons.

3. Theropoda. Triassic and Early Jurassic theropods are generally small to medium-sized (2-5 metres long) bipeds with large muscular tails; they are considered (by all) to be carnivores and had, as a correlate, much smaller guts than typical herbivores of equivalent size (Fig. 27A). The pelvis is propubic but the gut would have been positioned anterior to the centre of balance and was comparatively small so was unlikely to impair balance or mobility: the tail was an effective cantilever. The thoracic rib articulations are mobile and the abdomen was floored by gastralia; this implies that early theropods/theropod-like dinosauromorphs were capable of using both costal and cuirassal forms of aspiration. From the mid-Jurassic onward, the size-range and variety of theropods increased substantially.

The larger tetanuran theropods (e.g. *Allosaurus* – Fig. 27B) retained the classical body proportions and carnivorous adaptations (large skull, sharp recurved teeth, raptorial forelimbs) of basal dinosaurs, and also retained a well-developed set of gastralia. Other sub-clades (see below) diversified their body forms:

The generally lightly-built ornithomimosaurs (Fig. 27C) evolved small heads and toothless beaks/bills and resemble living omnivore-carnivore derivatives (ratites). In the case of the structurally similar and closely related alvarezsaurs, their jaws are lined by very small teeth instead of a beak/bill and some authors have speculatively linked their dental features to those in animals with a myrmecophagous (ant-based) diet (Longrich & Currie*,* 2009). Both of these groups were scored as herbivores by Macaluso & Tschopp (2018), yet both groups have lightly-built cursorially adapted skeletons, have long arms and grasping hands, are propubic and have long cantilever-like tails. This body configuration is more readily explained if they were comparatively small-gutted, pursuit adapted, carnivore/omnivores. Both groups retain a well-developed set of gastralia.

Therizinosaurs (see Fig. 27D) also exhibit comparatively small skulls with jaws lined by small leaf-shaped teeth; however, their body proportions include a capacious abdominal cavity, broadly flared iliac blades, an opisthopubic pelvis and a much-reduced tail (Zanno *et al.,* 2009). Their body form bears a passing resemblance to that seen in herbivorous xenarthrans (ground sloths). Therizinosaurs were scored, entirely appropriately, given their overall cranial and body form, as herbivores by Macaluso & Tschopp (2018). Gastralia have been reported in therizinosaurs.

Oviraptorosaurs (Fig. 27E) have medium-sized heads equipped with short, powerful toothless beaks. The pelvis is mesopubic, so the gut was positioned anterior to their centre of balance; they also have comparatively short tails and the femur lacks a prominent 4th trochanter. These two latter features are strong indicators of a bird-like alteration to their limb mechanics to compensate for the reduced cantilever effect of the tail. Furthermore, the length and raptorial structure of the forelimbs of oviraptorosaurs (Norell *et al.,* 2018) represent clear adaptations associated with prey capture (and hence carnivory). Oviraptorosaurs have short powerful jaws (indicating a strong bite – which could be interpreted either way in relation to diet), and there is a report of gastroliths (in *Caudipteryx*); these animals were scored as herbivores by Macaluso & Tschopp (2018).

The discovery of lizard remains in the body cavity of an *Oviraptor,* as well as those of juvenile troodontid skulls in association with a nest of *Citipati,* are both arguably suggestive of carnivory in these animals (Bever & Norell, 2009). Equally, crocodiles also have gizzards with gastroliths and can hardly be argued to be herbivores and, in the absence of teeth, gastroliths may have been important bone fragment processors in the gut of carnivorous oviraptorosaurs. As a general observation, the presence of a gastrolith-laden gizzard associated with an expansive and heavy gut (necessary, if these animals were indeed herbivores) that would have been positioned anterior to the centre of balance is incompatible with the build, mechanics of balance and indications of locomotor style seen elsewhere in their bodies. Common sense suggests that oviraptorosaurs were carnivores. Oviraptorosaurs also possess well-developed gastralia.

Finally, among the paravian-avialian (stem-lineage birds), of which *Deinonychus* (Fig. 27F) is a well-known example, the predatory adaptations seen in the skull as well as those of the fore- and hindlimbs are self-evident (Ostrom, 1969). The tail is long, but is thin and light, the femur lacks a 4th trochanter and the pubis is fully retroverted. The balance and pose of this animal would have been bird-like and necessitated a 'neoacetabular' knee joint; an adequate locomotor stride would have been achieved by lengthening the tibia-fibula and metatarsus. The posture depicted in Figure 27F (a common style of reconstruction of this animal) is not accurate to these principles because it indicates that the femur swung through a pendulum-like arc, which it could not have done because it was 'suspensory'. Gastralia are well developed in dromaeosaurs. This general paravian body pose would have been reproduced in *Archaeopteryx* (the so-called 'first bird' – which also exhibits gastralia, even though these bones are lost in true, flight-capable [ornithothoracine] birds).

A broader consideration of the morphofunctional organisation and fossil evidence that can be applied to a diversity of theropods suggests that the dietary assignments that have been proposed in the recent past are, in many instances, open to doubt. Furthermore, in each of these theropod taxa gastralia are known to be present, indicating that these animals had the potential to use cuirassal aspiration as a component of their respiratory repertoire. It is only among the more derived avialians that a large thoracic keel evolves, gastralia are lost, the ventral pelvic bones separate along the midline and the tail becomes so abbreviated that it forms a pygostyle – a suite of structural modifications that allow true birds to retain a bipedal pose and locomotor capacity in the complete absence of a cantilever tail.

[C] Conclusions

The range of anatomical configurations exhibited by the entire dinosaurian clade includes obligate bipedality, facultative bipedality and quadrupedality, and obligate quadrupedality. These locomotor postures are co-dependent on the positioning of the gut (and its mass) as well as general pelvic construction, irrespective of the respiratory system. The structural adaptations associated with the feeding apparatus have a direct bearing on diet and gut structure in these animals, which in turn influences the balance and pose of the body. Inferences about the dietary preferences of these animals require a holistic approach that incorporates jaw morphology, tooth shape, skull size, body proportions, locomotor mechanics, limb functionality and, rarely, the fortuitous discovery of fossilized gut contents. Using this range of criteria there is justification to doubt the scoring of the diets assigned to the various theropod sub-clades considered by Macaluso & Tschopp (2018). There is also clear anatomical evidence that contradicts the assignment of respiratory mechanisms among theropod dinosaurs proposed by Macaluso & Tschopp (2018).

<Figure 28 near here> theropod phylogeny with images – website for bird silhouette: http://clipart-library.com/bird-silhouette.html

Drawing broad physiological and functional comparisons between such disparate body forms as ornithischians, sauropodomorphs and theropods risks conflations and/or misunderstandings. Even among closely related and persistently bipedal theropod dinosaurs that all possess gastralia (and by implication cuirassal aspiration), taxa are variously specialized. Some (e.g. ornithomimids) reduce their dentitions, leading to the evolution of a bird-like keratinous beak/bill; some (e.g. therizinosaurs) shorten and reduce the mass of the tail and consequently partially or completely retrovert the pubis; some (e.g. 'paravialians') modify the pose of the hindlimb through the evolution of a suspension-style femur and alter the musculature that protracts and retracts the legs. However, these configurations are not consistent across all taxa and instead indicate a suite of adaptive morphologies that require explanation in light of the total body plan and a range of additional evidence that enhances the interpretation of the putative biology of each sub-clade (Fig. 28). The evidence available cannot be used to support the notion that there is a consistent, phylogenetically mappable, pattern implying that the aspiratory mechanism was the sole "evolutionary driver" of pelvic morphology among dinosaurs, as argued by Macaluso & Tschopp (2018).

[A] *SCELIDOSAURUS*: THE LOCOMOTOR SYSTEM

The biomechanical observations of Alexander (1976) followed by the review by Walter Coombs (1978c) prompted interest in the poses and relative proportions of dinosaur limbs, their musculature, locomotor capacity and trackway evidence (e.g. Gatesy, 1990; Carrano, 1998, 2000; Hutchinson & Gatesy, 2000; Hutchinson, 2000a, b; Carrano & Hutchinson, 2002; Hutchinson & Garcia, 2002; Hutchinson, 2004; Sellers & Manning, 2007). Trackway evidence does not exist for *Scelidosaurus* but its appendicular skeleton is now known (Norman, 2020b) and provides information concerning locomotor musculature, joint anatomy, limb proportions and potential limb excursion patterns for this animal.

[B] Pectoral girdle and forelimb myology

The pectoral girdle and forelimb musculature of thyreophorans have rarely been considered. Coombs (1978b) attempted a reconstruction of the principal forelimb muscles in ankylosaurs. Norman (1986: figs 75-77) provided origin and insertion maps and a lines-of-action reconstruction for the musculature of the pectoral girdle and forelimb in the ornithischian ornithopod *Mantellisaurus*. These reconstructions were based on comparative myological information derived from extant crocodilians. Birds (although extant theropods) were considered too specialized in their pectoral anatomy and myology for meaningful comparison. Meers (2003) provided a beautifully crafted redescription of crocodilian forelimb musculature. Maidment & Barrett (2011) reviewed the identification of forelimb musculature in basal ornithischians (with occasional reference to the stem thyreophoran *Scutellosaurus*) and used the Extant Phylogenetic Bracket (EPB) protocol advocated by Witmer (1995). Using this approach, they created origin and insertion maps for some of the shoulder and forelimb muscles of these dinosaurs based on a critical evaluation of the evidence of muscle distributions in living crocodilians and birds because they phylogenetically ‘bracket’ ornithischian dinosaurs. However, the efficacy of this approach is severely compromised by the profound differences between such disparate living representatives (Romer, 1923b; Gatesy, 1990, 1995; Carrano, 2000). The EPB approach offers a logical basis for the prediction of some soft-tissue features in fossil animals, but its application in this instance requires the exercise of considerable caution. The anatomy of the pectoral girdle of *Scelidosaurus* resembles that described in other basal ornithischians (Fig. 29) and this permits some plausible mapping of the origins and insertions of the principal support and locomotor muscles.

[C] Axial muscles

These support and stabilize the pectoral girdle and were considered in dinosaurs by both Coombs (1978b) and Norman (1986) – see also Meers (2003) for crocodiles. *M. trapezius* originates from fascia along the dorsal midline extending as far forward as the skull in crocodiles. It inserts along the anterior edge of the scapular blade and is mapped in this position in *Scelidosaurus* (Fig. 29A, tra-ls). N.B: A ventral slip of this muscle sheet forms the *m. sternomastoideus* (= *m.* cucullaris – Fig. 30, cuc) that inserts on the clavicular region of the pectoral girdle and has its origin on the ventrolateral surface ('mastoid region') of the braincase at the rear of the skull (Theis, 2010). The clavicles are preserved in *Scelidosaurus* and bear surface striations that suggest muscle insertions. There is also reason to suspect that the tendinous cranial portion of *m. cucullaris* may be causally linked to the presence of the epistyloid bones that have been recorded for the first time in *Scelidosaurus* (Norman, 2020a – see also Figs 19, 20).

M. levator scapulae (Figs 29, 30, tra-ls) and the *m. serratus* group of muscles typically originate on the surfaces of the cervical and dorsal ribs and insert on the distal portion of the medial surface and posterior edge of the scapular blade in crocodiles (Meers, 2003).

There is no reliable osteological evidence for the presence of either *m. rhomboideus* (present in extant crocodilians and birds – mostly attached to the suprascapula – Meers, 2003), or *m. costocoracoideus* that inserts on the coracoid. The latter bone is not well preserved in *Scelidosaurus*. The muscle typically originates on the sternal plate, sternal bones and sternal ribs and, to date, no remains of these latter bones have been reported in *Scelidosaurus*.

<Figure 29> Mapping of muscle origins/insertions on Scap, cor and hum.

[C] Dorsal muscles of the forelimb

[D] M. latissimus dorsi and *m. teres major*. The former is a large and extensive muscle that originates across the flanks in the thoracic region and inserts via a large tendon on the posterior surface of the humerus (Meers, 2003). The teres major originates on the distal, external surface of the scapular blade and shares a common insertion on the humerus with the *m. latissimus dorsi* (Fig. 29, ld-tm; Fig. 30, tm). Both are important forelimb retractors. No origin on the scapula was mapped for *m.* teres major by Maidment & Barrett (2011: fig. 7) although an insertion was indicated for *m. latissimus dorsi* on the posterior surface of the humerus.

[D] M. subscapularis was reconstructed occupying the entire medial surface of the scapular blade by Maidment & Barrett (2011: fig. 7B, SBS) and is shown inserting on the medial edge of the proximal humerus (Fig. 29B, ssc). The scapular origin corresponds to the area occupied by this muscle in crocodilians (Meers, 2003) and contrasts with the more restricted origin suggested for *Mantellisaurus* by Norman (1986: fig. 75B).

[D] M. scapulohumeralis caudalis is uncontroversial. In crocodiles it originates on the posterior proximal edge of the scapular blade (just distal to the glenoid – Meers, 2003) and inserts on the posterior surface of the humerus (Fig. 29, sh) adjacent to the subscapularis, just distal to the articular head.

[D] M. deltoideus scapularis (complex). In crocodiles this originates as a sheet attached to the anterolateral surface of the scapular blade and inserts on the lateral shoulder (tuberosity) of the humerus (Fig. 29, ds). A subdivision of this muscle (*m. deltoideus clavicularis*) has its origin (in the absence of a clavicle) on the anterior margin of the scapula (Meers, 2003) and inserts more distally on the posterolateral surface of the deltopectoral crest. Given the presence of a clavicle in *Scelidosaurus*, and the fact that it has a striated surface (as if for muscle attachment), this muscle probably shared an origin with *m. cucullaris* on the clavicle and adjacent acromial ridge (Figs 29, 30, dc). An area is available for the insertion of this muscle immediately distal to the well-preserved ld-tm muscle scar (sc) on the well-preserved humerus of BRSMG LEGL 0005 (Norman, 2020b: fig. 63A).

[D] M. triceps. In crocodiles this muscle is subdivided into a number of slips that originate either on the scapula or the posterior surface of the humerus

(Meers, 2003). In the absence of an equal number of comparable muscle slips in birds the triceps complex was reduced to origins for the 'brevis' on the posterior surface of the proximal humerus (Maidment & Barrett, 2011: fig. 7E, TRIB), and the 'longus' on the cuff above the glenoid on the scapula (fig. 7A, TRIL). Both of these slips insert via a common tendon on the olecranon process of the ulna. A more complex set of slips was identified in ankylosaurs by Coombs (1978b: figs 1-7). The organisation of this major limb extensor muscle is not clearly resolvable in *Scelidosaurus* so a simple scapular origin (Fig. 29A, tri - represented by a distinct pit on the lateral side of the glenoid buttress/cuff – Norman, 2020b: fig. 59A, dep) and a generalized humeral origin (Fig. 30, tri) accord with the interpretation of Maidment & Barrett (2011).

<Figure 30 near here> lines of actions of principal shoulder muscles.

[C] Ventral muscles of the forelimb

[D] M. pectoralis can be reconstructed originating on the ventral midline of the chest (in accordance with all sauropsid muscle maps), and inserting on the muscle-scarred distal portion of the deltopectoral crest on the humerus of *Scelidosaurus* (Figs 29C,D, p; 30, p).

[D] M. supracoracoideus has a radically different structure and function in birds and cannot be used for comparison. In crocodiles, this muscle originates along the scapulocoracoid suture and a slip also wraps around the anterior edge of the coracoid to insert on its medial surface (Meers, 2003). Its insertion is on the apex of the deltopectoral crest. Maidment & Barrett (2011) mapped the origin of this muscle solely on the tip of the acromial ridge, with an insertion adjacent to that for the pectoralis muscle on the deltopectoral crest. Both Coombs (1978b) and Norman (1986) indicated more extensive areas of origin that encompassed scapula and coracoid and suggested an insertion that spread proximally along the deltopectoral crest. The shallowly bowl-shaped external surface of the scapula adjacent to the coracoid, and the coracoid itself in *Scelidosaurus* offer a large area for the insertion of the *m. supracoracoideus* (Fig. 29A, sc). There is no evidence to determine whether this muscle wrapped around the anteromedial edge of the coracoid; in view of the attachments

suggested for the *m. cucullaris* and *m. deltoideus clavicularis* as well as the undoubted articular contact between the coracoid and sternal cartilages ventromedially, this seems less probable.

[D] M. subcoracoideus is absent in crocodiles (Meers, 2003) but present in lizards (Romer, 1944) and birds (Sullivan, 1962). Its absence in crocodilians could be interpreted as an autapomorphy. In lizards the origin of this muscle is broadly across the medial surface of the coracoid and it inserts on the medial corner of the proximal humerus. The origin of this muscle is mapped ("equivocally") on the coracoid of *Stormbergia* (Maidment & Barrett, 2011: fig. 7B, SBC). The coracoid is not sufficiently well preserved in *Scelidosaurus* to show muscle scars; however, the proximomedial surface of the scapula of the lectotype (NHMUK R1111 – Fig. 29B, scc) shows a large curved depressed area bordered by an irregular rugose ridge (Norman, 2020b: figs 54B, m.ri; 59B, med.r). This feature could be interpreted the margin of the attachment area for a large subcoracoideus muscle.

[D] M. coracobrachialis is consistently seen as a muscle group having a substantial area of origin on the posteroexternal surface of the coracoid and inserting on the anterior face of the humerus just below the humeral head and along the deltopectoral crest (Meers, 2003). The origin of this muscle is not defined on the coracoid of *Scelidosaurus* as it is in *Mantellisaurus* (Norman, 1986) or ankylosaurs (Coombs, 1978b) but a common area of insertion on the humerus, conforming to that seen in crocodiles adjacent to that for *m. scapulohumeralis* (Fig. 29, sh) seems probable.

D] M. biceps brachii originates adjacent to the supracoracoideus in crocodiles. The muscle is strap-like and inserts on the proximal end of the radius in a common tendon shared with the brachialis muscle (Figs 29,30, bi). A restricted area of the coracoid was mapped for this muscle in basal ornithischians (Maidment & Barrett, 2011: fig. 7A, BIC).

[D] M. brachialis originates on the posterolateral surface of the humeral shaft, distal to the deltopectoral crest and inserts on the proximal end of the radius (Fig. 29, 30, br). The biceps and brachialis together act as forearm flexors and humerus extensors.

[B] Myological interpretation of forelimb functionality

Judged from the evidence of this muscle-mapping exercise, the musculature in the shoulder region of *Scelidosaurus* is in some respects similar in its disposition to that described in extant crocodiles. This accords not only with the fact that the source of information about this musculature is the crocodile, but also the close similarity in the structure of the scapula and humerus of these two taxa. The principal difference lies in the structure of the coracoid: elongate and in profile dumbbell-shaped in crocodiles, whereas it is shorter and saucer-shaped in *Scelidosaurus*. This difference influences the interpretation of the associated roles of the shoulder muscles and their influence on limb movement.

In the crocodile, the elongate portion of the coracoid offers a strip of bone for origin of the *coracobrachialis* muscle complex that inserts on the deltopectoral crest; this muscle augments the adductor function of the massive *pectoralis* muscle and may help to stabilize the shoulder joint (Meers, 2003). The *supracoracoideus* complex and *m. deltoideus clavicularis* act as the main limb protractors. The dominant forces acting around the shoulder are associated with adduction and retraction during the terrestrial 'high walk'. Retraction is achieved by a combination of the lines of action of the *m. teres major, m. latissimus dorsi,* and to a lesser extent the *m. pectoralis* and *coracobrachialis*. Repositioning of the pectoral girdle modulates stride length and is linked to motion at the sternocoracoid joint (Meers, 2003).

In *Scelidosaurus* the coracoid is short transversely, the lines of action of the associated adductor muscles are short and may have needed to be large and powerful, especially if the forelimb was used for locomotion (as suggested below). Protraction would have been achieved by the clavicular deltoid musculature that was attached to the proximal leading edge of the scapula. There is also a large area available for the attachment of the *m. supracoracoideus* in the shallow basin-like area on the proximal surface of the scapula and extending medially, across the scapulocoracoid suture. The likely insertion on the proximal half of the deltopectoral crest suggests that the latter muscle was an important protractor (and part adductor) of the forelimb. Evidence for the presence of a *pectoralis* muscle is indicated by the robust and elongate deltopectoral crest; the main role of the muscle would have been adduction of the forelimb and protraction from the fully retracted position. The proximomedial anterior surface of the humerus is likely to have served as an area for attachment of the large *subcoracoideus* muscle, which is likely to have significantly augmented protraction and adduction of the forelimb. The clavicular deltoid muscle is likely to have been involved in repositioning of the forelimb during non-support use of the forelimb. The evidence for a sternum (or sternal plates) and well-developed sternal ribs, to which *m. pectoralis* would have been anchored, is wanting in *Scelidosaurus* and this muscle may have had a much less significant role in forelimb adduction and retraction compared to that needed for the 'sprawling' or 'high-walk' stances that can be adopted by the crocodile. The powerful retractors of the locomotor forelimb would undoubtedly have been the *m*. *latissimus dorsi*, *m*. *teres major* muscle complex that were anchored to the dorsal ribcage and scapular blade; these would have been augmented by the triceps group during retraction and lower limb extension.

One unknown factor is the relationship between the scapulocoracoids and the sternal cartilage(s). The rounded and thickened medial edges of the coracoids are suggestive of an articular (?synovial) relationship with the chest cartilages, perhaps indicating the existence of a sternocoracoid hinge of some type, though whether it functioned as it does in squamates and crocodiles remains in doubt.

[B] The role of the forelimb: previous interpretations

Only two individuals referable to *Scelidosaurus* provide measurable dimensions of their limb segments: the lectotype NHMUK R1111 (hindlimb only) and the referred specimen BRSMG LEGL 0005 (fore and hindlimbs) see Table-Appendix 1. The estimated total body lengths of these two skeletons are 4.4 metres and 3.1 metres respectively.

Simple forelimb:hindlimb or individual limb segment ratios have been used in the past as a measure of forelimb-hindlimb disparity and a proxy of body posture in fossil taxa (Galton, 1970; Norman, 1986; Padian, 2008). Such measures are however of limited value because, if used alone, they do not take account of the mass distribution (Alexander, 1976, 1985), biomechanical features of the limbs (Coombs, 1978c; Galton, 1970; Norman 1986; Maidment & Barrett, 2014) or their associated soft-tissue characteristics (Maidment & Barrett, 2011). In their review of the potential osteological correlates associated with quadrupedality in ornithischians, Maidment & Barrett (2014) proposed that there are five reasonably consistent osteological correlates: (i) an anterolateral process on the ulna; (ii) hoof-shaped manus unguals; (iii) a femur longer than the tibia; (iv) a reduced 4th trochanter; and (v) a transversely broadened ilium. Only two of these features relate to the structure of the forelimb. They noted that *Scelidosaurus* could only be scored for three postcranial characters (iii)-(v) and of these the femur had a prominent and pendent 4th trochanter. They rationalized that an intermediate pose may well be expected given that its ancestry was bipedal (dinosaurs in general, *Scutellosaurus* in particular) and its descendants i.e. stegosaurs and ankylosaurs, were quadrupedal. They noted the existence of the small partial skeleton (NHMUK R6704) but excluded it from consideration because its femoral length is less than 50% of that of the lectotype (NHMUK R1111). It was claimed, incorrectly (see Fig. 32), that this small specimen has a straight femur (another one of their suspected correlates of quadrupedality) and a low iliac width ratio.

Given what is now known of *Scelidosaurus*, (i) it has a modest lateral shelf on the ulna (whether this could be scored as a ‘process’ is dubious); (ii) does not have hoof-shaped manus unguals; (iii) its femur is longer than the tibia; (iv) it has a pendent 4th trochanter; and (v) there is a modest lateral expansion of the iliac blade. This unusual mix of character states (2 ‘quadrupedal’, 2 ‘bipedal’, one of uncertain value) confirms the ‘intermediate’ postural-locomotor status of *Scelidosaurus* that was suspected: *Scelidosaurus* was, plausibly, a facultative quadruped.

[B] Forelimb structure and potential functionality

The dominant pectoral girdle bones are the scapula and coracoid, which resemble in shape and proportions those seen in other basal ornithischians (e.g. Maidment & Barrett, 2011). No trace of a sternal plate or pair of sternal bones has been recovered to date, Owen’s comments (1863: 13) notwithstanding. The identification of small fusiform bony elements attached to the proximal leading edge of the scapula (Norman, 2020b: fig. 60) in *Scelidosaurus* is of interest. These bones occupy a position that is anatomically homologous with that of clavicles in other archosaur taxa. However, Vickaryous & Hall (2010) proposed that the furcula of birds is a homologue of the interclavicle of archosaurs and that the clavicles are therefore lost in birds (*contra* Yates & Vasconcelos, 2005; Nesbitt *et al.,* 2009 and many others). This new hypothesis has been argued to be more phylogenetically parsimonious than the longer established clavicles=furcula homology and has been applied to the dinosaurian outgroups of birds (Maidment & Barrett, 2011: fig. 5). The argument is critically dependent upon the preservation (presence or absence) and identification of bony elements that are small, fragile and may be unossified in ontogenetically immature individuals. As a consequence they may be unpreserved, potentially lost during fossilization or missed during field collection and preparation. The presence of what appear to be a pair of discrete articulated clavicles in this basal ornithischian casts doubt on the interclavicle=furcula hypothesis with respect to ornithischians, and it undermines the general phylogenetic parsimony argument that has been used to support this novel proposal.

Within the forelimb, the humerus is more robust than those described in basal ornithischians such as *Lesothosaurus* (Thulborn, 1972), *Scutellosaurus* (Maidment & Barrett, 2011) and *Heterodontosaurus* (Santa Luca, 1980). The deltopectoral crest is both broader and longer, and some muscle scars are clearly visible (even in juvenile individuals – Norman, 2020b: fig. 63) so it can be inferred that the humerus was mechanically loaded in life; this accords with a facultatively quadrupedal pose and locomotor style. The radius and ulna are shorter than the humerus, and more robust. The absence of an olecranon on the ulna (*m. triceps* insertion site) is unexpected because quadrupeds are generally characterized by the presence of a prominent olecranon process that increases the leverage of the limb extensor muscle (*m. triceps*). However, the only well-preserved ulna belongs to a juvenile individual (BRSMG LEGL 0005 – Norman, 2020b: fig. 64) and it is possible that tendon-induced metaplastic overgrowth of the ulna during ontogeny builds a more prominent olecranon in fully adult individuals. Equally, the absence of a well-developed olecranon may reflect the recency (in evolutionary terms) of the adoption of a quadrupedal pose.

The manus forms a compact, spreading structure capable of weight support and locomotion, but the three medial digits terminate in asymmetric, narrow, short, pointed unguals (Norman, 2020b: fig. 67) reminiscent of the pattern seen in Hettangian bipedal ornithischians (Thulborn, 1972; Norman *et al.,* 2004); but they cannot be described as 'raptorial' as appears to be the case in the manus of *Heterodontosaurus* – Santa Luca, 1980). The overall manus morphology suggests that it was 'unspecialised' or 'utilitarian' – capable of weight support, digging and grasping, as necessary. The structure and proportions of the manus of *Scelidosaurus* resemble those of the kangaroo (Shoaib, 2009). The latter is known from life observation to use its manus for transient weight support while feeding and during slow locomotion, as well as for scratching, digging and grasping. A similar set of capabilities is envisaged for the manus of *Scelidosaurus*.

There is now no unequivocal evidence of Late Triassic ornithischians so the earliest known ornithischian taxa are regarded as Hettangian (see Baron *et al*., 2017c) and all so far known examples have the characteristically short forelimbs and long, distally extended hindlimbs associated with cursorial bipeds (Coombs, 1978c; Carrano, 1999). *Scelidosaurus* is Sinemurian in age and therefore the first and earliest known armoured, facultatively quadrupedal ornithischian.

[C] The locomotor mode of Scelidosaurus *using fore- and hindlimb dimensions*

The relative proportions of the forelimb segments (Humerus [H]:Radius [R] and Radius:Metacarpal 3 [Mc3]) are known in few individual skeletal examples of *Scelidosaurus* (Table-Appendix 1). A calculation of the ratios of these dimensions allows them to be compared directly with the graphical summations of these values for a range of dinosaurs presented by Coombs (1978c: figs 8,9). Forelimb ratios of the limb segments R/H plotted against Mc3/R indicate that these values fall on the borderline between the morphospace polygons that encompass values of known *subcursorial* and *mediportal* quadrupedal mammals.

Equivalent hindlimb ratios of the Femur [F], Tibia [T] and Metatarsal 3 [Mt3]: (T/F vs Mt3/T) are also available (Table-Appendix 1) and when plotted on a graph of these values for dinosaurs, with a similar overlay of morphospace polygons for mammal values, *Scelidosaurus* was again placed on the boundary between the polygons for 'subcursorial' and 'mediportal' forms. Walter Coombs adopted the generalized distinctions between locomotor categories between mammals that had been suggested by William King Gregory (1912). The categories 'mediportal' and 'subcursorial' were described narratively:

"*Mediportal*. A mediportal animal is one with limbs primarily designed to meet the problems of bearing weight but with some elements of cursorial design, *commonly retained from a more cursorial ancestor* [my italics]. Cursorial features commonly retained included digitigrade stance, loss of lateral digits a single epipodium, interlocked or fused metapodials, and loss of ventral pectoral elements.

"*Subcursorial*. A subcursorial animal has moderate development of most cursorial adaptations and little or no limb modification for bearing weight. Some subcursorial animals are excellent runners, at least for short distances.

Coombs also offered what turned out to be an extremely apposite comment with respect to the observed limb-proportion ratios of *Scelidosaurus*:

"A runner of 'average' ability, if such exists, would be on the borderline between mediportal and subcursorial." (Coombs, 1978c: 394-395). This is precisely the position occupied by *Scelidosaurus* judged by the simple arithmetical and graphical analysis.

This essentially systematic approach to the categorization and partitioning of locomotor styles in vertebrates was reviewed by Carrano (1999), with particular respect to the interpretation of dinosaurian styles of locomotion. Using a bivariate and multivariate statistical approach applied to the limb bone dimensions in a large number of dinosaur taxa, and a greater range of anatomical variables measured on the hindlimb alone, Carrano was able to demonstrate that the notion of discrete boundaries separating locomotor categories was artificial – as Gregory (1912) clearly understood. Carrano argued that it was more appropriate to consider locomotor styles in individual taxa along a continuum between the end-points of 'graviportal' and 'cursorial'. Dinosaur taxa were simply distributed along a line between these extremes and any further subdivision of locomotor mode was arbitrary. When the limb dimensions of *Scelidosaurus* were analysed they produced a result 'intermediate' – precisely midway – between the locomotor end-points (Carrano, 1999: fig. 6), a result that is indistinguishable from the estimation derived using the Gregory-Coombs approach.

Scelidosaurus had an 'intermediate' (average) locomotor mode – it was neither cursorial nor graviportal and, as will be seen later (Phylogenetics Section) there is evidence that strongly supports the view that *Scelidosaurus* had evolved in a geological sense 'recently' from bipedal, cursorial ancestors.

[B] Pelvic girdle and hindlimb myology

The pelvic-hindlimb musculature of ornithischians has been more intensively studied than that of the pectoral-forelimb region. The most influential analysis was undertaken by Romer (1927a) in an attempt to reconstruct the pelvic and hindlimb musculature of *Thescelosaurus*. This was a synthesis derived from earlier work on the crocodile (Romer, 1923a), saurischian dinosaurs (Romer, 1923b) and the thigh musculature of the bird (Romer, 1927b). Galton (1969) applied Romer's analysis to newly prepared material of an ornithischian dinosaur *Hypsilophodon* that is anatomically similar to *Thescelosaurus* and mapped muscle origins and insertions as well as providing a line-of-action reconstruction. In similar fashion Norman (1986) applied this approach to *Mantellisaurus*.

These earlier myological reconstructions were reviewed by Maidment & Barrett (2011) using the EPB methodology (Witmer, 1995), but the same caveat applies: birds and crocodiles may be phylogenetically related, but are separated by >230Ma of evolutionary history and differ profoundly anatomically, biomechanically and biologically. The ground-breaking work by Hutchinson (2000a,b) incorporated phylogenetic analyses of shape change in the pelves and femora of theropods and birds; these, in combination with the origins and insertions of the principal hindlimb muscles were combined in order to better understand the locomotor consequences of anatomical changes along the theropod-bird phylogenetic tree. Unfortunately, the absence of unambiguous living descendants of ornithischians makes this type of coherent approach impossible, so the reconstructions that are attempted in the following section are dependent upon comparative modelling and a measure of applied plausibility.

<Figure 31 near here> pelves of thyreophorans compared

Coombs (1979) used the accounts of Romer and Galton to help model the principal pelvic muscles of ankylosaurs. Unfortunately, the anatomy of ankylosaur pelves and limbs differs strikingly from those of the ornithopods such as *Thescelosaurus, Hypsilophodon* and *Mantellisaurus* that had been used as the templates for earlier interpretations. To complicate matters a little more, pelvic muscle scars in ankylosaurs proved to be poorly defined (Coombs, 1979: 667). The anatomical conservatism shown in the pelvis of *Scelidosaurus*, when compared to those of typical stegosaurs and ankylosaurs (Fig. 31B,C), means that any attempt to model the musculature of the pelvic region of *Scelidosaurus* is largely dependent on the previously published accounts of non-thyreophorans.

[C] Limb extensors

[D] M. iliotibialis (it). This muscle group is present in both birds and crocodiles and originates along the dorsal margin of the ilium as three separate slips that insert via a common tendon on the cnemial crest of the tibia. In *Scelidosaurus* the dorsolateral edge of the main body of the ilium (supra- and postacetabular portion) bears a clear longitudinal rugosity that extends anteriorly to the proximal portion of the preacetabular process. There is no surface indication of subdivisions within this muscle scar for individual muscle slips (Figs 32, 33, it).

[D] M. iliofemoralis (if). In crocodiles this muscle originates from the lateral surface of the ilium dorsal to the acetabulum and inserts on the anterolateral surface of the femoral shaft. The homology with avian muscles in this area is confusing and it has been argued that a subdivision of this muscle may have inserted (bird-like) on the anterior trochanter of the femur (Hutchinson,

2000b). In the absence of clear osteological correlates in basal ornithischians Maidment & Barrett (2011) opted for a single origin on the lateral wall of the ilium and an insertion on the anterior trochanter only. In *Scelidosaurus*, the lateral surface of the iliac blade shows no evidence of muscular subdivisions. However if (as seen in birds) the equivalent *m. iliotrochantericus* had an origin on the preacetabular process then this may also have been the case in *Scelidosaurus*; the preacetabular process is long, laterally and ventrally deflected and would have provided a mechanically effective line of action if this portion of the muscle group inserted on the greater trochanter (Fig. 33, itr = the trochanteric crest in birds – Romer, 1927b; Hutchinson, 2000b). An anterodorsally positioned position of *m. iliofemoralis* on the deep part of the iliac blade probably inserted on the anterior trochanter (acting as a protractor when the femur is fully retracted). Another slip of this muscle group may also have inserted on the adjacent lateral surface of the greater trochanter (Fig. 32, if? – this latter slip serving to stabilise the femoral head by holding it against the acetabulum). The remaining bulk of this muscle is likely to have inserted on the proximal half of the anterolateral surface of the femoral shaft, lateral to the oblique ridge that extends distally from the base of the anterior trochanter (Figs 32, 33, if).

[D] M. flexor tibialis externus (fte). In crocodiles this muscle originates from the posterior edge of the postacetabular ilium and inserts on the posteromedial edge of the head of the tibia along with *m. flexor tibialis internus* (Romer, 1923a). The origin of this muscle can be localised on the ilium of *Scelidosaurus*, but its insertion is not defined on the tibia (Fig. 32, fte).

<Figure 32 near here> femora (both – for shape change) with muscle scars

[D] M. puboischiofemoralis internus (pifi). In crocodiles there are two parts to this muscle. The first originates on the medial surface of the ilium and first sacral rib, whereas the second originates as a fan of muscles attached to the posterior dorsal vertebrae. These muscles insert on the anterior and medial surfaces of the proximal end of the femur and a large tendon derived from these muscles also inserts on the femoral shaft dorsomedial to the 4th trochanter (Romer, 1923a). As observed by Maidment & Barrett (2011) the

preacetabular process of ornithischians is marked by a horizontal medial ridge and the area lateral to this ridge defines an area that could be most parsimoniously interpreted as the origin this muscle (or a part thereof). A medial ridge on the preacetabular process is present on *Scelidosaurus* ilia, but no other clear muscle scars can be identified on the dorsal vertebrae or the adjacent sacral rib. Additional components of this muscle group cannot be confirmed and it is always possible that the anterior extension and lateral expansion of the preacetabular process provided the necessary area for attachment of this group; if correctly surmised, this would give these muscle groups a more clear-cut femoral protractor and axial rotator function. The 4th trochanter is enlarged and bears muscle scarring on its medial surface as well as on the adjacent medial surface of the femoral shaft. This region may indicate a major insertion site for at least part of this muscle group (Figs 32, 33, pifi).

[D] M. puboischiofemoralis externus (pife). There has been much discussion concerning the homologies of this group of muscles (see Maidment & Barrett 2011). Their insertion site is, unequivocally, the greater trochanter in dinosaurs (Hutchinson, 2000b – see Fig. 32, pife?). However, the origin is varied across living taxa and therefore much more equivocal in the absence of obvious osteological correlates. Galton (1969), Coombs (1979) and Norman (1986) suggested that a slip of this muscle had its origin on the ischial shaft. The phylogenetic inference model used by Maidment & Barrett (2011) noted that the portion of this muscle group that is attached to the ischium is present in extant crocodiles (which have a radically different limb architecture to that seen in dinosaurs), but absent in extant birds (which adopt a parasagittal gait, as seen in dinosaurs, but deploy a ‘suspensory’ rather than ‘pendulum’ femur). On the basis of this inferential form of logic the identification of its area of origin on the ornithischian pelvis is not assured.

[D] M. ischiotrochantericus (ist). In crocodiles this muscle arises from the posteromedial surface of the ischium and inserts on the proximolateral surface of the femur. In birds the equivalent muscle originates on the lateral surface of the ischium and the sheet of tissue that spans the gap between the ischium and postacetabular ilium, but inserts on the trochanteric crest (roughly equivalent to the area of insertion in the crocodile). In *Scelidosaurus* its area

of origin is not clearly defined on the ischium, but the greater trochanter is robust and thickened posteriorly and, as argued by Maidment & Barrett (2011), this may indicate an insertion site for this muscle (Fig. 32, ist).

[D] M. ambiens (amb). This muscle originates on the proximal lateral and medial surfaces of the pubis in crocodiles, and has a generally similar origin on the stubby preacetabular portion of the pubis in birds; it inserts on the cnemial crest. A similar position was suggested in *Thescelosaurus* by Romer and an illustration of the prepubic blade of *Iguanodon* was interpreted as showing the muscle scar for this muscle (Romer, 1927a: fig. 9). Norman (1986: fig. 80) followed the reconstruction suggested by Romer. Maidment & Barrett (2011) also concurred and mapped an origin on the lateral surface of the prepubic blade in basal ornithischians. The reduction of the pubis to a small nubbin that is fused to the ilium in ankylosaurs left Coombs (1979: 672) equivocal about the presence of this muscle. There is a substantial area available on the lateral face of the prepubic blade in *Scelidosaurus* and an origin in this area can reasonably be inferred (Fig. 33, amb).

<Figure 33 near here> hindlimb muscles and lines of action

[C] Limb flexors

[D] M. iliofibularis (ifib). This muscle originates on the lateral surface of the postacetabular iliac blade, deep to *m. iliotibialis*. There is no clear osteological correlate for this muscle in *Scelidosaurus*, but it has been restored (Fig. 33, ifib)

[D] M. caudifemoralis brevis (cfb). As described in crocodilians by Romer (1923a) this muscle originates from the ventral portion of the postacetabular iliac blade and inserts lateral to the 4th trochanter of the femur. In *Scelidosaurus,* a modest brevis shelf is present and is considered to be the osteological correlate of the origin of this muscle (Fig. 33, cfb). The lateral surface of the 4th trochanter is bevelled and marked by a long muscle scar that is regarded as its insertion (Fig. 32D, cfb).

[D] M. caudifemoralis longus (cfl). In crocodiles this is a long cylindrical muscle of the tail that originates on the sides of the caudal vertebrae and the edges of the caudal ribs; it inserts on the blunt projection that forms the 4th

trochanter of the crocodile femur. Much reduced slip-like remnants of this muscle originate on the pygostyle in birds (George & Berger, 1966). In *Scelidosaurus* a similar origin of this muscle cannot be doubted (Fig. 33, cfl) and its insertion site would be on the medial surface of the 4th trochanter (Fig. 32B, cfl). As in other basal ornithischians the 4th trochanter of *Scelidosaurus* is pendent and its distal end probably marked the point of attachment of a gastrocnemial ligament (Sutton's tendon – Dollo, 1888; Norman, 1986). A femur of sub-adult size (NHMUK OR41322 – Fig. 34) retains a nearly complete fourth trochanter (not preserved in the lectotype) that is large and pendent as seen in the juvenile individual (Fig. 32A).

<Figure 34 near here> crushed femur with 4th trochanter

[D] M. adductor femoralis (add). In crocodiles the adductor complex arises on the ischium and inserts on the posterolateral distal half of the femoral shaft (Romer, 1923b). In birds this musculature has a generally similar pattern of origin (but extends on to the pubis) and insertion. In ornithischians it has been argued that the adductor complex (at least one part) originated on the lateral surface of the shaft of the ischium and inserted on the posterior face of the femur distal to the 4th trochanter (Coombs, 1979; Galton, 1969; Norman, 1986; Maidment & Barrett, 2011). The ischia of *Scelidosaurus* do not show clear evidence of muscle scars that accord with this general pattern, but there is a scarred area on the posterolateral surface of the femoral shaft (Figs 32B, 33, add).

[D] M. flexor tibialis internus. This muscle complex is present in squamates and crocodiles and is regarded as being represented, in part, by *m. ischioflexorius* of birds (George & Berger, 1966). The muscle was restored in ankylosaurs (Coombs, 1979) but Norman (1986) failed to recognize correlates in *Mantellisaurus*. Maidment & Barrett (2011) restored an origin near the proximal end of the lateral surface of the ischium; it would have inserted on the head of the tibia. No attempt has been made to reconstruct this muscle.

[D] M. femorotibialis group (ft)*.* This muscle group may have two (crocodilians) or three (birds) slips that originated on the shaft of the femur. Maidment & Barrett (2011: fig. 9C-F) were able to identify at least two areas

of origin for this muscle group on the femoral shaft. They are separated by a low ridge that arises at the base of the anterior trochanter and follows a curved course distomedially. In *Scelidosaurus* a similar femoral ridge is visible and may indicate the presence of at least two muscle slips (Fig. 32C,D, ft), although several other muscles claim areas of insertion in this region of the femoral shaft.

[B] Functional aspects of the pelvic muscle reconstruction

The primary limb retractor muscles are, as in all non-paravian sauropsids, the *caudifemoralis* group, which have a posteromedial line of action (Fig. 35A,B); these muscle groups are supplemented in their action by the crural (shin) flexors (e.g. *m. iliotibialis*), which also serve to fold and therefore raise the limb clear of the ground during the suspension phase of the locomotor cycle. The protractor muscles, principally the *m. iliofemoralis group*, *m. ambiens* and *m. puboischiofemoralis group*, attach to the anterodorsal ilium (and the prepubic blade) and draw the femur forward during the suspension phase (Fig. 35A); their action is supplemented later in the swing by the lower limb extensors (*m. iliotibialis* and *m. femorotibialis*). Various of the shorter muscles (e.g. *m. ischiotrochantericus* and slips of *m. iliofemoralis*) helped to stabilise the femoral head in the acetabulum. Muscles involved in facilitating outward long-axis rotation of the limb during protraction and extension, prior to foot placement on the substrate, include the *m. ischiotrochantericus* (ist) and the portion of the *m. puboischiofemoralis internus* that inserts adjacent to the 4th trochanter – Fig. 35C, pifi).

[C] Note on possibly co-opted aspiratory pelvic musculature?

Carrier & Farmer (2000a) suggested that the prepubic blades of some ornithischians might have acted as mobile ‘paddles’ that were capable of alternately compressing and decompressing the posterior abdomen to facilitate aspiration. This novel suggestion requires the presence of adductor and abductor (“iliopubic”) muscles that ran between the ilium/posterior dorsal vertebral area and inserted on the medial and lateral surfaces of the prepubic blade. The principle of pubic kinesis linked to aspiration is well established and understood in crocodilians (Gans, 1970; Carrier & Farmer, 2000b), but the musculature involved is associated with the ventral pelvis and gastral basket. The dorsal location of the prepubic blades in ornithischians renders the use of ventral musculature to move the pubis, such as that seen in crocodilians, extremely unlikely.

No living sauropsid taxa that have "iliopubic" muscles (Carrier & Farmer, 2000a) that originate on the ilium and insert on a kinetic pubis, so the application of a phylogenetic inference approach implies that an interpretation of this type is "extrapolatory" (*sensu* Bryant & Russell, 1992) or perhaps a "Class III" inference of Witmer (1995). Such interpretations may only be supportable in fossils when functional and biomechanical evidence is compelling, in preference to conservative phylogenetic inferences. It is conceivable that slips of muscle derived from the *m. puboischiofemoralis* muscle complex, which wrap around the pubis and proximate portions of the ilium, as well as sacral and posterior dorsal vertebrae, could have been 'co-opted' for the purpose of abducting-adducting the prepubic blades. Carrier & Farmer (2000a) noted from the biology and physiology of living sauropsids that costal aspiration is invariably supplemented by additional aspiratory systems (e.g. gular pumping and cuirassal aspiration). In extant archosaurs similar supplementation is observed (e.g. cuirassal aspiration, diaphragmatic aspiration and pelvic aspiration). Extinct ornithischians lack the osteological correlates associated with extra-costal respiration seen in theropods and sauropodomorphs (i.e. gastral baskets and pneumatic skeletal bones) and are inferred (not unreasonably, given the presence, in some, of indicators of high aerobic exercise capability – Carrano, 1999) to have required some unknown aspiratory mechanism to supplement costal respiration – particularly so when costal movements appear to have been limited or compromised by rib fusion (Gilmore, 1930; Coombs, 1971) or the presence of uncinate plates (Butler & Galton, 2008; Norman, 2020b). In the absence of any other alternative aspiratory mechanism pubic kinesis may stand for the time being as an improbable, yet plausible, hypothesis.

<Figure 35 near here> functionality of the hindlimb in cartoons

[C] Hindlimb excursions during the step-cycle

The structure and functionality of the archosaur-dinosaur pelvis-hindlimb have been a matter of considerable debate (e.g. Charig, 1972; Parrish, 1986; Padian, 1986; Padian & Olsen, 1989; Gatesy, 1990, 1995; Carrano, 2000). Gatesy (1995) listed the principal types of information that might be obtained to build an accurate picture of the locomotor capabilities of any organism: skeletal anatomy, limb posture, limb segment orientation, limb kinematics, muscular anatomy and neuromuscular control. In fossil organisms most of this information is missing and the remainder (skeletal and muscular anatomy) is rendered conjectural to varying degrees by the quality of preservation of the material in question. In addition, at a more philosophical level, such structure-function interpretations need to be correlated with the overall complexity of the organism's total biology and rationalized by reference to its phylogenetic context (Lauder, 1991). These considerations present the palaeontologist with a challenging set of problems.

Carrano (2000) adopted a structural-interpretative-phylogenetic approach to this topic and drew particular attention to a number of anatomical features and soft tissue interpretations in the pelves and hindlimbs of dinosauromorphs and dinosaurs, and mapped these on to a putative phylogenetic framework:

1. Acetabular structure and femoral head orientation. In dinosauromorphs and basal dinosaurs the acetabulum forms a deep, ventrally facing cupola that is walled medially and, laterally, produces a supra-acetabular crest whose lateral rim is downturned (e.g. Padian, 1986: fig. 5.2). The femoral head in these taxa is inturned relative to the femoral shaft, but also oriented anteromedially, whereas the proximal surface of the greater trochanter appears to have articulated with the downturned (pendent) rim of the supra-acetabular crest. It was suggested that the supra-acetabular crest may have formed a mechanical 'stop' that restricted femoral abduction as well as acting as a 'guide' that restricted femoral long-axis rotation. A correspondence in the shape of the femora and acetabula of various taxa (including the basal ornithischians *Lesothosaurus* and *Heterodontosaurus*) was used to support these inferences.

More derived dinosaurs (except stegosaurs and ankylosaurs) have an acetabulum that does not have a downturned lateral rim to the supra-acetabular crest, the femoral head is entirely medially directed, and the greater lateral width of the proximal surface of the femur butted up against the supra-acetabular crest and prevented undue femoral abduction (similar anatomical features have been noted convergently in pseudosuchian archosaurs with an erect stance).

2. Muscle re-orientation. Consequent upon the re-orientation of the femoral head and parasagittal pose of the limbs it was hypothesized that the *puboischiofemoralis* and *iliofemoralis* muscles would become femoral protractors (rather than abductor-rotators) and the bulk and power of the *iliofemoralis* in the line of action would be enhanced by expansion of the preacetabular process.

3. Anteroposterior expansion of the iliac blade. The dinosauromorph ilium is generally as long as it is deep, with a short triangular preacetabular process and a deeper, rounded postacetabular process. The acetabulum forms a laterally shrouded cupola as described above. *Scutellosaurus* and *Scelidosaurus* appear to be included (incorrectly) in this description of iliac morphology even though the acetabulum is open laterally, there is no downturned rim to the supracetabular crest, and the postacetabular blade is sub-rectangular and deep. Carrano (2000) correctly indicated that both have an “expanded anterior iliac blade”. An anterior extension of the preacetabular and postacetabular processes of ilium is the condition in derived dinosaurs (ornithischians, neotheropods and sauropods).

4. Muscle functionality linked to iliac blade expansion. The preacetabular process expansion is considered to be a way of augmenting the area of origin and leverage of the principal femoral protractors (and knee extensors): *mm. iliofemoralis, iliotibialis* and *puboischiofemoralis*. Equally, the postacetabular process expansion increases the area for origin of the femoral and knee flexors: *mm. iliofibularis, flexor tibialis* and *caudifemoralis brevis*, as well as increasing their leverage on the limb during retraction. Basal ornithischians are claimed (incorrectly) not to benefit from these structural changes to the limb retractors.

5. Morphology of the anterior trochanter. This structure is positioned distal (15-20% of femoral length) to the greater trochanter in dinosauromorphs. As the possible site of insertion of the *iliofemoralis* muscle, this position is interpreted as one in which the muscle acted as an abductor of the femur. Reorientation of the femoral head and the proximal migration of the anterior trochanter and expansion of the preacetabular blade in dinosaurs increased the potential of this muscle to act as a protractor of the femur.

Put into a phylogenetic context, the evolution of a dinosaur style of locomotion involved a distal-to-proximal suite of changes: ankle and knee joints that constrained limb motion to the parasagittal plane (and precluded significant abduction-adduction – Novas, 1996), was followed phylogenetically and temporally by the evolution of the femoral anterior trochanter and anteroposterior expansion of the iliac blade for the attachment of protractor and retractor musculature. Distal-to-proximal stabilization of the limb segments track in sequence from basal to higher nested nodes. This accords with the view that distal limb joints have little stabilizing musculature, so they require osteological modification of joint architecture that can be tracked in fossil taxa more readily than putative soft-tissue changes associated with the hip.

[C] Scelidosaurus *hindlimb structure and pose*

The pelvis and hindlimb of *Scelidosaurus* are better understood (Norman, 2020b) and can be more readily subjected to Carrano’s approach to limb structure and functionality. The ilium has a long, laterally-deflected preacetabular process and (contrary to previous views) a deep, rectangular postacetabular process and a brevis shelf. The acetabulum forms a partial cupola with a complete, curtain-like medial wall and a supra-acetabular crest with a horizontal rim (unlike the condition in dinosauromorphs and some basal dinosaurs).

The femur has an articular head that is medially offset from the shaft and not deflected anteromedially (as described to be the condition in dinosauromorphs and some basal dinosaurs – Carrano, 2000). The anterior trochanter is proximally placed and prominently positioned on the anterior margin of the greater trochanter. The implication from this configuration is that the femur could be swung parasagittally and was powered by musculature associated with the expanded iliac blade. The femoral shaft is slightly bowed (more so in juvenile individuals – see Fig. 32) and is notable for the presence of a prominent pendent 4th trochanter. The medium- to large-sized (~32 cms long) crushed femur of *Scelidosaurus* (NHMUK OR41322 – Fig. 34) has a prominent pendent 4th trochanter; however, on closer inspection this structure is noticeably thicker and considerably more robust than that of NHMUK R6704 (Fig. 32A). The 4th trochanter of the larger femur is thick, yet an outline of the slender 'juvenile' 4th trochanter morphology remains visible on its surface (Fig. 34, 4tr). The original structure has, in effect, been shrouded by a thickness of metaplastic bone (Fig. 34, mpb). It is probable that this secondary feature expanded and strengthened the anchoring of the caudifemoral tendons and reinforced the 4th trochanter.

A pendent 4th trochanter is consistently associated with ornithischians that, judged by their posture and limb proportions, were likely to have been cursorial (e.g. Maidment & Barrett, 2014 and references therein). The distal femoral condyles are laterally expanded, but show no clear evidence of an intercondylar extensor groove (but this is also a feature of the femur of the allegedly cursorial ornithischian *Hypsilophodon* – Galton, 1971, 1974).

Thick cartilages would have been present that capped the bones at the knee joint, and the structure of the preserved bones does not accurately reflect the extent to which this joint operated as a uni-axial hinge. The crus (shin) comprises a structurally dominant straight tibia and a shorter, but stout and bowed, fibula; this gives the impression that a limited amount of axial torsion might have been possible between the bones of the lower leg.

The tarsus is conventionally mesotarsal but the evidence, judged by what is currently known of the structure of the astragalocalcaneal roller surface, is that the ankle joint was not so strongly constrained to rotate in a transverse uni-axial plane because it does not display a deeply grooved (trochlear) joint surface. The distal tarsals, as preserved, also present an asymmetrical arrangement with the central (dT3) and lateral (dT4) tarsals forming well-ossified articular pads, whereas the medial tarsal (dT2), if present, was probably an unossified fibrocartilage pad or (less likely) entirely absent from the ankle joint (Norman, 2020b: figs 86, 87). The pattern of just two distal ankle bones (central and lateral) is found reasonably consistently among more derived ornithischians (in which this anatomy has been preserved – e.g. Norman 1980, 1986). The asymmetrical construction of this ankle joint would have left it potentially susceptible to (or able to accommodate) long-axis torsion during the limb excursion cycle.

In the context of ankle joint construction and joint mobility, it is interesting to note that the early (Hettangian) but unusually specialized ornithischian *Heterodontosaurus* has been reported as having three well-ossified distal tarsals (Santa Luca, 1980) or just two (Sereno, 2012). In either interpretation the distal tarsal structure that is preserved forms an ossified articular pad that caps all three weight-bearing metatarsals (2-4) that support functional pedal digits. In turn this tarsal structure articulated with a hinge-like and fused tibiotarsus. This ankle structure suggests that limb excursion was parasagittal and that ankle joint mobility was restricted to a single transverse plane of rotation.

The pes of *Scelidosaurus* is functionally tridactyl, being dominated by pedal digits 2-4 (Norman, 2020b: fig. 90). Metatarsals 2-4 are sutured proximally and form a splayed structure distally. Metatarsal 1 is short, but supports two phalanges, the terminal one of which forms a small pointed claw. Metatarsal 5 is represented by a splint bone. The three functional toes as preserved in the lectotype (NHMUK R1111 – the only currently known example that includes articulated feet) curve medially along their lengths, and the terminal unguals are pointed, slightly arched, but as with the phalanges are twisted medially along their lengths (Norman, 2020b: fig. 95).

[C] Scelidosaurus *pelvis and hindlimb: comparative comments*

The pelvis of *Scelidosaurus* (Fig. 31A) bears a much closer structural similarity to that of early ornithischians and euornithopods than to those of more derived stegosaurian and ankylosaurian thyreophorans (Fig. 31B,C – Carrano, 2000: figs 6, 7). The ilium has a long, arched (in mature individuals) dorsoventrally flattened preacetabular process, but it is not broadly expanded or downcurved to the extent seen in ankylosaurs and stegosaurs. The dorsal part of the iliac blade, though out-turned when articulated with the sacrum is not laterally flared, and its postacetabular blade is rectangular and has a modest brevis shelf. In both stegosaurs and ankylosaurs (Fig. 31B,C) the postacetabular blade is short and tilted horizontally. The ischium of *Scelidosaurus* is a Y-shaped thickened blade with a long stem. In stegosaurs the ischium is more transversely compressed and tapers distally (Maidment *et al.,* 2015), whereas those of ankylosaurs are considerably shorter, bar-shaped and decurved (Coombs, 1978a). The pubis of *Scelidosaurus* has a long, slender pubic shaft and a blade-like, laterally deflected prepubic process. The pubis of ankylosaurs is diminutive (a small oblong block fused to the ilium) from which projects a short, finger-shaped pubic shaft (Coombs, 1978a). In stegosaurs the pubis is a large, obtusely V-shaped bone with a parallel-sided pubic shaft that was ligamentously bound to the ischium, and a long rectangular prepubic blade (Gilmore, 1914).

Stegosaurs and ankylosaurs have much more robust and straight (pillar-like) femora (Gilmore, 1914; Coombs, 1978a). The femoral head is less clearly medially offset on the shaft (this is particularly so in ankylosaurid ankylosaurs, where the femoral head is terminal – Coombs, 1978a). The anterior trochanter tends to become indistinguishably fused to the greater trochanter. The 4th trochanter is represented by either a low mound or a large, depressed muscle scar on the lower half of femoral shaft. Their crural (shin) bones of are straight and the tibia is massive, with greatly expanded proximal and distal ends; the fibula is a comparatively slender, straight bone that had little to do with structural support. The ankle comprises a single proximal tarsal that is reduced to a flattened, warped plate formed by the astragalus, which is fused to the distal surface of the tibia. Distal tarsals have not, so far, been reported. The pes comprises short, dumbbell-shaped metatarsals and ‘stubby’ toes; these form a divergent ‘spreading’ arrangement that was most likely supported by a plantar pad of elasticated fibrous tissue. Their unguals are flattened, broad and rounded, distally forming a hoof, rather than a claw.

[B] Functionality of the hindlimb and pes summarised

1. Acetabulum. The acetabular joint surface is unusually large compared to the femoral articular head. It offers the possibility of a wide range of femoral head positions and consequential femoral excursions (Norman, 2020b: fig. 98) but the extent to which soft-tissues (notably cartilages) influenced the potential range of femoral excursions is uncertain (Hutson & Hutson, 2012).

2. Hindlimb joints. The knee has some of the osteological attributes of a simple hinge, but the extent to which this was constrained by soft-tissues to a transverse uni-axial plane of rotation is unknowable. The structure of the lower leg, which retains a short but stout, bowed fibula indicates that limited (modest) axial torsion may have occurred between the tibia and fibula. The ankle joint is weakly trochlear, as well as being osteologically asymmetrical. If there was a fibrocartilage pad covering the medial portion of the ankle, the entire ankle joint may have been susceptible to (or able to accommodate) long-axis torsion.

3. Hindlimb retractors. The lines of action of the caudifemoral muscles can be reconstructed (compare Figs 33, 35). The origin of the *m. caudifemoralis brevis* lies on the underside of the postacetabular process of the ilium and runs anteroventrally to the base of the 4th trochanter and its line of action is posteromedial (Fig. 35A, cfb). *M. caudifemoralis longus* is known to originate from the lateral surfaces of the caudal centra and the edges of the caudal ribs in all sauropsids (and even the equivalent pygostyle in birds) and inserts on the 4th trochanter. The line of action (Fig. 35A, cfl) of this retractor muscle runs anterolaterally from close to the caudal midline. In addition, the adductor muscle (Fig. 35, add) would both retract the femoral shaft (from its fully protracted state) and rotate the femoral shaft outward along its long axis (balancing some of the inward rotation imposed by the far more powerful caudifemoral muscles).

4. The pendent 4th trochanter is positioned on the posteromedial surface of the femoral mid-shaft (Fig. 35C) increasing the axial rotation generated by the femoral retractor muscles.

5. Hindlimb protractors. The lines of action of the *mm. iliotibialis, iliofemoralis* and *puboischiofemoralis internus* can be reconstructed with varying degrees of confidence. *M. iliotibialis* is consistently found to originate along the dorsal

edge of the iliac blade in sauropsids (including birds) and inserts on the cnemial crest of the tibia (Fig. 33, it). *M. iliofemoralis* originates on the dorsolateral surface of the iliac blade and inserts variously on the shaft of the femur and (with personal equivocation) on the anterior trochanter (Fig. 33, if) and lateral surface of the greater trochanter. At least one significant portion of the puboischiofemoralis complex originates from the proximomedial surface of the pubis, the surfaces of the posterior dorsal centra and the first sacral rib (in sauropsids). It has been suggested that a slip of this muscle attached to the ventral surface of the preacetabular process in ornithischians (Maidment & Barrett, 2011 – see also Fig. 33, pifi). This muscle inserts on the medial surface of the proximal femoral shaft and a major tendon of this muscle inserts adjacent to the 4th trochanter in crocodiles (there is a well-preserved muscle scar in this position on the femur of the lectotype – Fig. 32B, pifi). The lines of action of the first two muscles can be reconstructed with some confidence and vary a little along the length of the iliac blade because the preacetabular process swings markedly laterally along its length. *M. puboischiofemoralis* has a line of action that not only serves to protract the femur but imposes a torsional force that rotates the femoral shaft outward (laterally) in preparation for the next stride (Fig. 35C, E).

6. Dimensions of the abdominal cavity. *Scelidosaurus* was herbivorous and, judged from its teeth and jaw action, would have pulped and partly sheared its food prior to swallowing. This style of oral processing is unlikely to have prepared plant matter for immediate absorption in the intestine, so it would need to be processed further in the gut. A gizzard, lined with gastroliths, cannot be dismissed simply because no gastroliths have been recorded with any of the skeletons of this animal that have been discovered to date. A gizzard is present in living crocodiles and birds so may well have been present and used to comminute plant food in the anterior gut. However, further enzyme-mediated digestion would be necessary to release plant cell contents and can only have been achieved within gut caecae that housed permanent populations of microbes capable of secreting enzymes that can break down the tough polysaccharide (cellulose-based) cell walls of plants. Gut enlargement to accommodate caecae requires a capacious abdomen. The dorsal rib cage is indisputably broad (Norman, 2020b: fig. 34; see Figure 35D, E), and the body

shape is more similar to that seen in ankylosaurs (e.g. Gaston *et al.,* 2001) than stegosaurs (see also Fig. 22), which suggests that *Scelidosaurus* had a barrel-shaped abdomen.

7. Deflection of the prepubic blades. The lateral deflection of the prepubic blades that is evident in *Scelidosaurus* is also suggestive of the physical accommodation of a broadly expanded abdomen.

8. Asymmetry of the pes. The medial curvature that is evident when the digits of the pes are articulated might be an artefact of preservation in this specimen. However, the ungual phalanges of digits 2-4 are well-preserved and show comparatively little in the way of crushing plastic distortion, and yet they all indicate clear medial curvature. In the tridactyl pes of a 'normal' parasagittally-gaited dinosaur the axis of support tends to run through digit 3, which displays bilateral symmetry. The digits on either side splay: digit 2 curves medially, whereas digit 4 curves laterally so that the foot as a whole exhibits some degree of symmetry on either side of the principal axis of support (e.g. Norman, 1980: fig. 71; 1986: fig. 63). The persistent asymmetry evident across the digits of the pes of *Scelidosaurus* implies that torsional forces in the long axis of the hindlimb were acting on the foot during the support-retraction phase of the locomotor cycle (Fig. 35E).

[B] Conclusions

1. Motion at the hip joint between the femoral head and acetabulum, if osteological morphology is interpreted literally, may have been comparatively unconstrained, but this ignores major contributions that may have been made by the associated soft tissues (Hutson & Hutson, 2012; Manafzadeh & Padian, 2018).
2. The lines of action of the principal protractor and retractor muscles are likely to have imposed an oblique-to-parasagittal – anterolateral (protraction) and posteromedial (retraction) – plane of movement on the femur, and by implication the entire hindlimb.
3. A medially directed long-axis rotational force would have been imposed upon the body-weight-loaded femoral shaft (and by implication the

hindlimb) during caudifemoral muscle powered limb retraction because of the medial placement of the 4th trochanter on the shaft of the femur.

4. A laterally directed long-axis rotational force was imposed on the suspended femoral shaft during the limb protraction phase by the action of a component of *m. puboischiofemoralis internus* muscle (a slip of which has been inferred to have originated along a medial ledge beneath the preacetabular process of the ilium) that inserted adjacent to the 4th trochanter.
5. The volume and projected width of the abdomen, if correctly interpreted, would have presented a physical obstruction to the in-line parasagittal motion of the hindlimb during protraction. In effect the femur would have been deflected laterally as a consequence of proximity of the abdominal wall.
6. The asymmetry displayed in the distal tarsals of the ankle joint, and in the digits of the pes implies that the forces acting on the foot while it was placed on the ground involve medially-directed long-axis torsion transmitted through the foot via the more proximal hindlimb elements.

The extent of control of mobility exerted by the soft tissues surrounding the femoral head when it was in articulation with the acetabulum is currently unknowable. Similarly, the knee and ankle joints are ambiguous regarding the degree of constraint on their hinging capabilities. The lines of action of the principal protractor and retractor muscles of the hindlimb can be estimated with reasonable confidence. The torsional force exerted by the caudifemoral muscles during limb retraction, resulting from their asymmetrical attachment site on the femoral shaft, can be understood. The counter-torsional force exerted by the protractor musculature (notably *m. puboischiofemoralis*) is a matter of conjecture because its area(s) of origin exceed the bounds of phylogenetic inference. The size and general shape of the abdomen are equally conjectural, but can be inferred from the size of the gut in a range of living herbivores, the profile of articulated dorsal ribs and the lateral deflection of the preacetabular and prepubic blades. The asymmetry observed in the digits and ungual phalanges of the foot is an objective fact.

The hindlimb swung in an oblique-to-parasagittal arc, along an anterolateral-posteromedial plane facilitated by the mobility of the femoral head in the acetabulum. The retraction phase of limb motion imposed torsional forces on the hindlimb and foot, which are reflected in the medial curvature and asymmetry seen in the toes.

It has been suggested elsewhere (Carpenter *et al*., 2013: 3) that the hindlimb of the ankylosaur *Mymoorapelta* moved in an oblique-to-parasagittal manner, judged by the orientation of the articular axis of the acetabulum and "the expanded gut." These considerations probably apply more widely among ankylosaurs, particularly those with terminal femoral heads (Coombs, 1978a: fig. 15). The cupola-style of the acetabulum in stegosaurs and ceratopsians suggests that non-parasagittal hindlimb excursions may also have occurred in these groups of herbivorous ornithischian.

[B] Tail flexibility

The observation of a 'ball-and-socket' articular relationship between caudal vertebrae 1 & 2 in one skeleton of *Scelidosaurus*, but not in at least two other examples, poses questions that are both taxic and functional (Norman, 2020b).

There is no clear evidence for the presence of ossified tendons posterior to the sacrum in the specimens described to date. This observation implies that the flexibility of the tail was not constrained by these tendons and it could be swung freely laterally and dorsoventrally. The presence of rows of large ridged and cap-shaped osteoderms flanking the tail and running along the midline dorsally and ventrally may have limited extreme flexure, but they would also have provided an important weapon of defence (as commonly deployed by extant reptiles). It is probable that caudal osteoderms were capped by sharp-edged keratinous sheaths, judged by two recent ankylosaur discoveries (*Borealopelta* – Brown, 2017; *Zuul* – Arbour & Evans, 2017).

The presence of the equivalent of a ball-and-socket joint at the base of the tail in *Scelidosaurus* suggests that there was a particularly strong and stable pivot-point for tail swings. The caudal ribs of the anterior caudal vertebrae are also long and strong (Norman, 2020b: fig. 42), indicating that they provided areas for attachment, as well as improving the leverage, for flanking muscles (*m. caudifemoralis longus*) upon the tail. However, the articular surfaces of the zygapophyses between caudals 1 and 2 retain the 'normal' oblique angulation seen in proximal caudals generally, rather than the more horizontal orientation that might have been expected to correlate with increased lateral flexibility between these vertebrae.

For the present, the observation of the specialized articular relations at the base of the tail of just one individual of *Scelidosaurus* (BRSMG LEGL 0004) is regarded as a curiosity. It is hoped that future discoveries might clarify its significance.

[A] *SCELIDOSAURUS*: DERMAL SKELETON

The structure (Norman, 2020c), histology and biological role of the osteodermal skeleton of *Scelidosaurus* are topics that will be dealt with elsewhere (Norman & Baker, in preparation).

[A] THE SYSTEMATIC AND PHYLOGENETIC POSITION OF *SCELIDOSAURUS*

[B] Scelidosaurus*, early dinosaur classification and relationships*

Richard Owen established that *Scelidosaurus* was a member of his Dinosauria, based on the structure of its hindlimb:

> "The internal process [4th trochanter of the femur] is similarly well preserved, repeating the character of the herbivorous Dinosauria which is exemplified in the Iguanodon [italics]… The medullary or unossified cavity of the shaft of the bone has been more considerable, in relation to the compact shaft, than in the large femora previously described.
>
> From the foregoing characters it may be concluded that the present femur has belonged to a Dinosaur, allied to the Iguanodon [italics], …" (Owen, 1861: 5).

Despite the fact that Owen was describing the characteristics of a theropod femur (Owen, 1861: tab. I – see Norman, 2020a: fig. 2A), his words were still applicable to other genuine scelidosaur remains that he included in this preliminary description (Owen, 1861: tab. III – see Fig. 2). Owen was notably reticent when it came to expressing views about this new dinosaur's relationship to any of the other, then known, dinosaurs. His clearest remark was …

> "Upon the whole, I find the closest agreement to be between *Scelido*- and *Hylaeo-saurus* in the characters of the vertebral column; …" (Owen, 1863: 12).

And yet, despite Owen's extended description of parts of the dermal skeleton of *Scelidosaurus* (Owen, 1863: 20-26), there is neither a single mention of the osteoderms visible on the slab of Tilgate Stone containing the remains of *Hylaeosaurus*, nor a more detailed consideration of the potential relationship between these taxa.

Attempts to systematise and classify known taxa of Dinosauria began in the late 1860s, stimulated by the work of Edward Drinker Cope (1866). Cope established two groupings or "orders" of dinosaur based on his interpretation of their supposed ankle and foot structures: Orthopoda (including *Scelidosaurus*, *Hylaeosaurus*, *Iguanodon* and *Hadrosaurus*); and the Goniopoda (*Megalosaurus* and *Laelaps*). A year later Cope (1867) added a third order: Symphopoda, based upon his interpretation of the shin (crural), ankle (tarsal) and foot (pedal) structures in *Compsognathus*. The latter, he pointed out, suggested a resemblance between the feet of some dinosaurs and those of living birds. Subsequently, Thomas Henry Huxley (1868) demonstrated that the anatomical ("intermediate") similarities shared between the then-known dinosaurs and living reptiles and birds provided evidence that strongly supported Darwin's theory of evolution. Listing the anatomical differences between living reptiles and birds Huxley proceeded to fill the anatomical 'gap' between such distinctly different organisms by demonstrating that the fossil bird *Archaeopteryx* exhibits a number of reptilian features. Furthermore, he was able to demonstrate that the larger dinosaurs possessed many bird-like features in their sacra, pelves, hindlimbs and feet. The discovery of the small, lightly-built dinosaur *Compsognathus* compounded the similarities between dinosaurs, *Archaeopteryx* and living birds and allowed him to observe that "*Dinosauria* wonderfully approached … birds in their general structure, and therefore that these extinct reptiles were more closely allied to birds than any which now live" (Huxley, 1868: 73). This proposition was subsequently reinforced in a summary article (Huxley, 1870a) that led him to conclude "if the whole hind quarters, from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us from referring them to the *Dinosauria*." (Huxley, 1870a: 30-31). Huxley also began, in this same article, to dismantle Cope's classification of dinosaurs by pointing to anomalies in the leg and ankle structure among Cope's ordinal varieties. Subsequently, Huxley (1870b) reviewed and revised the classification of Dinosauria and, notwithstanding the primacy of Meyer's (1832) name Pachypoda, grudgingly accepted Owen's (1842) name Dinosauria:

> "… it may be well to allow justice to give way to expediency, and to retain the name of *Dinosauria* for these reptiles" (Huxley, 1870b: 33).

Huxley, using an approach that strikes us today as singularly prescient, provided a list of twelve diagnostic characters shared by known dinosaurs. The dinosaurs, thus diagnosed, were then divided into three "natural groups" (given familial ranking): Megalosauridae, Scelidosauridae, Iguanodontidae – and he added to these a group differentiated from the previous three by referring to it as Compsognatha. Each of these groups was supported by a list of diagnostic anatomical characters. However, Huxley stressed that the taxon Compsognatha (not given a familial suffix) was distinct anatomically from the three other dinosaurian families by virtue of possessing a slender, elongated neck and cursorial hindlimb proportions. All these features were demonstrable in the nominal taxon *Compsognathus*. He concluded that it was necessary to create a new Order of fossil reptiles that he named Ornithoscelida (because all of them exhibited bird-like limbs) and within this Order he identified two sub-orders that he named Dinosauria (characterized by being short-necked and having stout graviportally adapted limbs) and Compsognatha (with long necks and slender cursorial limbs). Given that Huxley was dealing with just seven recognised dinosaur taxa, and how little of their anatomy was known, this work was remarkable.

[B] Huxley's (1870b) classification

Order: ORNITHOSCELIDA
    Suborder: DINOSAURIA
        Family Megalosauridae
        Family Scelidosauridae
        Family Iguanodontidae
    Suborder: COMPSOGNATHA
        Nominal taxon *Compsognathus*

Developing his concept of ornithoscelidans by comparing them to other then-known reptile groups, Huxley introduced a confusing set of alleged affinities (=relationships) that resulted in his creating further higher-level taxonomic groupings based upon vertebral column morphology alone. These superordinal categories – Suchospondylia, Erpetospondylia, Pleurospondylia and Perospondylia – were neither acknowledged nor formally adopted by contemporary taxonomists and systematists and – perhaps fortunately – went the way of Cope's ill-fated Orthopoda, Goniopoda and Symphopoda.

During subsequent decades a greater range and variety of better-preserved dinosaur fossils were discovered, largely as a result of the prodigious efforts of Cope and Othniel Charles Marsh in the United States, as well as Louis Dollo in Europe (Colbert, 1968; Desmond, 1975). A clearer but more complicated picture of the range and variety of dinosaurian anatomy and morphology began slowly to emerge. Marsh (1881, 1884, 1891, 1895) assembled, illustrated and defined groupings of dinosaurs whose names and general attributes are still recognized today: Theropoda, Sauropoda, Ornithopoda, Stegosauria and Ceratopsia. Harry Govier Seeley (1887[1888]) also developed a utilitarian classification of dinosaurs that was based primarily upon pelvic morphology (using the term "ischia" to mean pelvis in an Aristotelian sense) and the presence of vertebral pneumatism. Seeley's system divided all known dinosaurs into two fundamentally distinct groups that he named Saurischia and Ornithischia. The clear-cut anatomical differences accommodated Marsh's groupings consistently and rationally, and were taken by Seeley to be so fundamental as to imply that Dinosauria *per se* was not a natural group (clade):

> "Dinosauria has no existence as a natural group of animals, but includes two distinct types of animal structure with technical characters in common, which show their descent from a common ancestry rather than their close affinity." (Seeley, 1887[1888]: 170)

and a little later (page 171) "I see no ground for associating these two orders in one group".

[B] Seeley's (1887[1888]) *classification*

Order: SAURISCHIA
    Suborder: Theropoda
    Suborder: Sauropoda

Order: ORNITHISCHIA
    Suborder: Ornithopoda
    Suborder: Ceratopsia
    Suborder: Stegosauria

Although there were fundamental disagreements concerning the monophyly or (Seeley's preference) diphyly and even polyphyly of dinosaurs with respect to their origin from archosaurian predecessors (e.g. Romer, 1933, 1968; Charig *et al.,* 1965; Bakker & Galton, 1974; Charig, 1982), Seeley's fundamental classificatory scheme proved robust in the face of continuous discoveries of new dinosaur taxa. In a major cladistic review of the Archosauria, Gauthier (1986) finally established a consensus over the matter of the monophyly of the Dinosauria and one that incorporated Seeley's two principal taxa as sister-taxa. It is only comparatively recently that the underlying topology of the constituent members of the clade Dinosauria has been challenged (Baron *et al*., 2017b,c).

[B] Scelidosaur classification and relationships

Scelidosaurus was (and still is) commonly referred to in general classificatory schemes of dinosaurs because it has been long recognized as one of the earliest known armoured ornithischian dinosaurs (e.g. Nopcsa, 1928; Kuhn, 1946; Romer, 1933, 1956, 1966). These latter accounts classified *Scelidosaurus* as a primitive (=basal) stegosaur. Romer (1968) revised his opinion about its stegosaurian affinities following the examination of freshly acid-prepared pelvic bones of the juvenile scelidosaur (NHMUK R6704 – Norman, 2020b) and subsequently referred *Scelidosaurus* to Ankylosauria. The authority implicit in this re-assignment was followed thereafter (e.g. White, 1973; Carroll, 1988).

<Figure 36 near here> Norman cladogram

A non-numerical cladistic revision of Seeley's Ornithischia (Norman, 1984b – Fig. 36) suggested that *Scelidosaurus* was a thyreophoran (='shield-bearer') and in doing so resurrected the taxonomic category Thyreophora (Nopcsa, 1915) but reduced its composition to two primary taxa: Stegosauria and Ankylosauria. Nopcsa (1915) had originally applied this name to all the then-known quadrupedal armoured ornithischians (Ankylosauria, Stegosauria and Ceratopsia); this was based upon the long-held (but incorrect) understanding that ceratopsians were also shielded/armoured (see Norman, 2020a). Within the revived Thyreophora, Norman posited *Scelidosaurus* as the sister-taxon to the clade Ankylosauria (=Nodosauridae + Ankylosauridae). At the same meeting Sereno (1984: Fig. 37) also reviewed the systematics of Ornithischia (although he did not include the taxon *Scelidosaurus*). Sereno coincidentally sought to revive Nopcsa's name Thyreophora, but proposed that it should comprise Stegosauria, Ankylosauria, Pachycephalosauria and

Ceratopsia (closer, in taxonomic content, to the original conception of Nopcsa). These preliminary analyses prompted further attempts to rationalize ornithischian relationships (Cooper, 1985; Maryańska & Osmólska 1985). Subsequently, Sereno (1986 – Fig. 38) tacitly accepted Norman's restricted conception of Thyreophora; he included *Scelidosaurus* in this revision but positioned it as the proximate sister-taxon to a clade that he named Eurypoda (=Stegosauria + Ankylosauria) rather than as a sister-taxon to Ankylosauria. The clade name Thyreophoroidea was emended to recognize the proposed sister-taxon relationship between *Scelidosaurus* and the clade Eurypoda (Fig. 38).

<Figure 37 near here> Sereno cladogram 1

The view that *Scelidosaurus* is a non-eurypodan stem thyreophoran (along with *Scutellosaurus* and *Emausaurus*) now prevails and has been reinforced by almost all subsequent systematic reviews of ornithischian-thyreophoran relationships (e.g. Coombs & Maryańska, 1990; Sereno, 1999; Norman *et al.,* 2004; Butler *et al*., 2008; Maidment *et al,*. 2008; Thompson *et al.,* 2012; Arbour & Currie, 2016; Baron *et al*., 2017b; Raven & Maidment, 2017). The only published exceptions to this consensus are Carpenter (2001), whose unconventional analytical approach (see discussion in Thompson *et al.,* 2012: 303) generated topologies that placed *Scelidosaurus* as the proximate sister-taxon to the Ankylosauria (=basal ankylosauromorph). Parish (2005: fig. A7.1) came to a similar conclusion, although Parish's data were later incorporated into a co-authored article (Thompson *et al.,* 2012) that promoted the consensus view that *Scelidosaurus* was a stem-lineage thyreophoran. Most recently, Wiersma & Irmis (2018) re-analysed ankylosaur relationships, by reference to a character set developed by Mark Loewen and James Kirkland, in light of a newly discovered and described ankylosaurid (*Akainacephalus*). This analysis positioned *Scelidosaurus* as a basal ankylosaur, whereas *Scutellosaurus* and *Emausaurus* were positioned (more conventionally) as successive basal thyreophorans. There was, however, no discussion of the implications of their revised positioning of *Scelidosaurus* but, in fairness, their study was solely focused on derived ankylosaur taxa and their interrelationships, rather than on basal thyreophoran relationships.

<Figure 38 near here> Sereno cladogram 2

The more detailed description of the anatomy of *Scelidosaurus* that is now available (Norman, 2020a,b,c) permits a re-evaluation of the anatomical characters and the character-scoring used in previous systematic analyses, and a consequential reassessment of its phylogenetic position within Ornithischia.

[A] SYSTEMATIC ANALYSIS: THE POSITION OF *SCELIDOSAURUS*

[B] Previous analyses and data sources

1. Walter Coombs' (1971, 1978a) reviews of Ankylosauria clarified and greatly improved our understanding of their anatomy, and offered a logical basis (through the listing of sets of anatomical characteristics – effectively synapomorphies) that established a classification for the then known ankylosaurians. Coombs recognized two distinct ankylosaur families, Nodosauridae and Ankylosauridae, and speculated upon their evolutionary history. The identity of a common ancestor shared by the two ankylosaur families was discussed briefly and declared to be unknown. Equally, the potential role of *Scelidosaurus* in the ancestry of Ankylosauria was considered in the light of Romer's (1968) assessment of it as an ankylosaur rather than a stegosaur. *Scelidosaurus* was dismissed as an ankylosaur ancestor on the basis of a number of (what are now known to be) incorrect anatomical observations:

> "The type of *Scelidosaurus* (*fide* Newman, 1968) has ankylosaur-like armour plates, but lacks the diagnostic cervical half-rings. The upper temporal fenestrae of *Scelidosaurus* are open, and there are no armour plates fused to the skull roof (Owen, 1863). *Scelidosaurus* has a single supernumerary cranial element above the orbit (Coombs, 1972), whereas *Pinacosaurus* and presumably other Ankylosauridae have three (Maryańska, 1971). Nodosaurid skull roof composition is unknown. Therefore,

> *Scelidosaurus* is not morphologically suitable as an ancestor of the family Ankylosauridae, and in so far as no features diagnostic of the Ankylosauria have yet been described in *Scelidosaurus*, I do not accept the genus as an ancestor for any ankylosaurs. (See noted added in proof, p. 168)" (Coombs 1978a: 164)

As a measure of support for his stated position on the matter, Coombs was able to refer (using the note added in proof) to an account of *Scelidosaurus* (Thulborn, 1977), in which it was argued (incorrectly) that this dinosaur was ornithopodan rather than an ankylosaurian. The extent to which Coombs had been misled about the anatomy of *Scelidosaurus* reflects the want of a descriptive revision, rather than any shortcoming of his own.

Many of the anatomical characters listed by Coombs (1978a) in his review of the classification of Ankylosauria have been translated into character-state formats in numerous subsequent numerical cladistic analyses.

2. Sereno (1986) summarised ornithischian relationships and provided synapomorphy lists to support the clade Thyreophora: *Scutellosaurus* + *Scelidosaurus* + Eurypoda). Five characters supported a more exclusive clade named Thyreophoroidea (*Scelidosaurus* + Eurypoda – see Fig. 38):

i. A sinuous dentary tooth row in lateral view.
ii. A supraorbital bone forms the dorsal orbital margin.
iii. Enlargement of the medial portion of the mandibular condyle.
iv. A basisphenoid that is much shorter than the basioccipital.
v. Median palatal pterygovomerine keel.

3. Tumanova (1987) and Coombs & Maryańska (1990) did the same in supporting a cladogram summarising in-group relationships among ankylosaurs that reinforced the conclusions reached by Coombs (1978a). Sereno & Dong (1992) provided an updated description of the early stegosaur *Huayangosaurus* (Dong, Tang & Zhou, 1982). In this account a discussion of the anatomical features found in *Huayangosaurus*, as well as those shared by other known stegosaurs, was provided as a basis for justifying a synapomorphy-based cladogram (Sereno & Dong, 1992: fig. 14) that placed

Huayangosaurus as the most basal known stegosaur. Several comments concerned unpublished comparative observations on the anatomy of *Scelidosaurus* and were used to justify exclusion of *Scelidosaurus* from the Eurypoda and reinforce Sereno's (1986) topology (Fig. 38).

4. Lee (1996) offered the first matrix-based analysis of ankylosaur relationships, but used a limited range of taxa and concentrated only upon cranial character-states. Similarly, Kirkland (1998: 273) analysed cranial and postcranial characters and doubled the number of taxa considered, but scored *Scelidosaurus* as the default outgroup in his matrix. Carpenter *et al.,* (1998) undertook another analysis, but introduced suprageneric taxa (Nodosauridae and Ankylosauridae) that were determined prior to the cladistic analysis. The value of adopting an approach that makes *a priori* decisions about monophyletic groupings (suprageneric taxa) was criticised methodologically by (Wilkinson *et al.,* 1998) who determined that the results were phylogenetically uninformative. While strict application of logic renders their determination correct, it is the case that many of more recent analyses of thyreophorans (and other, sometimes broader-based taxonomic analyses) commonly make pragmatic *a priori* decisions about suprageneric taxa in order reduce data-processing time and 'improve' resolution. A 'compartmentalized' suprageneric taxon approach was nevertheless also employed by Carpenter (2001) in an attempt to manage the high levels of homoplasy that have been reported to occur among ankylosaurs (Penkalski, pers. comm. March 2020).

5. Sereno (1999) provided a more comprehensive review of dinosaur relationships by offering lists of characters (and their coding protocols) for each of the major dinosaur clades and their subordinate taxa. However, there were continuing methodological problems with this analysis through his use of suprageneric taxa (see Wilkinson *et al*., 1998): only a limited number of ornithischian taxa were included and the monophyly of particular named clades was assumed prior to the analysis. The thyreophoran dataset included 118 characters that were used to code 17 thyreophoran taxa. The clade Thyreophoroidea (*Scelidosaurus* + Eurypoda) was supported by the five character-states listed above, but these had been modified in response to the

discovery of a new, apparently more basal, taxon *Emausaurus* (Haubold, 1990).

6. Subsequent analyses by Vickaryous *et al.* (2001) and Hill *et al.* (2003) were more narrowly focused upon cranial characters alone and, as can be seen from the scores in the matrix produced by Hill *et al.* (2003: 28), it is not at all surprising that *Scelidosaurus* defaults as an outgroup to Ankylosauria (along with *Emausaurus* and the basal stegosaur *Huayangosaurus*).

7. Vickaryous *et al.* (2004) provided what became the default phylogenetic analysis for ingroup ankylosaurs because it included cranial and postcranial characters, used a wide range of taxa and made no *a priori* assumptions about ingroup relationships. It was used for a number of years, with subtle modifications to character-states and the addition of new taxa. Unfortunately, this analysis used *Lesothosaurus* and *Huayangosaurus* as outgroups, and did not include basal thyreophorans such as *Scelidosaurus* and *Emausaurus.*

8. Butler *et al.* (2008) provided a re-assessment and more exhaustive set of analyses of the systematics of the clade Ornithischia. These were undertaken in the light of many new discoveries and the inconsistencies in the non-numerical systematic analyses that emerged from this new material (Norman, 1984b; Sereno, 1984, 1986; Cooper, 1985; Maryańska & Osmólska 1985). Butler *et al*. (2008) again used a number of suprageneric taxa (notably, in this instance, Ankylosauria) and generated a larger ornithischian dataset than that presented by Sereno (1999). Regarding the placement of *Scelidosaurus* their results were consistent with those published by Sereno (1986, 1999) because they used the same characters, apart from one additional character:

   i. The presence of cortical remodelling on cranial bones (after Carpenter (2001)

It was however noted that *Scelidosaurus* had not been described (by 2008), with the implication that characters and character-state codings may differ once its anatomy is known in greater detail. It was also admitted that the analysis involved the coding of supraspecific operational taxonomic units:

e.g. Stegosauria and Ankylosauria, and that a fuller consideration of the phylogenetic position of *Scelidosaurus* would (ideally) require consideration of a range of individual eurypodan taxa. This was, however, considered to be beyond the scope of their analysis.

Overall, the analysis cast doubt upon the interpretation of *Scelidosaurus* as a stem ankylosaur (Norman, 1984b; Carpenter, 2001). Constraining the resolved tree so that *Scelidosaurus* is positioned as the sister taxon to Ankylosauria increased tree length by 8 steps (among trees of 485 steps), but they did note that this was not a significantly worse explanation of the data (Templeton Test, p=0.04-0.13).

9. Several more taxonomically restricted analyses of thyreophoran ornithischians have been undertaken since the work of Butler *et al*. (2008). The most relevant among these, because they incorporate *Scelidosaurus*, are Thompson *et al.* (2012), Arbour & Currie (2016 – with a supplementary by Arbour & Evans, 2017) and Wiersma & Irmis (2018) for Ankylosauria; and Maidment *et al*. (2008), Mateus *et al.* (2009), Maidment (2010) and Raven & Maidment (2017) for Stegosauria. All of these studies provide taxon lists as well as detailed character descriptions and coding.

The output of these sets of analysis differ markedly. For ankylosaurs, large numbers of equally most parsimonious trees (MPTs) were generated from data tables in which the codes assigned to characters were unweighted and unordered (4248 MPTs [52 taxa and 170 characters] – Thompson *et al.,* 2012; 3030 MPTs [44 taxa and 177 characters] – Arbour & Currie, 2016); and finally 21 MPTs [35 taxa (31 thyreophorans) and 293 characters – none of which were weighted, but 48 were ordered] – Wiersma & Irmis (2018). For stegosaurs the datasets were smaller: Maidment *et al*. (2008) used just 18 taxa (11 of which were ingroup stegosaurs) and 85 characters, whereas the most recent analysis (Raven & Maidment, 2017) used 23 taxa (13 of which were ingroup stegosaurs) and 114 characters. In contrast to the ankylosaur analyses, some characters were assessed (*a priori*) and selectively weighted or ordered. This procedure generated respectively 5, 41 and finally a single MPT seemingly considerably better resolved. Thorough though the analytical processing of all these studies has been they are, somewhat paradoxically, limited with respect to their consideration of basal taxa (including

Scelidosaurus). As a consequence, in all instances but one (Wiersma & Irmis, 2018) *Scelidosaurus* occupies an entirely consistent position as the sister taxon to Eurypoda.

In each analysis character lists are notable for their choice of codable anatomical characters intended to differentiate *between* a range of derived, but anatomically conservative and in many instances fragmentary/incomplete in-group taxa (note for example the discussion in Thompson *et al.,* 2012: 308 *et seq.* regarding the status of the clade Polacanthinae/Polacanthidae). The cumulative effect of scoring large numbers of derived character-states is that it introduces substantial statistical bias within the dataset that results in the outgroup OTUs and/or 'basal' taxa being scored "absent"/"0" for large numbers of characters (e.g. Butler *et al*., 2008; Thompson *et al.,* 2012, *et seq*) despite the fact that these characters enable resolution between more derived taxa within the overall analysis; these particular issues are discussed in greater detail by Brazeau (2011). Interestingly Wiersma & Irmis (2018) compared the results of their analysis with those achieved by Arbour & Currie (2016 – and its reworked and heavily pruned iteration: Arbour & Evans, 2017). They noted a profound lack of resolution among most nodosaurid and ankylosaurid taxa in the strict consensus tree, and that a degree of resolution was only be achieved by calculating a 50% Majority Rule consensus (which should not be used to explore phylogenetic relationships – Sumrall, Brochu & Merck, 2001); and a Maximum Agreement subtree which, although it identifies consistent phylogenetic structure common among the MPTs, also removes a large number of taxa and is inherently unstable (Wiersma & Irmis, 2018). Weirsma & Irmis' trees also lacks resolution although this does not appear to be as severe as that evident in Arbour & Currie's data. Both studies highlight weak levels of tree support, which point toward fundamental character-related problems (high levels of homoplasy and missing data for many taxa) in ankylosaur systematics.

Scelidosaurus, Emausaurus and *Scutellosaurus* cluster at the base of most trees because they can be scored for only a restricted number of anatomical characters, many of which were identified originally by either Sereno (1986, 1999) or Butler, *et al.* (2008). Other factors that have influenced the phylogenetic reconstructions based on these analyses (notably the placement of *Scelidosaurus* but also including *Scutellosaurus* and *Emausaurus*) are:

- The comparatively high levels of missing data for all three taxa.
- Anatomical characters were incorrectly identified and/or scored because so little detailed anatomy of these taxa was known.

In the case of *Scelidosaurus,* despite the skeleton having been cleared of matrix, authors have until now been obliged to rely on the monographs of Owen (1861, 1863), a small amount of anatomy illustrated by Charig (1972) or, on rare occasions, brief examination of material in the collections of the Natural History Museum (e.g. Carpenter *et al.,* 2013; Arbour & Currie, 2016). An illustrative example of this particular problem can be seen in the matrix created by Arbour & Currie (2016) in which ~50 out of a total of 177 characters were scored incorrectly for *Scelidosaurus*; this observation has no bearing on the competence of these authors but simply reflects how little was then known of this important taxon.

[B] New analysis

For the present analysis, the author surveyed, assessed, and sampled previously published character lists and their codings, then constructed a matrix of 15 taxa and 115 characters (Table-Appendix 2). The approach used was to identify characters that could be scored for currently known early (or apparently anatomically basal) taxa, as well as some exemplar well-preserved and well-described stegosaurs and ankylosaurs (see also Table-Appendix 2). This resulted in the production of a near equal split between cranial and postcranial characters (cranial 55 : 60 postcranial). A number of characters were added, whereas others were redefined, corrected and re-coded. This process of winnowing avoided the incorporation of many highly specific characters that have no relevance to a consideration of basal taxon systematics (Brazeau, 2011).

[B] Analytical protocols

[C] Taxon sampling

The primary purpose of a palaeontological systematic assessment of any particular taxon is to assess the extent to which its anatomical characteristics resemble, in a comparative sense, those of either contemporary taxa or ones that span the chronostratigraphic time interval in which it occurs. Equally, attempts can be made to enlarge the range of taxa with which it shares some of its principal characteristics, irrespective of their chronostratigraphic occurrence, so that it can be placed (topologically) and then interpreted in a broader phylogenetic and deeper temporal context. The taxa listed below were chosen because they are generally well preserved and described, are roughly contemporaneous (Early Jurassic), and share anatomical features seen in *Scelidosaurus*. Additional taxa were added because they have been widely recognized in the literature as representative of the two principal thyreophoran subclades.

Scelidosaurus is exclusively from the Early Jurassic Charmouth Mudstone Formation (late Sinemurian) of south-west England. It is a facultatively quadrupedal ornithischian with a well-developed dermal cuirass – and is thus considered to be *de facto* thyreophoran (Norman, 2020a,b,c). Exactly contemporaneous and taxonomically valid ornithischians have yet to be discovered and described.

Lesothosaurus is an Early Jurassic (Hettangian) slender-bodied, bipedal and, by consensus, non-thyreophoran ornithischian (but see Butler *et al.,* 2008) from southern Africa. It is known from abundant skeletal and cranial material (Thulborn, 1970, 1972; Santa Luca, 1984; Sereno, 1991; Porro *et al.,* 2015; Baron *et al*., 2017a). This taxon has been regarded as the most basal ornithischian and has been used consistently as an outgroup in ornithischian/thyreophoran analyses.

Pisanosaurus from Argentina of Late Triassic (Carnian-Norian) age has long been claimed to be ornithischian (Casamiquela, 1967; Sereno, 1991, 1999, 2012; Martinez *et al.,* 2013) but doubts about the association of the skeletal elements and the systematic position of this taxon have been raised in the past (Norman *et al.,* 2004; Padian, 2013). In the light of recent suggestions made by Baron *et al.* (2017c) this taxon (*Pisanosaurus*) has been re-described and re-assessed (Agnolin & Rozadilla, 2018). It is now considered probable that this material belongs to a silesaurid dinosauromorph. *Lesothosaurus* can therefore be justly regarded as one of the most basal, and earliest, adequately known ornithischians.

Scutellosaurus has been recovered from the Early Jurassic Kayenta Formation of North America (Colbert, 1981; Breeden, 2016). The chronostratigraphic age of this Formation has been a matter of prolonged dispute: ranging from latest Triassic (see the discussion in Colbert, 1981) through the Hettangian, Sinemurian and Pliensbachian stages of the Early Jurassic (note the discussion in Steiner & Tanner, 2014). Current views suggest an early Pliensbachian age. This taxon exhibits similar characteristics to those seen in the bipedal/cursorial *Lesothosaurus*. *Scutellosaurus* also has an extensive cuirass of osteoderms, making it 'thyreophoran' in a literal sense, and an obvious choice as a comparator for *Scelidosaurus*.

Emausaurus is an enigmatic thyreophoran, having been recovered from the Early Jurassic (Toarcian) of Europe (Haubold, 1990). It is known from only an incomplete, dermally ornamented articulated skull and partial mandible, a small number of isolated postcranial bones and a few conical osteoderms that indicate the presence of a dermal cuirass. Some features seen in the skull and postcranium indicate anatomical affinities to *Scelidosaurus* and *Scutellosaurus*.

Looking further afield stratigraphically for other ornithischians that are technically thyreophoran because they possess a dermal skeleton, as well as being well preserved and described, there are several candidate Jurassic taxa:

Huayangosaurus is a regarded as a basal stegosaur that has been recovered from the Middle Jurassic (Bathonian-Callovian) of China (Zhou, 1983, 1984; Sereno & Dong, 1992, Maidment *et al.,* 2006). The taxon is represented by two skulls and a substantial portion of its postcranial skeleton (which includes a variety of dermal plates and spikes).

Kentrosaurus is another stegosaur taxon known from abundant disarticulated cranial, postcranial and dermal bone material collected from the

Late Jurassic (late Kimmeridgian-early Tithonian) of East Africa (Hennig, 1925; Galton, 1988).

Stegosaurus from the Late Jurassic Morrison Formation of North America (Kimmeridgian-Tithonian) is an approximate contemporary of *Kentrosaurus*, and is the eponymous stegosaur. Several skulls and skeletons of this taxon have been recovered and these have been described in detail by Gilmore (1914) and this work was supplemented more recently by Maidment *et al.* (2015).

Ankylosaurian thyreophorans are predominantly Cretaceous in their stratigraphic distribution, although the earliest known example described to date are Late Jurassic (Kimmeridgian). Exemplar taxa used in this analysis include:

Kunbarrasaurus from the early Late Cretaceous (Albian-?Cenomanian) of Australia includes at least one articulated skeleton and skull and several other postcranial fragments. Its postcranium was partly described by Molnar (1996) and a detailed skull description was completed more recently (Leahey *et al.,* 2015). The postcranial skeleton preserves parts of its articulated dermal skeleton including partial parasagittal rows of conical osteoderms.

Jinyunpelta from the early Late Cretaceous (Albian-Cenomanian) of China comprises a substantial portion of a skull and the postcranium of an armoured dinosaur that has been described by Zheng *et al.* (2018). The skull is crushed obliquely dorsoventrally, but much of its external anatomy has been described, as has its postcranial skeleton and dermal armour. The latter is extensive and augmented by the presence of a bony tail club.

Sauropelta is represented by several partial skeletons and skulls collected from the Early Cretaceous Cloverly Formation (Aptian) of North America (Ostrom, 1970).

Silvisaurus was recovered from the late Early Cretaceous Dakota Formation (Aptian-Cenomanian) of North America and includes a skull and partial skeleton (Eaton, 1960).

Pinacosaurus is a Late Cretaceous (Santonian-Campanian) taxon from Mongolia and China, represented by a considerable number of skulls and skeletons that encompass a size range (from juvenile to adult). First described by Gilmore (1933) this work has been added to by Maryańska (1971, 1977), Godefroit *et al*., (1999) and Hill *et al.* (2003).

Edmontonia is a Late Cretaceous (Campanian) taxon from North America represented by several of skulls and a number of postcranial skeletons (Gilmore, 1930; Russell, 1940; Coombs, 1971, 1978a).

Euoplocephalus is another well known Late Cretaceous (Campanian-Maastrichtian) taxon from North America (Lambe, 1902; Coombs, 1971, 1978a; Vickaryous & Russell, 2003; Vickaryous *et al.,* 2004; Arbour & Currie, 2013) has been claimed to be represented by numerous specimens. However it should be noted that a recent revision of the taxonomic assignment of remains attributed to *Euoplocephalus tutus* (Penkalski, 2018) has considerably reduced the number of specimens attributable to *Euoplocephalus* and assigns those excluded from this taxon to a number of other ankylosaurian taxa such as *Oohkotokia* (Penkalski, 2014) and *Zuul* (Arbour & Evans, 2017).

Struthiosaurus is widely distributed across the Late Cretaceous (Campanian-Maastrichtian) of Europe and its remains include both skull and postcranial material (Nopcsa, 1915, 1929; Pereda Suberbiola & Galton, 2001).

Outgroup and additional taxa. *Silesaurus* was specified as an outgroup following Baron *et al.* (2017b,c). *Silesaurus* (Dzik, 2003) is a Late Triassic (late Carnian-early Norian) dinosauriform. Two additional taxa: *Hypsilophodon* (Galton, 1974) and *Dryosaurus* (Janensch 1955; Galton 1981, 1983), both of which are well-described bipedal ornithopod dinosaurs, were included as unspecified comparative ornithischian taxa.

[C] Scoring

Anatomical characters were scored by direct observation of specimens (where possible) otherwise scoring was derived from the original descriptive accounts and accompanying illustrations. A full list of the taxonomic material and sources is provided in Table-Appendix 2. All characters were unweighted and unordered.

[C] Analysis

The compiled data file (available as a supplementary NEXUS file) comprises 18 taxa scored for 115 anatomical characters. The matrix was constructed in MacClade v4.06 (Maddison & Maddison, 2003) and then exported into TAXEQ3 (Wilkinson, 2001) in order to check whether there are taxa that lack unique character combinations. Any such taxa can be removed without compromising the statistical algorithm that generates the cladogram topology, but no taxa failed this test so none were deleted.

<Figure 39 near here> Strict Consensus tree with Bremer support

Analyses were performed using PAUP* (Swofford, 2002) using both Heuristic with Tree Bisection-Reconnection implemented (22,569 replicates examined), and Branch & Bound search algorithms. When parsimony-based analyses generate ambiguity (an array of equally most parsimonious solutions) it is normal practice to resolve character change by using optimization algorithms (Farris, 1970; Swofford, 2002). Analyses were therefore run using both ACCTRAN (which, on balance, accelerates character change so that they occur as near to the root as possible) and DELTRAN (which delays character change as close to the tips as possible) optimizations so that the evolutionary implications of character state changes could be compared and evaluated (Swofford & Maddison, 1992). It has more often than not been considered preferable to favour ACCTRAN optimizations, but this is unfounded – see Agnarsson & Miller (2008).

A Strict Consensus tree (Fig. 39) was generated from the resultant MPTs. MacClade offers an option to create a Decay Index (Bremer, 1994) file that generates a PAUP* command which can be used to calculate decay indices of branch support for individual clades as a measure of overall branch-tree stability. The command file can be executed on the active dataset in PAUP* which runs a series of calculations on each of the clades generated by the dataset. A log file stores the sequence of numerical outputs. The tree length attained (before a specified node collapses) can be used to calculate individual decay indices (Fig. 39 – Bremer support numbers on branches). The MPTs were also subjected to a bootstrap analysis set to 10,000 replicates (Fig. 40). The bootstrap percentage figures offer an assumption-limited, statistical measure of confidence in the cladogram's topology (Sanderson, 1989).

<Figure 40 near here> Bootstrap results of MPTs

The tree file of MPTs generated in PAUP* was also imported into MacClade and then manipulated using its tree editing tools to investigate the influence of alternative topologies on tree length and statistical support ('testing' by mimicry of the topologies generated in recently published analyses).

[B] Results and topological manipulations

Both the Heuristic and Branch & Bound analyses produced 10 MPTs of 226 steps (min: 164, max: 629) with a consistency index (CI) = 0.73, retention index (RI) = 0.87 and homoplasy index (HI) = 0.27. The strict consensus tree (Fig. 39) has a topology that conforms in most respects with previous analyses. However, a cluster of taxa: *Scutellosaurus, Emausaurus* and *Scelidosaurus* are a positioned on the stem of Ankylosauria rather than on the stem of Thyreophora.

Ingroup resolution among individual nodosaurid taxa is lacking (Fig. 39), which is a result that is entirely consistent with previously published analyses that have attempted to resolve nodosaur relationships (see Thompson *et al.,* 2012, for a discussion of this problem). The uncertainty concerning nodosaurid positioning is responsible for the majority of the differences among the 10 MPTs. There is also a subsidiary ambiguity over the positions occupied by *Jinyunpelta* and *Kunbarrasaurus* (Fig. 39) that contribute to the differences between MPTs. There is a general correspondence between the tree support offered by the Bremer indices (Fig. 39) and bootstrap values (Fig. 40). These values are as robust as, or more robust, than those published in recent analyses (e.g. Thompson *et al.,* 2012: fig. 2; Arbour & Currie, 2016: fig. 11; Wiersma & Irmis, 2018). However, these latter analyses had much larger ranges of ankylosaurian taxa, many of which are fragmentary (high levels of missing data) and exhibit substantial levels of anatomical conservatism and homoplasy, all of which challenge the analytical algorithms (and subsidiary statistical manipulations) deployed in an attempt to obtain resolved trees.

<Figure 41 near here> Tree manipulation of *Scutellosaurus* and *Jinyunpelta*.

Exploration of tree topology (intended to reproduce and investigate the topology of previously published cladograms) can be undertaken by importing an MPT tree file (.tre) generated in PAUP* into the Tree Window of MacClade. Taxon repositioning automatically generates corresponding tree length and statistical support data. It is equally possible to use MacClade to explore tree topologies that are generated using PAUP* when the original dataset is re-analysed following the addition or deletion of taxa:

1. When *Scelidosaurus* (0.9 % missing data) is repositioned so that it occupies what might be regarded as a 'traditional' thyreophoroidean position (as the proximate sister taxon to Eurypoda), tree length increases by 18 steps (244 steps).

2. Repositioning *Emausaurus* (56.5% missing data) as the basal sister taxon to *Scelidosaurus* on the eurypodan stem further increases tree length by three steps (247 steps).

3. When *Scutellosaurus* (28.7% missing data) is repositioned as the basal sister taxon to *Emausaurus* a tree length drops to 231 steps, which is just five steps longer than that of the most parsimonious trees. This latter result reflects a combination of the 'gravitational pull' on the data exerted by the basal ornithischian characters exhibited by *Scutellosaurus,* combined with the missing data for this taxon.

Scutellosaurus possesses several character-states that correlate with a cursorial-bipedal style of life (seen in *Lesothosaurus*, *Hypsilophodon* and *Dryosaurus*); it also has a less specialised jaw morphology (reminiscent of that seen in *Lesothosaurus*). These basal ornithischian characters conflict with the presence of two key ankylosauromorphan characters: cranial exostoses, and multiple parasagittal rows of osteoderms on its torso. An indication of the latter character conflict is revealed by the fact that reverting the positions of *Scelidosaurus* and *Emausaurus* as successively more remote ankylosauromorphans to Ankylosauria, while leaving *Scutellosaurus* as the proximate sister taxon to Thyreophora (see Figure 41), produces a tree length of 229 which is just three steps longer than that of the fundamental MPTs. Statistically, this topology cannot be dismissed from consideration, even if it is not favoured by the author.

4. *Jinyunpelta* (45.2% missing data) can also be repositioned on the ankylosaurid stem (see Figure 41); this accords with Coombs (1978a) because this taxon exhibits a tail club. It is interesting to note that this tree topology increases tree length by just a single step (230 steps, CI: 0.71, RI: 0.86).

5. *Kunbarrasaurus* (27.8% missing data) appears to be stably positioned as the most basal ankylosaurian currently known. All other locations on the tree produce substantial increases in tree length.

5. Deleting the comparatively poorly resolved taxa *Kunbarrasaurus* and *Jinyunpelta* from the original dataset in PAUP* and then re-running the analysis using the same parameters results in 6 MPTs (all residual tree conflict reflects the lack of resolution within the nodosaurid clade). Tree length is reduced to 212 steps (min: 164, max: 585) and these trees have a CI: 0.77 and RI: 0.89. The Strict Consensus tree is presented as Figure 42. The topology of the fundamental consensus tree (Fig. 39) is retained but benefits from a substantial (14 step) decrease in tree length.

<Figure 42 near here> Deletion of Kunbarra & Jinyun cladogram

[B] Discussion

The strict consensus tree (Fig. 39) generated by the dataset re-affirms the 1970s hypothesis concerning the main ankylosaurid-nodosaurid dichotomy (Coombs, 1978a) and the 1980s hypothesis concerning the general composition of the clade Thyreophora (Norman, 1984b; Sereno, 1986). Both general hypotheses have indeed been supported in subsequent studies (Coombs & Maryańska, 1990; Sereno, 1999; Butler *et al.,* 2008; Thompson *et al.,* 2012; Arbour & Currie, 2016; Raven & Maidment, 2017) and are therefore regarded as secure. The decay indices (Fig. 39) and bootstrap support values (Fig. 40) add a measure of support for these hypotheses. One result generated by this analysis is controversial: the positioning of *Scelidosaurus* (and related taxa) on the stem of Ankylosauria (Figs 39-42), given the near universal support for the clade named Thyreophoroidea (*Scelidosaurus* + Eurypoda – see Fig. 38). Note in particular the discussion in Thompson *et al.* (2012: 306-308). In this new topology Thyreophoroidea and Eurypoda as envisioned since Sereno (1986) become meaningless.

There are several points that arise in the light offered by this new analysis and the tree topology that it has generated:

- Anatomical updates. This has been the first opportunity to incorporate accurate anatomical information concerning *Scelidosaurus* into any systematic analysis (note the comments in Butler *et al.,* 2008: 20). It is worth noting that one of the more recent detailed analyses of thyreophoran relationships had a near 30% error rate in its scoring of *Scelidosaurus*. This analysis has benefitted from some preliminary information on *Scutellosaurus* (Breeden, 2016) that supplements that which was available in Colbert (1981); the former account is also expected to be updated in the near future (Breeden, pers. comm. March 2020). *Emausaurus*, another key taxon, although it is represented by a well-preserved but partial skull lacks a great deal of anatomy and would benefit from fresh discoveries of this taxon.
- Dataset review. The new data matrix represents a process of addition to, as well as culling, editing and scoring/re-scoring of characters listed in previously published datamatrices. These were constructed originally in attempts to assess either global ornithischian interrelationships (notably Butler *et al*., 2008 and Sereno, 1999); or those found within specific ornithischian sub-clades (e.g. Stegosauria and Ankylosauria – notably Maidment *et al.,* 2008; Arbour & Currie, 2016; Raven & Maidment, 2017).
- Character choice. The characters that have been retained, as well as a smaller number of novel characters, focus mainly upon the anatomies displayed by currently known basal thyreophoran ornithischians. This represents a deliberate attempt to redress the balance which, in most analyses, has tended to favour ever-increasing numbers of anatomical

characters that pertain only to more derived taxa – with the understandable aim of increasing the statistical support for the discrimination between, and placement of, a substantial number of anatomically more derived, taxa.

- Topological plasticity. Phylogenetic definitions (node-based and stem-based) are used in some palaeontological systematic analyses following the pioneering work of Farris (1976), de Queiroz & Gauthier (1990, 1992) and de Queiroz (1992). This style of taxon-clade definition is driven by the desire to remove ambiguity in the way that relationships are defined, and works well in a framework provided by a stable cladogram topology. Unfortunately palaeontology is a research discipline in which the discovery of additional material, the re-description of established taxa, and the discovery of completely new taxa are commonplace. As a consequence any fossil-based cladogram can be little more than an interim hypothesis of relationships.

The fossil record of terrestrial vertebrates (in this particular instance that of armoured dinosaurs of the Jurassic and Cretaceous) is logically and inescapably incomplete (Darwin, 1859; Retallack, 1984). As a consequence, systematic analyses have shown consistently that palaeontologically-based cladograms, although they often maintain some degree of large-scale coherence (but note Baron *et al.,* 2017b as an exception), are inherently internally labile (as demonstrated here). Adopting a preferentially stem-based (rather than node-based) approach to taxon definitions may prove to be a more pragmatic way of maintaining some degree of nomenclatural stability (and reducing the rate of propagation of new taxonomic names) in the face of changing fossil-based tree topologies.

[C] Thyreophoran clades and apomorphy lists

Serve as summaries of the character acquisitions in (anatomical) support of the topology presented in Figures 39 & 40, and the simplified summary cladogram (Fig. 42). The lists generated below represent a summary of the apomorphies that were generated in PAUP* and found to be common to both ACCTRAN & DELTRAN optimizations. The (larger) total numbers of ACCTRAN and DELTRAN characters produced by these analyses are listed in parentheses (for the comparatively unambiguous clades) and are available for scrutiny in Table-Appendix 3.

Phylogenetic definitions are provided for some clades, but these are not suggested for taxonomic groupings that are well known but not comprehensively surveyed in this analysis, e.g. Stegosauria, Ankylosauridae, Nodosauridae.

Clade THYREOPHORA

Stem-based definition: all taxa more closely related to *Euoplocephalus* and *Stegosaurus* than to *Hypsilophodon*.

The possibly node-based definition: the common ancestor of Stegosauria (*Stegosaurus*) and Ankylosauria (*Euoplocephalus* and *Edmontonia*) and all of its descendants, is exclusive and risks leading to the generation of new taxonomic names for stem-lineage thyreophorans when they have been discovered – or currently known taxa are re-positioned there following revision/updating.]

Total characters under ACCTRAN 17, DELTRAN 12 – (see Table-Appendix 3 for details).

1. Anterior supraorbital (palpebral) bound to the anterodorsal orbital margin
2. Postorbital (and posterodorsal orbit margin) obscured by osteoderm(s)
3. Mandibular condyles of the quadrate: medial condyle larger than the lateral
4. Median vomeropterygoid keel is deep (approaching or touching snout roof)
5. Dorsal margin of the dentary in occlusal view mildly bowed medially
6. Fourth trochanter positioned at mid-length on the femoral shaft
7. Transverse width of the distal femur greater than the depth of the medial condyle
8. Osteoderms form parasagittal rows either side of the dorsal midline
9. Osteoderms extend along the caudal series

Clade STEGOSAURIA

Total characters under ACCTRAN 23, DELTRAN 22

1. Quadrate head rectangular
2. Pterygoids partially fused along the midline
3. Maxillary and dentary crown surfaces bear long vertical ridges
4. Scapula blade stout and parallel-sided (homoplastic: also present in derived ankylosaurs)
5. Lateral profile of the ilium bowed dorsally (homoplastic: also present in derived ankylosaurs)
6. Postacetabular blade less than 30% of the length of the ilium (homoplastic: also present in derived ankylosaurs)
7. Supraacetabular crest projecting laterally and creating a partially laterally open cupola
8. Pubis, the femoral articular surface forms a laterally facing oval depression
9. Pubic shaft stout and bar-shaped
10. Femur tall, narrow and straight-shafted
11. Femoral anterior trochanter exhibits partial fusion with the greater trochanter (homoplastic in some nodosaurids)
12. Femoral fourth trochanter forms a raised ridge (homoplastic: present also in basal ankylosaurs and nodosaurids)
13. Cnemial crest of tibia robust and curved (homoplastic: present in derived ankylosaurs)
14. Fibula stout, but smaller than the tibia (homoplastic: present in derived ankylosaurs)
15. Pedal digit 1 lost
16. Parasagittal midline osteoderms form hypertrophied plates or spines
17. Lateral flank osteoderms are absent (except for parascapular spines). One row of lateral flank osteoderms has been reported in *Huayangosaurus* (Sereno & Dong, 1992: 340) but they reference an indistinct fieldwork photograph (Zhou, 1984:pl. 1) of a partial

articulated skeleton. I have been unable to identify these osteoderms, and none were mounted on the skeleton in plate 13.

18. Distal caudal osteoderms form tall, paired conical spines
19. Parascapular spine present (secondarily lost in stegosaurines)

Clade: Ankylosauromorpha

Stem-based definition: all taxa more closely related to *Euoplocephalus* and *Edmontonia* than to *Stegosaurus*.

Scutellosaurus

1. Cortical remodelling on the external surface of the skull partially developed
2. Jugal-quadratojugal exostotic ornamentation present
3. Humerus:femur length ratio greater than 80%
4. Orientation of the principal cross-sectional long-axis of the preacetabular process is horizontal (rather than vertical)
5. Osteoderms form multiple parasagittal rows on either side of the dorsal midline
6. Parasagittal osteoderms on the torso adjacent to the midline are low, and either ridged or roughly conical
7. Caudal osteoderms are oval based and generally low ridged

Emausaurus

1. Dorsal margin of the dentary is sinuous in lateral view
2. Proportions of metacarpal 1 'medium' (neither elongated nor squat)

Scelidosaurus

1. External antorbital fossa/fenestra is small
2. Skull has some additional (non-supraorbital) osteoderms
3. Partial cortical remodelling of the skull surface present and includes a small number of osteoderms
4. Postorbital has a medial wall that partitions the orbit from the adductor chamber

5. Prominent exostosis on the lateral surface of the mandible, but an overlying osteoderm may not be present (unless the holotype mandibles preserve remnants of a superficially placed osteoderm)

Clade ANKYLOSAURIA

Stem-based definition: all taxa more closely related to *Euoplocephalus* and *Edmontonia* than to *Scelidosaurus*.

Kunbarrasaurus and *Jinyunpelta*

1. Skull shape in occipital view, long-axis horizontal
2. Premaxilla edentulous (homoplastic: among Nodosauridae, Ankylosauridae and Stegosauria)
3. Premaxillary palate wider than long
4. Median marginal premaxillary notch present
5. Postorbital, posterodorsal orbit margin obscured by osteoderms
6. Predentary shape in occlusal view: extreme transverse extension to form a horizontal bar
7. Mandibular glenoid ventrally offset relative to the occlusal plane of the dentition
8. Long shallow symphyseal ramus of the mandible
9. Premaxillary tooth count reduced to zero (reversed in some nodosaurids)
10. Scapula blade shape: stout and parallel-sided (homoplastic: Stegosauria)
11. Acetabular medial wall forms an imperforate cupola
12. Femoral shaft shape in anterior view: stout and straight shaft
13. Femoral anterior trochanter: completely fused to the greater trochanter (reversed in *Kunbarrasaurus* and *Struthiosaurus*)
14. Fourth trochanter has the form of a raised ridge (rather than being pendent, or a depression in the femoral shaft) – homoplastic in Stegosauria
15. Cnemial crest of tibia is large and curved (homoplastic in Stegosauria)
16. Fibula smaller than tibia, but is a robust bone (homoplastic in Stegosauria)

Clade ANKYLOSAURIA [Traditional node]

Node-based definition: the common ancestor of *Euoplocephalus* and *Edmontonia* and all of its descendants. [This node has the potential to become the new taxon Euankylosauria but this additional clade name is neither essential nor particularly desirable.]

Total characters under ACCTRAN 16, DELTRAN 28) – additional to the previous listing.

1. External surface of the skull covered extensively by a 'carapace' formed by interconnected osteoderms in fully mature individuals.
2. Quadrate shaft anteroventrally inclined
3. Paroccipital processes oriented posteroventrolaterally
4. Discrete and large, ridged osteoderm present on the lateral surface of the mandible
5. Lateral profile of the dorsal surface of the ilium long and bowed dorsally
6. Preacetabular process of the ilium expanded distally
7. Shaft of the ischium rod or bar-shaped
8. Obturator foramen/process absent
9. Pubis fused to the ilium (and ischium)
10. Pubic shaft reduced to a small finger-shaped process (or entirely absent)
11. Pubic shaft considerably shorter than that of the ischial shaft
12. Pedal ungual phalanges broadly rounded, flattened (hoof-like)
13. Conical lateral flank osteoderms

Clade ANKYLOSAURIDAE (total characters under ACCTRAN 10, DELTRAN 14)

1. Maximum skull width equal to or greater than skull length
2. Presence of paranasal fossae on the premaxilla
3. Number of discrete antorbital osteoderms (caputegulae) greater than ten
4. Skull roof osteoderms (caputegulae) have the form of small mostly rounded plates
5. Lateral (infra) temporal fenestra occluded by osteoderms

6. Femoral head terminally positioned on the femoral shaft
7. Fourth trochanter of the femur is low-mound that surrounds a depressed muscle scar
8. Fourth trochanter positioned on the distal half of the femoral shaft
9. Distal tibia and proximal tarsals fused together
10. Terminal caudal osteoderms combine to form a bony club

Clade NODOSAURIDAE (total characters under ACCTRAN 11, DELTRAN 10)

1. Skull profile in lateral view arched or domed posterior to the orbit, creating the appearance of ventral flexure
2. Occipital condyle hemispherical and separated from the braincase by a constricted neck
3. Basisphenoid and pterygoids fused together
4. Quadrate head fused to the squamosal-paroccipital
5. Lateral (infra-) temporal fenestra reduced to a narrow slit
6. Maxillary and dentary crowns possess well-developed cinguli
7. Acromial process of the scapula twisted laterally
8. Ischial shaft with a pronounced bend at mid-length
9. Lateral cervicopectoral osteoderms develop into tall, conical-subconical plates or spikes

[A] SYSTEMATIC CLASSIFICATION

Indented hierarchy:

- DINOSAURIA Owen, 1842
  - ORNITHOSCELIDA Huxley, 1870b
    - ORNITHISCHIA Seeley, 1887[1888]
      - THYREOPHORA Nopcsa, 1915
        - ANKYLOSAUROMORPHA Carpenter, 2001

Genus and species: *Scelidosaurus harrisonii* Owen, 1861

[A] THE PHYLOGENETIC CONTEXT OF *SCELIDOSAURUS*

The topology of any palaeontological cladogram derived from a dataset is little more than a statistical artefact generated by a combination of the objective protocols deployed by the algorithm, and the subjective choice, definition and scoring of anatomical characters (Smith, 1994). The challenge for palaeontologists has always been to convert such constructs (hypotheses of relationship) into evolutionary trees that represent plausible sequences of anatomo-biological changes whose coherence implies phylogenetic meaning.

> *"There are three kinds of lies: lies, damned lies and statistics."*
> Benjamin Disraeli (1804-1881)

One test (using the term figuratively) that can be applied in order to establish whether the data contain a phylogenetic signal (beyond simplistic measures of statistical support for a particular topology), is to determine to what extent the succession of character acquisitions generated by the analytical regime are biologically plausible within the context of a transformational ancestor-descendant (evolutionary) series. The taxon narratives below incorporate many of the apomorphies from the lists generated by this analysis, with the addition of a few further observations taken from the complete apomorphy lists generated under both optimizations (Table-Appendix 3).

1. ***Thyreophora*** is recognized as a clade of herbivorous ornithischian dinosaurs that first appear in the Early Jurassic (Hettangian-Sinemurian). Their teeth are comparatively small, 'beech leaf shaped' and arranged *en echelon* in the dentition. Two of the most basal thyreophoran taxa known: *Scutellosaurus* (Colbert, 1981) and the stegosaur *Huayangosaurus* (Sereno & Dong, 1992) retain straight dentitions (as seen in the basal ornithischian *Lesothosaurus*). In contrast, more derived thyreophorans develop lingual bowing of their dentitions. The curvature of opposing dentitions creates structural guides that prevented fore-aft translation of the mandible during

(orthal) jaw closure; this system promoted oral food processing through a combination of orthal pulping and intermittent shearing. The mandibular symphysis was probably flexible, and permitted limited long-axis mandibular torsion (and wishboning) to occur during the chewing cycle. The mandibular joint is expanded transversely and represents a structural adaptation to limit or control mandibular torsion. A deep internasal partition in the snout (formed by the vomers and pterygoids) may be linked to the posterior extension, from the premaxillary hard palate, of a soft palate that separated the nasal and oral cavities; this latter feature would have allowed respiration while food was being processed in the mouth (and was probably the case for most, if not all, ornithischians).

The dermis in thyreophorans was imbued with the capacity to grow large osteoderms. This ability probably reflect either the retention (or re-expression) of the archosaur trait (or it could have evolved *de novo*). Osteoderm development was expressed in the skull through the evolution of a row of three supraorbital bones that arc around the dorsal orbital margin and create a prominent brow ridge. Postcranially, parasagittal osteoderm rows evolved.

The postcranial skeleton displays a general shift away from cursoriality (seen among all basal dinosaurs) and toward the adoption of a quadrupedal stance. Their limbs start to evolve the proportions (femur > tibia) and comparative robustness seen in graviportally-adapted animals; and their forelimbs develop a non-raptorial and more 'utilitarian' morphology that would have permitted weight support as well as grasping suggestive of a trend toward quadrupedality within this clade. Remnant features linked to an evidently bipedal-cursorial ancestry are shown in some of the earliest known thyreophorans. For example, *Scutellosaurus* shows features associated with bipedality and cursoriality in the construction of its hindlimb.

2. ***Stegosauria*** represent a distinct branch of thyreophorans currently recognized first in the Bathonian-Callovian. They evolved characteristics that differentiate them from all other (ankylosauromorph) thyreophorans. However, they adopt a broadly similar quadrupedal-graviportal body form and

consequently evolved a number of morphofunctional features in their girdle and limb construction that converge, to varying degrees, upon those seen in derived ankylosaurians.

Among thyreophorans, stegosaurs developed a distinctive morphology: long, narrow skull and low snout. This character suite was not used in the dataset because it is only clearly expressed in *Stegosaurus* (many reconstructions of stegosaur taxa tend to follow the cranial proportions of the eponymous taxon). It should be noted that the most basal stegosaur so far described (*Huayangosaurus*) exhibits a long, low snout (Sereno & Dong, 1992: fig. 1B) even though the skull reconstructions provided in this account do not really reflect this peculiarity. The quadrate head is rectangular rather than hemispherical/condylar, so the quadrate is fixed in position and stabilizes the mandibular joint; this may be an adaptation that is functionally linked to the long, slender snout (and mandible). The dentition is characterized by large numbers of small, laterally-flattened, low, broadly leaf-shaped crowns with apical abrasion facets. The sides of the crowns bear distinctive radiating patterns of ridges confluent with the apical cusps, and there are basal cinguli. Jaw mechanics in these animals is poorly understood. Richard Swann Lull (1910: 367) suggested that stegosaurs ate "food of a yielding character which did not require [del] forcible mastication".

Postcranially, the dorsal vertebral column is characterized by the dorsoventral 'stretching' of the neural arches and transverse expansion of the apices of the neural spines (Gilmore, 1914; Maidment *et al.,* 2006). In the shoulder girdle the scapula becomes stout and reinforced, eventually fusing along its suture with the coracoid. The humerus is stout and has a massive deltopectoral crest; these changes reflect the adoption of a quadrupedal gait. Modifications are also seen in the pelvis and hindlimb with the lengthening and vertical deepening of the preacetabular process and the flexure (dorsal bowing) of the ilium. The postacetabular iliac blade becomes abbreviated and this may be associated with increasing lateral tail flexibility. The acetabulum becomes more cupola-like and the pubis evolves a large, oval and laterally facing facet for articulation against the anteromedial surface of the femoral head. The femur is long, narrow and straight (particularly so when compared to the stout, but squat, morphology seen in derived ankylosaurians), whereas the tibia is short and very stout. Although the tibia is the dominant bone of the shin the fibula is still stout and dumbbell shaped rather than reduced to a narrow splint. The foot structure is essentially 'elephantine' with short, robust, oblique-to-vertically arranged metatarsals and short digits that terminate in bluntly truncated unguals (rather than the broadly rounded, more 'hoof-shaped' unguals that are seen in the generally similarly constructed feet of ankylosaurs). The loss of the 1st digit of the pes (Sereno, 1986) may be an apomorphy among derived stegosaurs, but the point at which this loss occurred within this lineage is uncertain.

In their early evolutionary history stegosaurs establish a very characteristic body form; this is most notable in the distribution of their torso and tail osteoderms, which form two paramedian rows of tall plates and/or spines that appear to have been anchored to the laterally expanded apices of adjacent neural spines. The restricted osteoderm distribution may be linked causally to the pronounced narrowing and deepening of the thoracic and abdominal region (see Fig. 22), which conforms structurally with the lengthening of the femur in the hindlimb. The distal end of the tail is 'armed' with pairs of tall, sharp spines and the ability to swing this defensive structure laterally may account for the restructuring of the postacetabular blade of the ilium and the dorsoventral expansion of proximal caudal ribs. The distal portion of the blade of the scapula is also commonly adorned with a sharply-pointed parascapular spine, although this feature appears to have been lost secondarily in stegosaurines (Raven & Maidment, 2017).

3. ***Ankylosauromorpha*** (=Ankylosauroidea [Norman, 1984b] – the latter taxonomic name was created for the exclusive clade (Scelidosauridae (Ankylosauridae + Nodosauridae)). In contrast to its sister-clade Stegosauria, Ankylosauromorpha is represented by a succession of stem taxa that accumulate anatomical characters in a near step-like manner as they 'evolve' toward Ankylosauria *sensu stricto*.

The skull becomes progressively strengthened externally through the evolution of exostoses that overgrow intracranial sutures (and anchored a keratinous carapace). In this analysis *Scutellosaurus* represents the earliest member of this branch. Unlike the stegosaur lineage, and more closely resembling derived ankylosauromorphs, *Scutellosaurus* has a shorter, more box-like skull (Breeden, 2016); and the skull surface is ornamented by exostotic growth, notably on portions of the preserved skull roof and jugal arch. However, the jaws and teeth (so far as they are currently known) suggest that the dentition was straight (rather than bowed) and the mandible was slender (e.g. Colbert, 1981: fig.10) and reminiscent of that seen in the basal ornithischian *Lesothosaurus* (Sereno, 1991).

Postcranially, the forelimb:hindlimb proportions indicate that the limbs are more comparable in length, suggestive of facultative quadrupedality (Colbert, 1981: 42-46) in spite of the presence of several anatomical features in the hindlimb (pendent fourth trochanter, femur shorter then tibia and a long slender pes) that are more often associated with cursoriality (Galton, 1971; Coombs, 1978c). The holotype of *Scutellosaurus* is preserved with a large number of low-ridged osteoderms that can best be restored as multiple parasagittal rows along its torso and tail (Colbert, 1981); this general pattern differentiates members of Ankylosauromorpha from Stegosauria.

4. ***Emausaurus***. Although this taxon is far from complete (Haubold, 1990), it includes a partial articulated skull that is box-shaped and exostotic (rather than being low, long snouted and unornamented). Its jaw profile, unlike the rectilinear morphology seen in *Scutellosaurus*, is sinuous as in all more derived ankylosauromorphans. The alteration in the morphology of the jaw is suggestive of modifications linked to the diet and jaw mechanics in these dinosaurs.

The remainder of the skeleton is poorly represented. The vertebrae show no evidence of the proportional changes in the height of the neural arches and spines that characterize stegosaurs. A few conical osteoderms are preserved but these give no indication of how extensively they were distributed across the torso. It is clear from the proportions of the preserved metacarpals that the forelimb is adapted for weight support rather than grasping and the ungual phalanges are conical and only slightly decurved. Equally, the few known proximal pedal phalanges are short and block-like, and have proportions very similar to those seen in the pes of *Scelidosaurus.* All these features are suggestive of graviportality and quadrupedality.

5. ***Scelidosaurus****.* Now that this taxon is known more completely, it can be seen to be undergoing consolidation of its cranial structure. The antorbital fossa/fenestra is much reduced compared to that of *Emausaurus*, reinforcing the snout. Exostoses are also far more widespread across the skull surface, and additional osteoderms are present posterior to the orbit. The mandible also shows the onset of the development of posterolateral dermal reinforcement reminiscent of that seen in more derived ankylosaurs.

Postcranially, the trunk is broad, rather than narrow and deep as seen in stegosaurs; its limb proportions indicate that this taxon was facultatively quadrupedal, judged by its limb proportions and the 'utilitarian' adaptations seen in the manus. Anomalously, the femur retains a pendent fourth trochanter similar to that seen in *Scutellosaurus* (and reminiscent of those seen in cursorially-adapted bipeds such as *Lesothosaurus*, *Hypsilophodon* and *Dryosaurus*) but positioned mid-shaft, rather than proximally as it is in these latter cursors. The femur is also a little longer than the tibia, indicative of a 'sub-cursorial' (less fleet-footed) locomotor mode. In this context, it is unfortunate that so little is known of the structure of the femur and hindlimb of *Emausaurus*. Nevertheless, it is considered likely that remnant features associated with a bipedal ornithischian ancestry persist among these ankylosauromorphs as they shifted (in an evolutionary sense) toward the obligate quadrupedality seen in more derived ankylosaurs.

The dermal skeleton is well developed with multiple parasagittal rows across the body of this taxon. In the cervical region there is a set of four partial bony collars (five, if the tricorn plates immediately behind the skull are included) comprising transverse bands of baseplates that anchor arrays of osteoderms; this arrangement is anatomically similar to the reduced number of osteoderm-bearing collars seen in nodosaurids and ankylosaurids.

6. Stem-based **Ankylosauria** (*Kunbarrasaurus* and *Jinyunpelta*). Insofar as their anatomy is currently known, these two taxa apparently demonstrate the

onset of a shift in the morphology of their skulls: becoming lower and broader and more consolidated (approaching the form seen in the more derived ankyosaurids and nodosaurids). These taxa also show a continuation of the development of an osteodermal covering (carapace) over the skull surface. The snout also develops a substantially broader beak (approaching, again, the condition seen in more derived ankylosaur taxa). There is loss of premaxillary teeth and their replacement by a more extensive keratinous beak/rhamphotheca, notably in *Jinyunpelta* (although the condition in *Kunbarrasaurus* is uncertain). The transition from dentulous to edentulous premaxillae occurs homoplastically among ankylosaurids, nodosaurids and stegosaurs. The mandible evolves a ventrally-offset glenoid to increase adductor muscle leverage and improve food-processing efficiency.

Postcranially, the breadth of the trunk region is shown in the articulated skeleton of *Kunbarrasaurus*. Some changes associated with graviportality include the development of an imperforate acetabulum and a femur that is straight, stout and its anterior trochanter becomes fused against the greater trochanter. The fourth trochanter is ridged (rather than pendent) and positioned midway down the femoral shaft. The tibia is robust and there is a shorter, but still stout, fibula.

Jinyunpelta. The presence of a tail club in *Jinyunpelta* (Zheng *et al.,* 2018) is of interest because this anatomical character has been regarded as a marker of taxa that are members of the Ankylosauridae (Coombs, 1978a). The systematic analysis undertaken by Zheng *et al.,* (2018: figs 9, 10) suggested that this taxon was an ankylosaurine; however, their analysis was based upon the dataset of Arbour & Currie (2016) with the addition of their new taxon and some additional nodosaurid taxa. The strict consensus of their MPTs demonstrates no resolution at all – perhaps not surprising because it repeats the original outcome. Selective manipulation of their MPTs allowed them to position *Jinyunpelta* as an ankylosaurine ankylosaurid. However, their adjusted topology contains a fundamental but unremarked inconsistency: *Hylaeosaurus*, a taxon universally accepted as a nodosaurid ankylosaur is shown as a basal member of Ankylosauridae.

7. Node-based **Ankylosauria** are recognised by the total consolidation of the skull through the evolution of a substantial cranial ‘carapace’ formed by either fused osteoderms or a combination of osteoderms and exostoses. The quadrate shaft is anteroventrally inclined and the paroccipital processes are posteroventrolaterally oriented. A discrete, large ridged osteoderm covers the external surface of the mandible (and there may be osteoderm plates that reinforced the fleshy cheek, lateral to the dentition).

Postcranially, the preacetabular process of the ilium is broadly expanded distally and the role of the pubis, which is considerably diminished in size (as, to some extent, is that of the ischium), are usurped by the expansion of the ilium. The acetabulum is completely imperforate and forms a cup-like enclosure for the femoral head. The limbs are stout and there is in general less extreme disparity between fore- and hindlimb length; this can range from approximate equality in *Hungarosaurus* to 75% in *Sauropelta* (in comparison to that seen particularly in more derived stegosaurs). The feet are short and convergently ‘elephantine’ in their general proportions (as seen homoplastically in stegosaurs) with splayed toes forming a semi-vertical cone (which would have been supported in life by a wedge-shaped fibrous heel-pad) and the toes are stubby; however, unlike stegosaurs their toes terminate in broad, rounded and flattened, genuinely hoof-shaped unguals.

8. **Ankylosauridae** have compact skulls that tend to be wider than long. Rostrally there are paranasal fossae on the premaxillae (and the latter remain free of dermal ossifications). The antorbital region of the skull is covered by a large number of relatively small (polygonal-to-subcircular) osteoderms (rather than the smaller number of large polygonal elements seen in nodosaurids). The lateral (infra-) temporal fenestra is occluded by osteoderms.

Postcranially, the femur is stout and has a terminally positioned femoral head. The fourth trochanter has the form of a low crater-like rim that surrounds a depressed muscle scar, and is also positioned on the distal half of the femoral shaft. The tibia is also stout and the proximal tarsal (astragalus) is little more than a thin warped plate that is fused to its distal articular surface. The osteoderms at the distal end of the tail are modified to create a bony club.

9. **Nodosauridae** have long skulls with a ventrally flexed, domed postorbital portion of the skull; this effect is augmented by an occipital condyle that projects posteroventrally from the occiput on a distinct neck. The anteroventral rotation of the braincase may also be linked to the fusion that occurs between the basisphenoid and posterior palate (pterygoids). The lateral (infra-) temporal fenestra is reduced to a narrow slit (visible posterolaterally), and the quadrate becomes fused to the squamosal/paroccipital process.

Postcranially, there is a highly distinctive prominent posterolaterally everted acromial process on the scapula. A mid-length bend in the shaft of the ischium is also characteristic of this clade.

The osteodermal skeleton is also distinctive because in most nodosaurid taxa, there is a 'protective' fringe of prominently spiked osteoderms formed by the most laterally positioned cervicopectoral and anterior flank osteoderms.

[D] Commentary. The anatomo-biological character changes that have been listed (and subsequently described in the narrative account) in the successional arrangement of taxa established by the topology of the new cladogram (Figs 39, 42) are largely consistent and biologically plausible. In marked contrast, the stratigraphic occurrences (particularly those of the basal ankylosauromorphs that are the primary focus of this article) are incongruent with the topology of the cladogram; they occur in the fossil record in the following chronological order: *Scelidosaurus* (Sinemurian) – *Scutellosaurus* (Pliensbachian) – *Emausaurus* (Toarcian). Stratigraphic incongruence is a common feature of cladograms and prompts debates concerning the veracity of morphological-only parsimony-based analyses, and the incompleteness of the (vertebrate) fossil record (e.g. Norell & Novacek, 1992; Norell, 1993; Zou & Zhang, 2016; Marshall, 2019).

Taken at face value, the present analysis implies that scutellosaurs existed (but are currently unrecorded) in the late Hettangian, and that emausaurs should similarly be present in the early-middle Sinemurian. These predictions provide a rationale for future exploration of Early Jurassic continental deposits. It should also be noted that the positioning of the tail-club-bearing *Jinyunpelta* may be anomalous, if it is a genuine ankylosaurid (Zheng *et al.,* 2018 – as implied by the branch re-positioning shown in Figure 41 and its minimal (one step) increase in tree length); this suggests either the need to identify more critical anatomical characters in new specimens attributable to this genus, or a requirement to supplement the current dataset with a greater range of ankylosaurian anatomical characters.

Despite these latter caveats the general coherence of the character changes implicit in the cladogram topology offers a measure of credence to the hypothesis that this analysis and its cladogram depicts a series of morphological stages by which the evolution of Thyreophora might be understood.

> "Nothing occurs contrary to Nature except the impossible, and that never occurs."
> Galileo Galilei (1564-1642)

However, this hypothesis of relationships will be supported, improved and/or modified with the discovery of more complete material of currently known taxa, the discovery and description of new taxa, or the generation of new (or revised) anatomical characters and their associated coding.

[A] CONCLUSIONS

Scelidosaurus harrisonii Owen, 1861 was a facultatively-quadrupedal, dermally-armoured ankylosauromorph ornithischian dinosaur from the Early Jurassic (Sinemurian) of England. It is currently the earliest known representative of the clade Thyreophora (Nopcsa, 1915).

The skull and lower jaw of *Scelidosaurus* were encased in a protective (and ornamental) layer of tough keratinous scutes. A curiously unornamented portion of the skull surface anterior to the eye, and immediately above the antorbital fossa, might reflect the existence of an inflatable(?) diverticulum of the cranial sinus system; this may have had some role in the behavioural repertoire of this animal. The sensory systems of this dinosaur are only indirectly understood. Some individual sclerotic ossicles are preserved but not as a complete ring, so the size of the orbit and the acuity of the eye are unknown. The ossified proximal portion of the stapes and adjacent braincase structure permits a tentative reconstruction of the external and middle ear. The structure and general anatomy of the neurocranium and its associated soft tissues (brain, cranial nerves and vasculature) have been described as far as possible. The epistyloid bones that project obliquely from either side of the posterior of the skull are interpreted as metaplastic ossifications of tendinous portions of the cucullaris muscle (a cranioclavicular subdivision of the trapezius musculature) that was involved in the control of neck flexure and head movement. Parts of the cranial musculature are described and the relationship among these muscles and the osteological evidence pertaining to jaw action in this animal are summarised. A limited capacity for oral food processing suggests that food was swallowed in a partially comminuted state. The abdominal cavity needed to be capacious to accommodate the gut and its associated caecae necessary to adequately digest and then absorb the nutrients from this fodder. The transverse width of the torso in this dinosaur revealed by the span of the ribcage and modifications to the pelvis means that the body profile is most similar to that seen in more derived ankylosauromorphs.

The epivomers may have been involved in the support of nasal turbinates. The respiratory system and its functionality in diapsids is reviewed and these findings are applied to *Scelidosaurus*. It is probable that this dinosaur used a combination of costal and abdominal aspiration. A previous analysis (Macaluso & Tschopp, 2018) attempted to identify the "evolutionary driver" of opisthopuby across Dinosauria and concluded that respiratory constraints were of primary importance, rather than those associated with herbivory. Reviewing this analysis has revealed that a number of factors have been either misrepresented or avoided and that such "drivers" of opisthopuby were considerably more complex than they suggest.

Locomotor musculature and the functionality of the locomotor system in *Scelidosaurus* indicate that this dinosaur was a facultative quadruped (having evolved comparatively recently – during the earliest Jurassic – from ancestors that were bipedal cursors). The locomotor capacity of *Scelidosaurus* is best described as 'average' (midway on the scale between the extremes represented by graviportal and cursorial). The hindlimb was constrained, by the girth of the abdomen, to undertake oblique-to-parasagittal excursions; this is reflected in the structure of the pelvis, the limb joints and structure of the toes of the feet. A curious ball-and-socket articular structure reported between the vertebrae at the base of the tail in one near-adult specimen (BRSMG LEGL 0004) may reflect a marked degree of controlled tail flexibility, which could be interpreted as a defensive adaptation (being able to powerfully swing the sharply-bladed osteoderm-bearing tail); whether this feature might also be linked to reproductive behaviour and the adoption of a specific mating position is inevitably more subjective.

The recently-published anatomy of *Scelidosaurus* permits a better-informed assessment of its systematic position. Following on from a critical review of several datasets published in recent years, aimed at resolving relationships between a wide range of known ornithischian taxa or more specifically within the ornithischian clade Thyreophora, a revised and updated dataset has been prepared. Analysis of this new dataset produces a strict consensus cladogram (well-supported statistically) that conforms in most respects with previous analyses. However, the topology of the cladogram indicates that *Scelidosaurus* as well as the closely related taxa *Emausaurus* and *Scutellosaurus*, occupy positions on the stem of the clade Ankylosauria, rather than as sister-taxa to the clade Thyreophora. There is a plausible case for removal of the taxonomic category Eurypoda (and perhaps Thyreophoroidea – contingent upon the emergence of an agreed position for *Scutellosaurus*) from the thyreophoran classificatory hierarchy.

Palaeontologically-derived cladograms are inherently less stable than those created using data from extant taxa. Fossil data are degraded by loss and absences, creating a profound epistomological gap: an incomplete range of morphological characters are available, and taxon representation is very far from complete. As a consequence fossil-based cladograms are labile and phylogenetic definitions based upon such topologies ought to be used parsimoniously (with a greater emphasis being placed on more inclusive stem-based definitions); this latter approach may be beneficial if it reduces clade name proliferation that otherwise generates a legacy of nomenclatural confusion.

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It has been a personal delight to be able to show Ron Croucher the proof pages of a succession of monographs on *Scelidosaurus* because they represent the materialisation of a substantial part of his working life spent as a preparator (and laboratory superintendent) at the Natural History Museum, London.

Yet again I must applaud the friendship, kindness (and critical acumen) of Kevin Padian (University of California, Berkeley) and David Weishampel (Johns Hopkins University) who were willing (and felt completely at liberty) to 'wield the intellectual knife' over a pre-submission version of this manuscript. I deeply appreciate the time and effort they expended in doing such dreadfully unrewarding work – friendship apparently knows no bounds! I am also indebted to the editors (particularly Nick Fraser, National Museums of Scotland, Edinburgh) and two non-anonymous reviewers: Attila Ösi (Hungarian Academy of Sciences) and Paul Penkalski (University of Wisconsin-Madison), working on behalf of the Linnean Society, for their time and effort spent reading and commenting critically (and informatively) upon the submitted manuscript. It is still the case that persistent errors and misinterpretations remain the responsibility (and fault) of the author.

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FIGURE LEGENDS

Figure 1. Charmouth is a coastal village located about one kilometre due east of Lyme Regis. The Spittles-Black Ven is an eroding cliff from which the remains of *Scelidosaurus* have been recovered since the late 1850s. Fresh slips and cliff falls continue to expose the remains of individual bones or in some cases articulated skeletons belonging to this dinosaur.

Figure 2. *Scelidosaurus harrisonii* Owen, 1861 (LYMPH 1998 6.1-6.7). The small ('foetal') specimen from Charmouth. Part of the paratype series belonging to the name *S. harrisonii*. These specimens belong to a small individual and appear to be associated. They were illustrated in Richard Owen's first monograph (Owen 1861: tab. III).

Figure 3. *Scelidosaurus harrisonii* Owen, 1861 (The lectotype – NHMUK R1111). The encased skeleton restored as it might have appeared when first discovered, exposed on a series of more or less contiguous blocks of areno-argillaceous limestone (marlstone). The majority of the neck and both forelimbs may have been present originally but were not recovered by the quarrymen who excavated the skeleton.

Figure 4. *Scelidosaurus harrisonii* Owen, 1861. Cranial anatomy reconstructed in A, lateral and B, dorsal views (modified from Norman, 2020a: figs 8, 9).

Figure 5. *Chelonia mydas* (Linnaeus, 1758) – the Green Turtle. External skull anatomy. A, lateral and B, dorsal view, illustrating the superficial cranial osteology. C, lateral and D, dorsal views showing the distribution of keratinous scutes. Norman, pers. colln (ex-University of Cambridge Zoology Department teaching collection). Scale bar indicated.

Abbreviations: au – auditory recess, au.sc – auditory recess scute covering, tom – the chelonian tomium (= rhamphotheca of *Scelidosaurus*).

Figure 6. *Scelidosaurus*. An interpretation of the cranial keratinous scute pattern on the skull and mandible in A - lateral and B - dorsal views.

Abbreviations: asc – angular scute, fsc – frontal scute, dsc – dentary scute or sheath, hsc – occipital horn scute, itsc – infratemporal scutes, jsc – jugal arch scutes, lsc – lacrimal scute, msc – maxillary scute (there may have been several), nmsc – nasal median scute, nsc - nasal scutes restored as overlapping plates, pdsc – predentary scute (rhamphotheca), posc – postorbital crater-like scute, qjsc – quadratojugal-quadrate scute, rsc – rhamphothecal scute of the premaxilla, sosc – supraorbital (brow-ridge) scute (there may have been several), stsc – supratemporal scutes, tym – tympanic membrane, ? – area on the surface of the lacrimal lamina that is devoid of exostoses and may mark the location of a diverticulum of a cranial sinus.

Figure 7. *Ovis aries* Linnaeus, 1758. A. lateral view of cranial osteology showing the horn core. B. The horn core with its keratinous horn superimposed, showing the lack of correspondence in shape between the horn core and its overlying keratinous casque (horn). Norman, pers. colln (Rough Fell sheep, Sedbergh, Cumbria).

Abbreviations: hc – horn core, kh – keratinous horn. Scale bar indicated.

Figure 8. *Scelidosaurus harrisonii* Owen, 1861. The lectotype NHMUK R1111. A. Jugal showing sclerotic plate. B, Stapes.

Abbreviations: do – dermal ossification, ec.s – ectopterygoid suture, est – surface for the extrastapes, ftp – footplate, ls – lacrimal suture, pal.s – palatine suture, Po – postorbital, Qj – quadratojugal, sc.os – sclerotic ossicle. Scale bar indicated.

Figure 9. *Scelidosaurus*. Attempted reconstruction of the posterodorsal region of the skull showing the general disposition of the stapes-extrastapes, middle ear cavity and tympanum,.

Abbreviations: bo – basioccipital condyle, cnVII – foramen for cranial nerve VII, est – extrastapes (reconstructed), pap – paroccipital process, Pro – proötic, Q – quadrate, Qj – quadratojugal, rw – round window (fenestra rotunda), Sq – squamosal, st – stapes, tym – tympanic annulus and membrane (reconstructed). Shaded area: reconstruction of the middle ear cavity and a ventral branch leading to the throat (eustachian tube).

Figure 10. *Scelidosaurus*. Diagrammatic longitudinal section through the skull showing an attempted reconstruction of the nasal passage. The latter is shown floored anteriorly by a connective tissue sheet that forms a soft secondary palate that spans the gap between opposing maxillae and was probably attached sagittally to the ventral margin of the vomers. The epivomers are interpreted as sheet-like ossifications that form within the connective tissue that roofs the nasal passage; these bones are sutured to the dorsal edges of the vomers (Norman, 2020a).

Abbreviations: Epi – epivomers, Mx – maxilla, np – nasal passage, ol.b – olfactory bulb, Pt – pterygoid, sp – soft palate. Arrows indicate air flow. Dark tone – bones in section. Pale tone approximate shape of the nasal passage.

Figure 11. *Scelidosaurus harrisonii* Owen, 1861. The lectotype (NHMUK R1111). What remains of the formerly fully articulated skull: the skull roof, neurocranium, part of the right suspensorium and cheek, as preserved (sketched in 2018).

Abbreviations: bo – basioccipital condyle, bot – basioccipital tuberosity, bpt – basipterygoid process (right), J – jugal, La – lacrimal, Ls – laterosphenoid (left), Mx – maxilla (right), N – nasal bones, pap – paroccipital process (left), Q – quadrate (right).

Figure 12. *Scelidosaurus*. Diagrammatic lateral view of the neurocranium, showing the identifiable cranial nerve foramina and fossae.

Abbreviations: Bo – basioccipital, bot – basioccipital tuberosity, bpt – basipterygoid process, Bs – basisphenoid, cart – cartilage, cn.[Roman] –

cranial nerves, fo – fenestra ovalis, fr – fenestra rotunda, Ls – laterosphenoid, Op – opisthotic, Os – orbitosphenoid, P – parietal, Pro – proötic, Ps – parasphenoid (cultriform process), vag-jug – foramen occupied by cranial nerves (vagus) and venous blood vessels (jugular vein), vcd – fissure for passage of the vena capitis dorsalis, vid – vidian [=carotid artery] canal.

Figure 13. Partially transparent neurocranium to show the approximate structure of the brain, the principal cranial nerves and blood vessels.

Abbreviations: c.art – carotid artery, Cbl – cerebellum, Ce – cerebral lobes, cn. [roman] – cranial nerve, jug.v – jugular vein, med – medulla (brain stem), p – pituitary body. Dotted outline – approximate profile of the endocranial cavity.

Figure 14. *Varanus exanthematicus* (Bosc, 1792). Mapping the areas of origin and insertion of the principal jaw closing muscles in a living sauropsid. A, lateral. B, oblique dorsolateral. C. lower jaw in oblique dorsolateral aspect (redrawn from Holliday, 2009: fig. 1).

Abbreviations: MAMEM – m. adductor mandibulae externus medialis. MAMEP – profundus, MAMES – superficialis, MAMP – posterior, MLPt – levator pterygoideus, MPPt – protractor pterygoideus, MPST – pseudotemporalis, MPT – pterygoideus.

Figure 15. *Scelidosaurus.* The principal jaw adductor muscles identified. A, dorsal muscle origin map. B-D, muscle reconstructions.

Abbreviations: AN.OR – m. anguli oris, bod – bodenaponeurosis, MAMEM – m. adductor mandibulae externus medialis, MAMEP – profundus, MAMES – superficialis, MAMP – posterior, MLPt – levator pterygoideus, MPST – pseudotemporalis, MPT – pterygoideus.

Figure 16. *Scelidosaurus*. The matching of the curvature of opposing dentitions. A. Right mandible in dorsal view (NHMUK R1111). B.

Reconstruction of the left half of the skull in ventral view (after Norman, 2020a: fig. 10).

Figure 17. *Scelidosaurus*. Occlusal views of maxillary and dentary dentitions. A, separated dentitions. B, alignment of dentitions during occlusion – the bowing of each dentition match to permit orthal pulping or intermittent tooth-tooth occlusion. C, malocclusion modelled by the propalinal displacement of the dentary, creating a zone where the dentitions cross over (starred). D, two modes of jaw closure: Di, represents the non-occlusal orthal pulping of vegetation; Dii shows high-angle occlusion between opposing crowns that creates shear to cut vegetable fibres and generates steep wear facets on adjacent crown surfaces. Both modes of occlusion occur at intervals along the dentitions.

Abbreviations: Dent – dentary dentition, Max – maxillary dentition, Malocc – malocclusion created by propalinal displacement of the dentary, Occ – normal occlusal relationship of the dentitions. Arrows indicate direction of movement. Starred symbol indicates region where dentitions cross, creating the potential for damage to the teeth caught in opposition.

Figure 18. *Scelidosaurus*. Skull diagrammatics. A, pivot point between the squamosal and quadrate head viewed laterally, joint (q-sq.j) highlighted in black. B. Posterior view of the quadrate pivoting transversely (small arrows) against the squamosal. The structure of mandibular joint shows that the quadrate is cupped by the articular-surangular articular surfaces. C. The principal lines of action of the jaw closing muscles in cross-sectional view to show imposed medial torsion exerted by the adductor mandibulae (AM) complex, as well as the counter-torsion effected by the sling-like *m. pterygoideus* complex (MPT).

Abbreviations: AM – *mm. adductor mandibulae* (overall direction of force), An – angular bone, Ar – articular bone, MPT – *m. pterygoideus* (overall direction of force), q-sq.j – articular joint between the head of the quadrate and the squamosal cotylus, Sa – surangular bone, Sp – splenial bone.

Figure 19. *Scelidosaurus*. A. Epistyloids as preserved in the large articulated referred skeleton (BRSMG LEGL 0004 – after Norman, 2020a). B. An isolated epistyloid as preserved in lateral view in the considerably smaller referred individual (CAMSM X39256). Scale bars in centimetres.

Abbreviations: at – atlas, at.r – atlas rib, ba – baseplate, ep (l,r) – epistyloids, ost – osteoderm, pap – paroccipital process, Q – quadrate. Scale bars in cms. Pale tone – sediment.

Figure 20. *Scelidosaurus*. A reconstruction of the head-neck and shoulder girdle based on Norman (2020a,b). Highlighting the *m. cucullaris* (= *m. sternocleidomastoideus*) muscle that has been hypothesized to be associated with the presence of epistyloid bones.

Abbreviations: Cor – coracoid, Sca – scapula.

Figure 21. *Scelidosaurus* (BRSMG LEGL 0004). The left side of the facial region showing a discrete patch of smooth bone just dorsal to the antorbital fossa (also smooth surfaced). All the surrounding bone surfaces are roughened by exostoses. After Norman (2020a: fig. 14).

Abbreviation: aof – antorbital fossa.

Figure 22. Cartoons approximating pelvic region cross-sectional body profiles of A, an ankylosaur and B, a stegosaur.

Figure 23. A theoretical model of pelvic aspiration in ornithopod ornithischians (based on a hadrosaur pelvis). A, B. Dorsal views of the pelvic region showing the transverse motion suggested for the pubes that serially compressed and decompressed the abdominal cavity. Note: the ischia should meet distally on the midline, rather than remaining separate as shown here. C. Lateral view of the pelvis showing a reconstruction of a hypothetical pubic abductor muscle. After Carrier & Farmer (2000a: fig. 10B).

Abbreviations: Exp – expiration (pubes adducted), Insp – inspiration (pubes abducted), il – ilium, ipm – (hypothetical) iliopubic muscle, is – ischium, pu – pubis.

Figure 24. A simplified phylogeny of dinosaurs (after Baron *et al*., 2017b). Note that gastralia are lost independently in sauropods and ornithischians but retained in all other clades (being also lost independently in the derived, powered flight-capable, Theropoda [=birds]).

Figure 25. Ornithischian skeletal forms. A. *Eocursor*. B. *Edmontonia*. C. *Stegosaurus*. No gastralia are present in these or any other known ornithischians.

Images kindly provided by Scott Hartman who retains the copyright of each. Scale bars in centimetres.

Figure 26. Sauropodomorph skeletal forms. A. *Plateosaurus* (a prosauropod). B. *Nigersaurus* (a sauropod). Gastralia are present in the prosauropod, but no sauropods possess gastralia.

Images kindly provided by Scott Hartman who retains the copyright of each. Scale bars in centimetres.

Figure 27. Theropod skeletal forms. A. *Herrerasaurus* (a dinosauriform, stem-dinosaur or a basal theropod – according to various analyses). B. *Allosaurus* a tetanuran theropod – see Figure 28). C. *Ornithomimus* a coelurosaur. D. *Nothronychus*, a coelurosaur. E. *Oviraptor*, a maniraptoran. F. *Deinonychus*, a paravian. *Herrerasaurus* and all other theropods possess gastralia.

Images kindly provided by Scott Hartman who retains the copyright of each. Scale bars in centimetres.

Figure 28. Simplified theropod phylogeny. All tetanuran theropods have gastralia; these are only lost in true birds (n.gast). The orientation of the pubis varies across these clades and is dependent upon multiple factors:

dietary preference (herbivory, omnivory, carnivory); body proportions (notably the reduction in length and mass of the tail); and more specific locomotor adaptations and habits of individual theropods within each subclade. There is no simple and unambiguous correspondence between pelvic structure and posture, habit, locomotor style, or putative diet and respiratory mechanics.

Dinosaur images kindly provided by Scott Hartman, who retains the copyright of each. The raptor silhouette was made available through the following website: http://clipart-library.com/bird-silhouette.html

Figure 29. *Scelidosaurus*. Myological mapping. Scapula and Coracoid, based on the lectotype NHMUK R1111 (A, lateral. B, medial). Humerus, based on the referred specimen BRSMG LEGL 0005 (C, posterior. D, anterior). After Norman (2020b: figs 56, 58, 63).

Abbreviations: bi – *m. biceps*, cuc – *m. cucullaris*, br – *m. brachialis*, dc – clavicular deltoid, ds, scapular deltoid, ld-tm – *mm. latissimus dorsi-teres major*, p – *m. pectoralis*, sbs – *m. subscapularis*, sh – *m. scapulohumeralis*, sc – *m. supracoracoideus*, scc – *m. subcoracoideus*, tra-ls – *mm. trapezius-levator scapulae*. Scale bars in centimetres.

Figure 30. *Scelidosaurus*. Pectoral girdle and forelimb elements associated with the posterior skull and neck (after Norman, 2020b), showing the distribution of some of the principal girdle and forelimb muscles and providing an indication of their lines of action.

Abbreviations: bi – *m. biceps*, br – *m. brachialis*, cuc – *m. cucullaris* (derived as a slip of the trapezius muscle – often referred to as the sternocleidomastoid muscle), dc – clavicular deltoid, ds – scapular deltoid, p – *m. pectoralis*, sc – *m. supracoracoideus*, tm – *m. teres major*, tra-ls – *mm. trapezius-levator scapulae*, tri – *m. triceps*.

Figure 31. Pelvic reconstructions in left lateral view. A. *Scelidosaurus* (after Norman 2020b: fig. 77). B. *Euoplocephalus* (after Coombs 1978a). C. *Stegosaurus* (after Gilmore 1914).

Figure 32. *Scelidosaurus*. Femoral muscle maps. Includes small and large femora to show the change of curvature of shaft that occurs during ontogeny. A. 'Juvenile' (NHMUK R6704 – after Norman, 2020b: fig. 79). B-D. 'Adult' (NHMUK R1111 – the lectotype, after Norman, 2020b: fig. 78) in medial (B), anterior (C) and lateral (D).

Abbreviations: add – adductor, cfb – *m. caudifemoralis brevis*, cfl – *m. caudifemoralis longus*, ft – *m. femorotibialis*, if – *m. iliofemoralis*, if? – possible area for attachment of a slip of the *m. iliofemoralis*; itr-pife? – area available for insertion of the *m. iliotrochantericus* (*m. iliofemoralis*) and perhaps the *m. puboischiofemoralis externus* (site of origin uncertain), ist – *m. ischiotrochantericus*, pifi – *m. puboischiofemoralis internus*.

Figure 33. *Scelidosaurus*. Myology of the principal pelvis and hindlimb reconstructed as lines of action.

Abbreviations: add – adductor, amb – *m. ambiens*, cfb – *m. caudifemoralis brevis*, cfl – *m. caudifemoralis longus*, ft – *m. femorotibialis*, fte – *m. flexor tibialis externus*, if – *m. iliofemoralis*, ifib – *m. iliofibularis*, ist – *m. ischiotrochantericus*, it – *m. iliotibialis*, itr – *m. iliotrochantericus* (avian-equivalent subdivision of the iliofemoralis), pifi – *m. puboischiofemoralis internus*.

Figure 34. *Scelidosaurus* cf. *harrisonii*. Femur (NHMUK OR41322) crushed proximally, but showing a well-developed 4th trochanter that is secondarily thickened by the addition of a layer of metaplastic bone over its surface. The metaplastic bone derives from calcification of the caudifemoral tendons where they attach to the trochanter.

Abbreviations: 4tr – fourth trochanter, fc – fibular condyle, mpb – metaplastic bone, tc – tibial condyle. Scale bar in centimetres.

Figure 35. *Scelidosaurus*. Femur and hindlimb motion examined. The principal lines of action of retractor muscles and their influence upon the femur and hindlimb poses have been reconstructed as a series of cartoons. A. Dorsal view of the femur in 'neutral' pose with lines of action of main muscles: note in particular the lateral or medial attachment of these muscles on the femoral shaft. B. Vertical pose of the femur with an indication of the posteromedial lines of action of the powerful limb retractors (*m. caudifemoralis* – cfb/l, and *m. adductor* – add). C. Cross-section through the femoral shaft at the level of the fourth trochanter showing the torsion inducing lines of action of the principal protractors (pifi, ist) and retractors (if, cfb, cfl). D. Mechanical influence on hindlimb protraction resulting from the breadth of the gut. E. Oblique-to-parasagittal hindlimb excursion during the protraction-retraction cycle.

Figure 36. Early (non-numerical) cladistics-based attempt to establish a topology for armoured dinosaurs within the clade Ornithischia. The topology was created by Norman (1984b: fig. 2).

Figure 37. Early (non-numerical) cladistics-based attempt to establish a topology for armoured dinosaurs within the clade Ornithischia. This topology is derived from Sereno (1984: fig. 1).

Figure 38. Early (non-numerical) cladistics-based attempt to establish a topology for armoured (thyreophoran) dinosaurs within the clade Ornithischia. This topology is derived from Sereno (1986: fig. 3).

Figure 39. Strict Consensus Tree based on the 10 equally most parsimonious trees (MPTs) generated by the new analysis. The lack of resolution lies in the topographic ambiguity of *Kunbarrasaurus*, *Jinyunpelta* and that of the four nodosaurid taxa. Overall, the topology supports many aspects of previously published cladograms. However, and controversially, *Scutellosaurus*, *Emausaurus* and *Scelidosaurus* are positioned as successive out-groups on the branch leading to Ankylosauria. Convention places these taxa on the branch leading to Thyreophora. *Kunbarrasaurus* may well prove to be a stem

ankylosaur once it has been fully described; furthermore, *Jinyunpelta* is positioned as a basal ankylosaurian. However, Zheng *et al*., (2018) propose that it is an ankylosaurine ankylosaur (despite the lack of resolution in their strict consensus tree) – see also Figure 41.

Numerical Decay Indices (Bremer support) for the individual clades are indicated in italics adjacent to the relevant branches.

Figure 40. A bootstrap analysis (Heuristic) of the dataset using 10,000 replicates. Bootstrap support percentages are indicated on individual branches.

Figure 41. Cladogram manipulation using MacClade. In this example *Scutellosaurus** has been positioned as the proximate sister taxon to the clade Thyreophora. Tree length is calculated to be 229 steps, which is three steps longer than the most parsimonious trees obtained by the analysis of this dataset. The re-positioning of *Scutellosaurus*, if it could be supported by additional data, might justify a redefinition of the taxon Thyreophoroidea, as indicated on this branch. Note: an additional adjustment, which involves a single step increase (230 steps) positions *Jinyunpelta* (albeit tentatively = ?) as a basal ankylosaurid on the basis of its possession of a tail club (in conformity with Coombs, 1978a).

Figure 42. Taxon deletion tree. *Kunbarrasaurus* and *Jinyunpelta* have been deleted. Tree length (of the 6 MPTs) is 212 steps, 14 steps fewer than found in the MPTs of the original dataset (Fig. 39). The principal clades: THYREOPHORA, STEGOSAURIA, ANKYLOSAURIA, Nodosauridae and Ankylosauridae conform topographically with those established by previous analyses. However, the ankylosauromorph branch and its composition, if confirmed in subsequent analyses, implies that the way Sereno (1986, *et seq*.) envisioned Eurypoda and Thyreophoroidea are meaningless.

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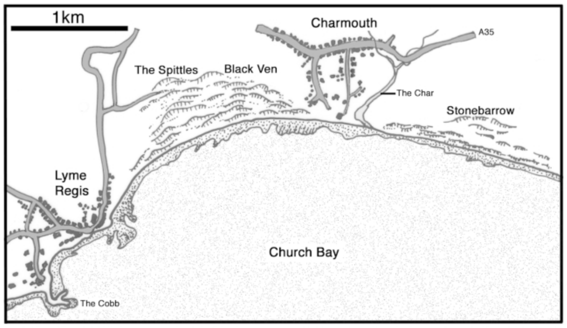

Fig. 1. 2 COLUMN WIDTH

Figure 1. Charmouth is a village about 1 km due east of Lyme Regis. Black Ven is an eroding cliff from which the remains of Scelidosaurus have been recovered since the late 1850s. Fresh slips and cliff falls continue to expose the remains of individual bones or in some cases articulated skeletons belonging to this dinosaur taxon.

209x297mm (300 x 300 DPI)

FIGURE 2 - ONE COLUMN WIDTH

Figure 2. Scelidosaurus harrisonii Owen, 1861 (LYMPH 1998 6.1-6.7). The small ('foetal') specimen from Charmouth. Part of the paratype series belonging to the name S. harrisonii. These specimens belong to a small individual and appear to be associated. They were illustrated in Richard Owen's first monograph (Owen 1861: tab. III).

209x297mm (300 x 300 DPI)

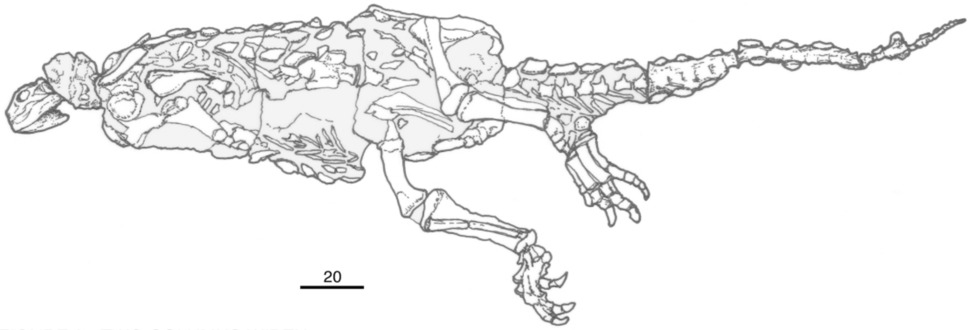

FIGURE 3 - TWO COLUMNS WIDTH

Figure 3. Scelidosaurus harrisonii Owen, 1861 (The lectotype – NHMUK R1111). The skeleton restored as it might have appeared when first discovered, exposed on a series of more or less contiguous blocks of argillaceous limestone (marlstone). Most of the neck and both forelimbs were not recovered.

265x100mm (300 x 300 DPI)

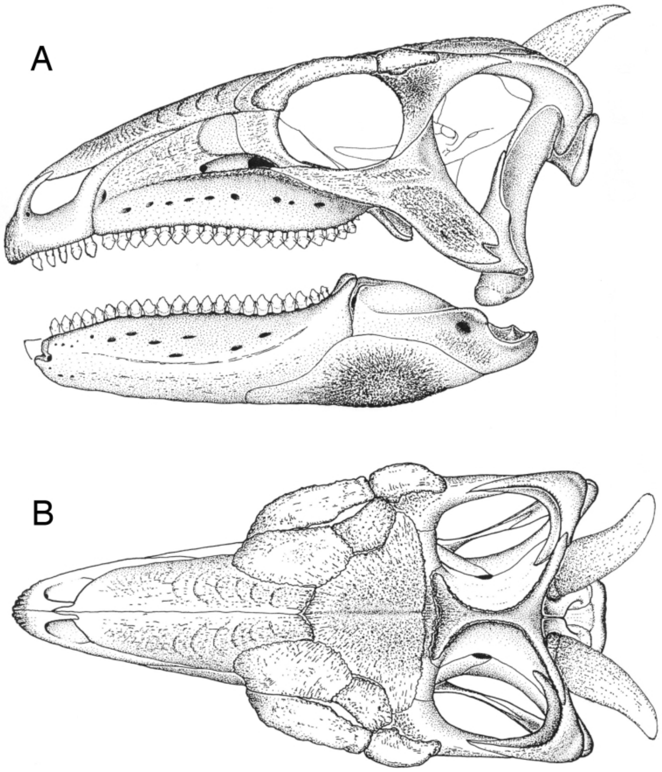

FIGURE 4 - TWO COLUMNS WIDTH

Figure 4. Scelidosaurus harrisonii Owen, 1861. Cranial anatomy reconstructed in A, lateral and B, dorsal views (modified from Norman, 2019a: figs 8, 9).

209x296mm (300 x 300 DPI)

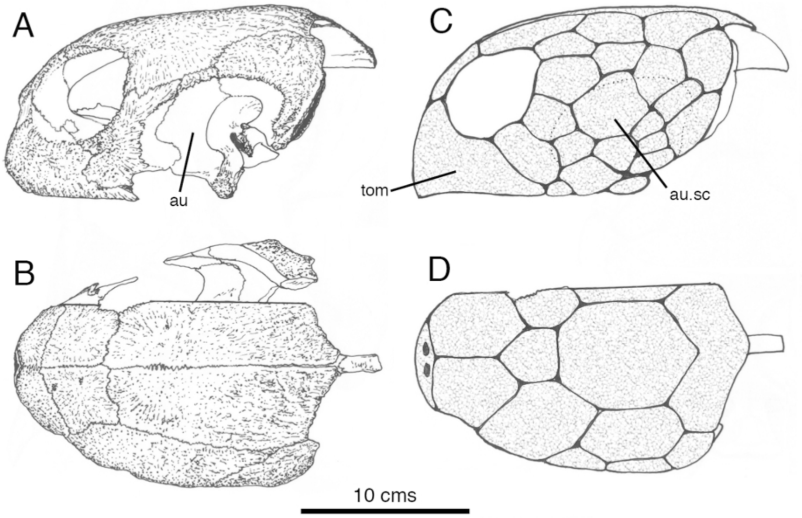

FIGURE 5 - TWO COLUMNS WIDTH

Figure 5. Chelonia mydas (Linnaeus, 1758) – the Green Turtle. External skull anatomy. A, lateral and B, dorsal view, illustrating the superficial cranial osteology. C, lateral and D, dorsal views showing the distribution of keratinous scutes. DBN personal collection (ex-University of Cambridge Zoology Department teaching collection). Scale bar indicated.

Abbreviations: au – auditory recess, au.sc – auditory recess scute covering, tom – the chelonian tomium (= rhamphotheca of Scelidosaurus).

209x297mm (300 x 300 DPI)

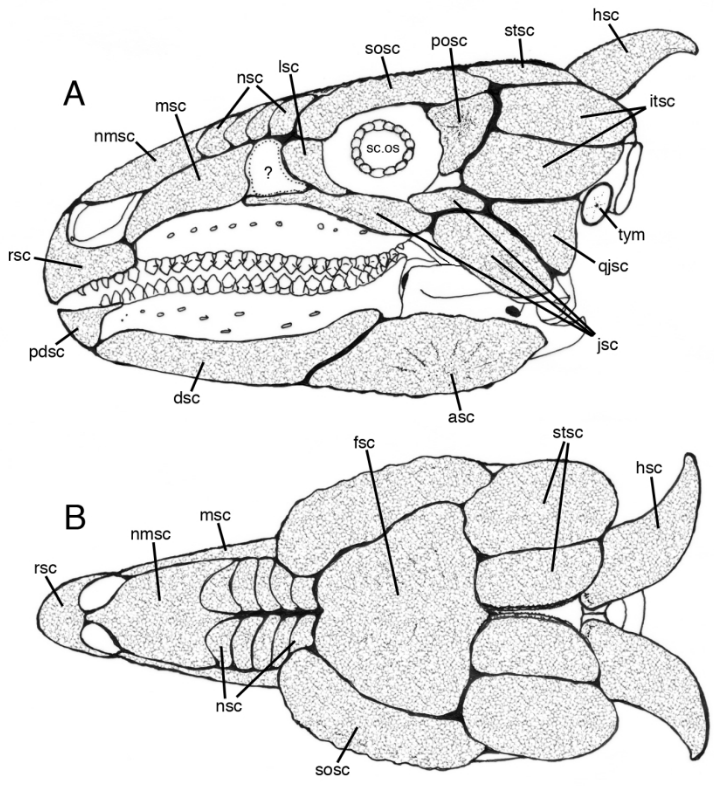

FIGURE 6 - TWO COLUMNS WIDTH?

Figure 6. Scelidosaurus. Interpretative scute pattern on skull and lower jaw in A - lateral and B - dorsal view.

Abbreviations: asc – angular scute, fsc – frontal scute, dsc – dentary scute or sheath, hsc – occipital horn scute, itsc – infratemporal scutes, jsc – jugal arch scutes, lsc – lacrimal scute, msc – maxillary scute, nmsc – nasal median scute, nsc - nasal scutes restored as overlapping plates, pdsc – predentary scute (rhamphotheca), posc – postorbital crater-like scute, qjsc – quadratojugal-quadrate scute, rsc – rhamphothecal scute of the premaxilla, sosc – supraorbital (brow-ridge) scute(s), stsc – supratemporal scutes, tym – tympanic membrane, ? – area on the lacrimal lamina devoid of exostoses.

209x296mm (200 x 200 DPI)

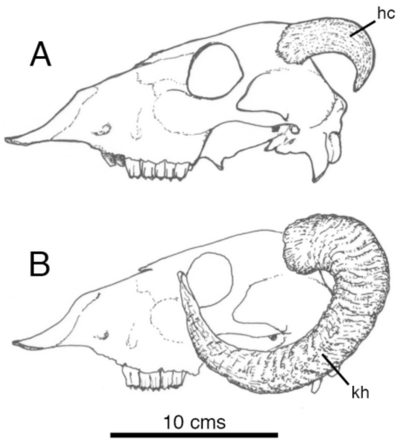

FIGURE 7 - SINGLE COLUMN WIDTH

Figure 7. Ovis aries Linnaeus, 1758. A. lateral view of cranial osteology showing horn core. B. Horn core with superimposed keratinous horn showing the lack of correspondence in shape between the horn core and its overlying keratinous casque (horn). DBN personal collection (Rough Fell sheep, Sedbergh, Cumbria).

Abbreviations: hc – horn core, kh – keratinous horn. Scale bar indicated.

209x297mm (200 x 200 DPI)

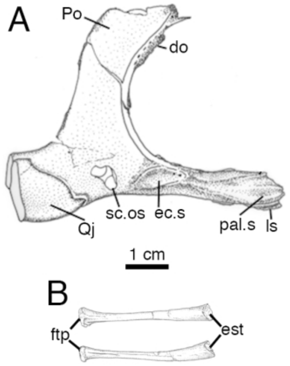

FIGURE 8 - ONE COLUMN WIDTH

Figure 8. Scelidosaurus harrisonii Owen, 1861. The lectotype NHMUK R1111. A. Jugal showing sclerotic plate. B, Stapes.

Abbreviations: do – dermal ossification, ec.s – ectopterygoid suture, est – surface for the extrastapes, ftp – footplate, ls – lacrimal suture, pal.s – palatine suture, Po – postorbital, Qj – quadratojugal, sc.os – sclerotic ossicle. Scale bar indicated.

209x297mm (200 x 200 DPI)

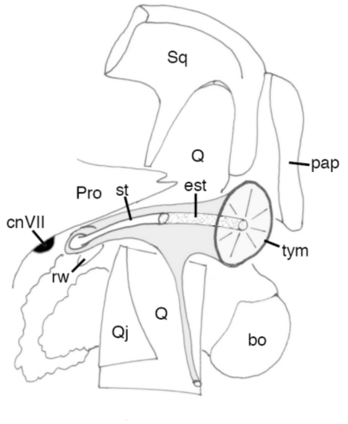

FIGURE 9 - SINGLE COLUMN WIDTH

Figure 9. Scelidosaurus. Reconstruction of the posterodorsal region of the skull showing the location of the tympanum, stapes-extrastapes and middle ear cavity.

Abbreviations: bo – basioccipital condyle, cnVII – foramen for cranial nerve VII, est – extrastapes (reconstructed), pap – paroccipital process, Pro – proötic, Q – quadrate, Qj – quadratojugal, rw – round window (fenestra rotunda), Sq – squamosal, st – stapes, tym – tympanic annulus and membrane (reconstructed). Shaded area: reconstruction of the middle ear cavity and a ventral branch leading to the throat (eustachian tube).

209x297mm (200 x 200 DPI)

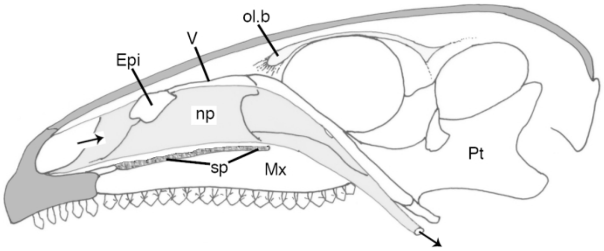

FIGURE 10 - SINGLE COLUMN WIDTH

Figure 10. Scelidosaurus. Diagrammatic longitudinal section through the skull to show the approximate position of the nasal passage and presence of the soft palate spanning the maxillae and ventral edge of the vomers.

Abbreviations: Epi – epivomers, Mx – maxilla, np – nasal passage, ol.b – olfactory bulb, Pt – pterygoid, sp – soft palate. Arrows indicate air flow. Dark tone – bones in section. Pale tone approximate shape of the nasal passage.

209x297mm (200 x 200 DPI)

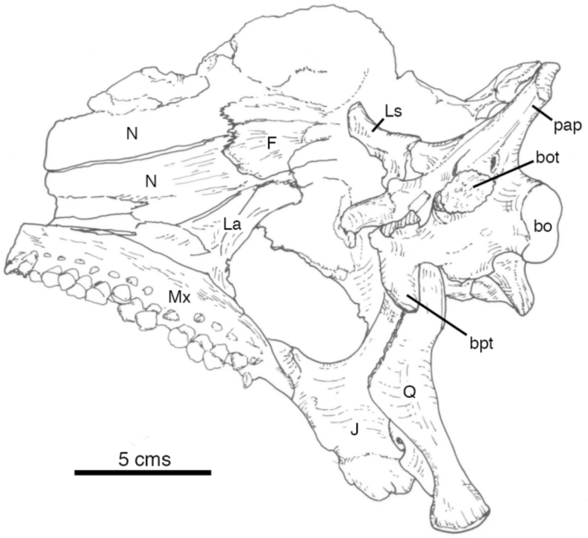

FIGURE 11 - DOUBLE COLUMN WIDTH

Figure 11. Scelidosaurus harrisonii Owen, 1861. The lectotype (NHMUK R1111). The skull roof, neurocranium, part of the right suspensorium and cheek, as currently preserved (sketched in 2018).

Abbreviations: bo – basioccipital condyle, bot – basioccipital tuberosity, bpt – basipterygoid process (right), J – jugal, La – lacrimal, Ls – laterosphenoid (left), Mx – maxilla (right), N – nasal bones, pap – paroccipital process (left), Q – quadrate (right).

209x297mm (200 x 200 DPI)

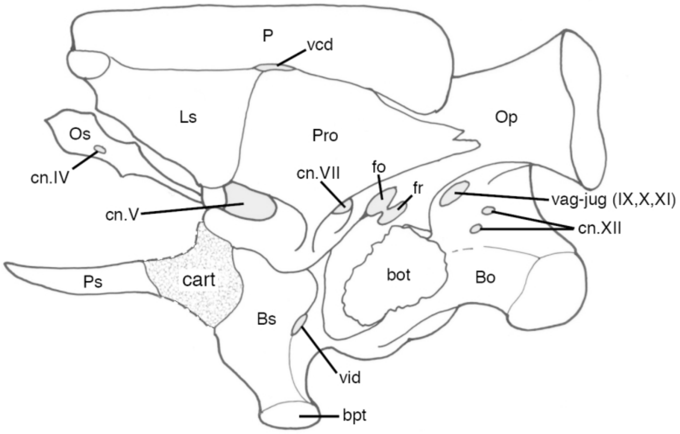

FIGURE 12 - DOUBLE COLUMN WIDTH

Figure 12. Scelidosaurus. Lateral view of the restored neurocranium, showing the identifiable cranial nerve foramina and fossae.

Abbreviations: Bo – basioccipital, bot – basioccipital tuberosity, bpt – basipterygoid process, Bs – basisphenoid, cart – cartilage, cn.[Roman] – cranial nerves, fo – fenestra ovalis, fr – fenestra rotunda, Ls – laterosphenoid, Op – opisthotic, Os – orbitosphenoid, P – parietal, Pro – proötic, Ps – parasphenoid (cultriform process), vag-jug – shared foramen occupied by cranial nerves and venous blood vessels, vcd – fissure for the vena capitis dorsalis, vid –vidian [=carotid] canal.

209x297mm (200 x 200 DPI)

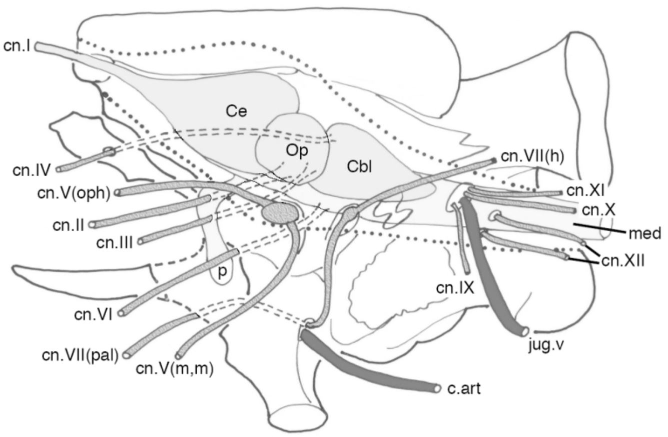

FIGURE 13 - DOUBLE COLUMN WIDTH

Figure 13. Partially transparent neurocranium to show the approximate structure of the brain, the principal cranial nerves and blood vessels.

Abbreviations: c.art – carotid artery, Cbl – cerebellum, Ce – cerebral lobes, cn. [roman] – cranial nerve, jug.v – jugular vein, med – medulla (brain stem), p – pituitary body. Dotted outline – approximate profile of the endocranial cavity.

209x297mm (200 x 200 DPI)

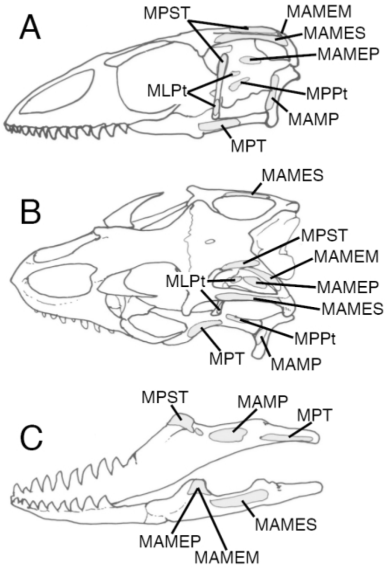

FIGURE 14 - SINGLE COLUMN WIDTH

Figure 14. Varanus exanthematicus (Bosc, 1792). Mapping the areas of origin and insertion of the principal jaw closing muscles in a living sauropsid. A, lateral. B, oblique dorsolateral. C. lower jaw in oblique dorsolateral aspect (redrawn from Holliday, 2009: fig. 1).

Abbreviations: MAMEM – m. adductor mandibulae externus medialis. MAMEP – profundus, MAMES – superficialis, MAMP – posterior, MLPt – levator pterygoideus, MPPt – protractor pterygoideus, MPST – pseudotemporalis, MPT – pterygoideus.

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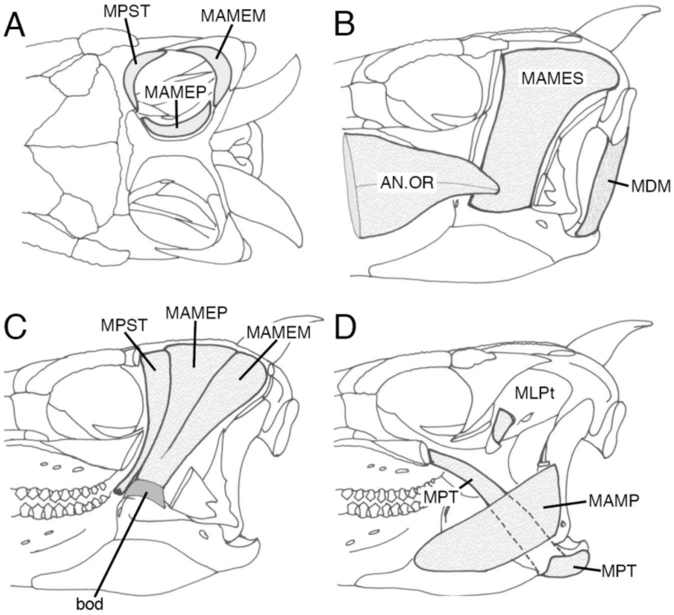

FIGURE 15 - TWO COLUMNS WIDTH

Figure 15. Scelidosaurus. The principal jaw muscles identified. A, dorsal muscle origin map. B-D, muscle reconstructions.

Abbreviations: AN.OR – m. anguli oris, bod – bodenaponeurosis, MAMEM – m. adductor mandibulae externus medialis, MAMEP – profundus, MAMES – superficialis, MAMP – posterior, MLPt – levator pterygoideus, MPST – pseudotemporalis, MPT – pterygoideus.

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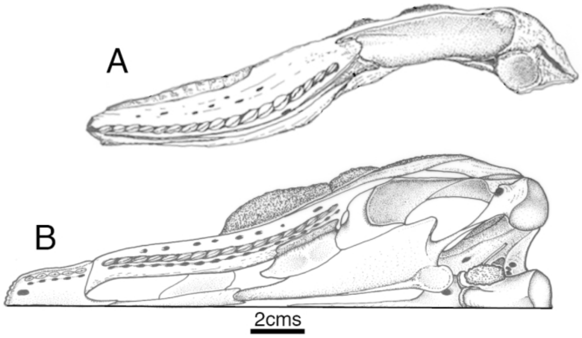

FIGURE 16 - ONE COLUMN WIDTH

Figure 16. Scelidosaurus. The mutual matching of the curvature of the opposing dentitions. A. Right mandible in dorsal view (NHMUK R1111). B. Reconstruction of the left half of the skull in ventral view (after Norman, 2019a: fig. 10).

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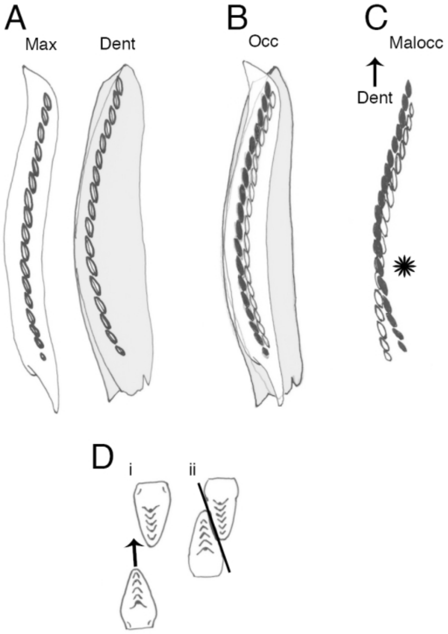

FIGURE 17 - ONE COLUMN WIDTH

Figure 17. Scelidosaurus. Occlusal views of maxillary and dentary dentitions. A, unoccluded dentitions. B, normal aligned occlusion – the bowing of each dentition match to permit orthal pulping or occlusion. C, malocclusion created by propalinal displacement of the dentary, creating a zone where the dentitions cross over (starred). D, two modes of jaw closure: Di, represents the non-occlusal orthal pulping of vegetation; Dii shows high-angle occlusion between opposing crowns that creates shear to cut vegetable fibres and generates steep wear facets on adjacent crown surfaces. Both modes of occlusion occur at intervals along the dentitions.

Abbreviations: Dent – dentary dentition, Max – maxillary dentition, Malocc – malocclusion created by propalinal displacement of the dentary, Occ – normal occlusal relationship of the dentitions. Arrows indicate direction of movement. Starred symbol indicates region where dentitions cross, creating the potential for damage to the teeth caught in opposition.

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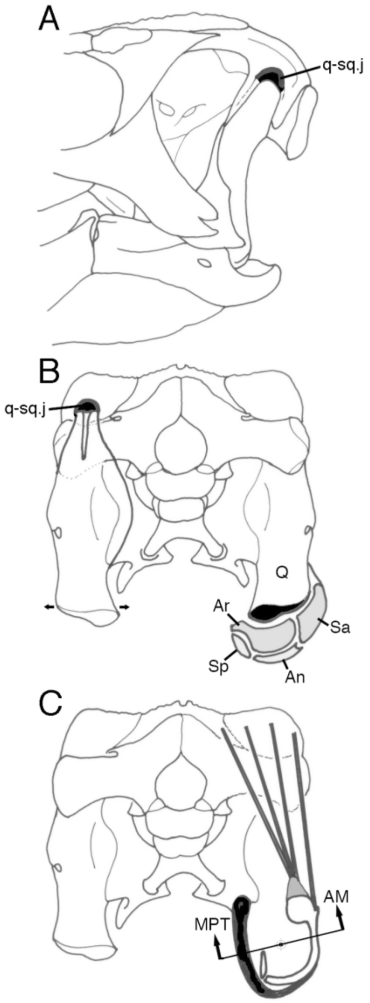

FIG. 18
SINGLE
COLUMN
WIDTH

Figure 18. Scelidosaurus. Skull diagrammatics. A, pivot point between the squamosal and quadrate head viewed laterally, joint (q-sq.j) highlighted in black. B. Posterior view of the quadrate pivoting transversely (small arrows) against the squamosal. The structure of mandibular joint shows that the quadrate is cupped by the articular-surangular articular surfaces. C. The principal lines of action of the jaw closing muscles in cross-sectional view to show imposed medial torsion exerted by the adductor mandibulae (AM) complex, as well as the counter-torsion effected by the sling-like m. pterygoideus complex (MPT).

Abbreviations: AM – mm. adductor mandibulae (overall direction of force), An – angular bone, Ar – articular bone, MPT – m. pterygoideus (overall direction of force), q-sq.j – articular joint between the head of the quadrate and the squamosal cotylus, Sa – surangular bone, Sp – splenial bone.

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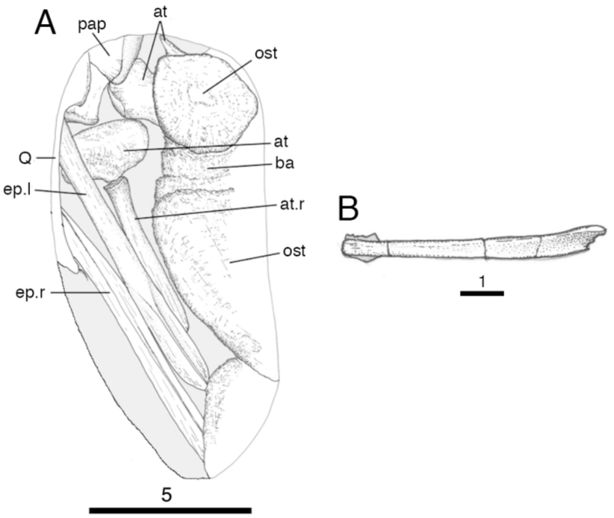

FIGURE 19 - ONE COLUMN WIDTH
(unless illegible)

Figure 19. Scelidosaurus. A. Epistyloids as preserved in the large articulated referred skeleton (BRSMG LEGL 0004 – after Norman, 2019a). B. An isolated epistyloid as preserved in lateral view in the considerably smaller referred individual (CAMSM X39256). Scale bars in centimetres.

Abbreviations: at – atlas, at.r – atlas rib, ba – baseplate, ep (l,r) – epistyloids, ost – osteoderm, pap – paroccipital process, Q – quadrate. Scale bars in cms. Pale tone – sediment.

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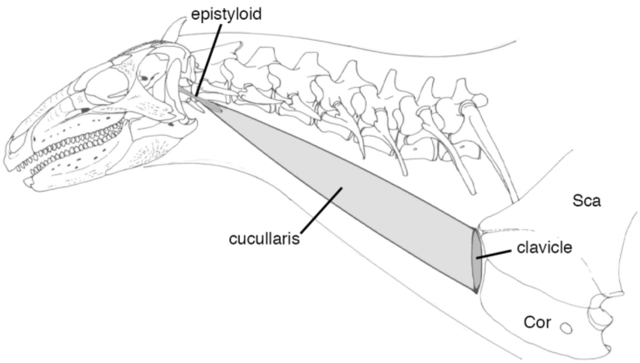

FIGURE 20 - TWO COLUMNS WIDTH

Figure 20. Scelidosaurus. A reconstruction of the head-neck and shoulder girdle based on Norman (2019a,b). Highlighting the m. cucullaris (= m. sternocleidomastoideus) muscle that has been hypothesized to be associated with the presence of epistyloid bones.

Abbreviations: Cor – coracoid, Sca – scapula.

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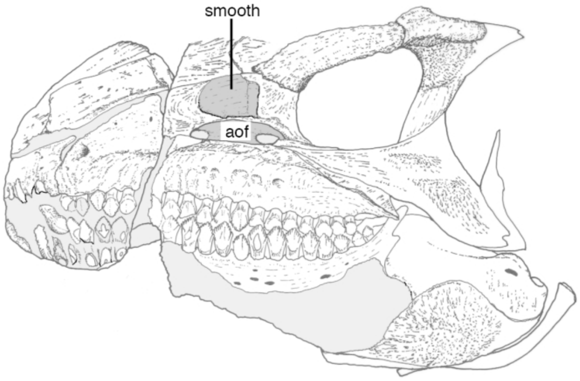

FIGURE 21 - ONE COLUMN WIDTH IF RESOLUTION IS OK

Figure 21. Scelidosaurus (BRSMG LEGL 0004). The left side of the facial region showing a discrete patch of smooth bone just dorsal to the antorbital fossa (also smooth surfaced). All the surrounding bone surfaces are roughened by exostoses. After Norman (2019a: fig. 14).

Abbreviation: aof – antorbital fossa.

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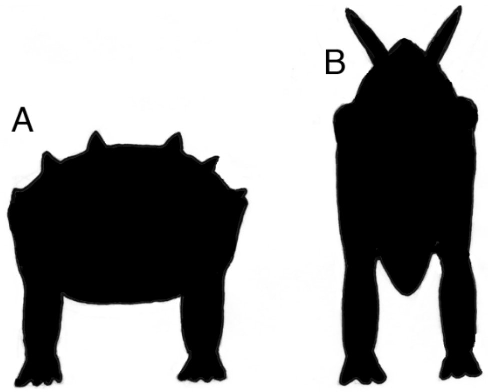

FIGURE 22 - ONE COLUMN WIDTH

Figure 22. Cartoons approximating pelvic region cross-sectional body shapes of A, an ankylosaur. B, a stegosaur.

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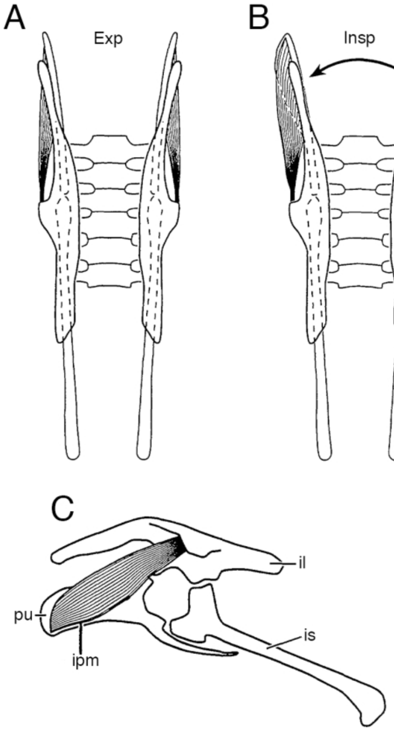

FIGURE 23 - ONE COLUMN WIDTH

Figure 23. A theoretical model of pelvic aspiration in ornithopod ornithischians (based on a hadrosaur pelvis). A, B. Dorsal views of the pelvic region showing the transverse motion suggested for the pubes that serially compressed and decompressed the abdominal cavity. Note: the ischia should meet distally on the midline, rather than remaining separate as shown here. C. Lateral view of the pelvis showing a reconstruction of a hypothetical pubic abductor muscle. After Carrier & Farmer (2000a: fig. 10B).

Abbreviations: Exp – expiration (pubes adducted), Insp – inspiration (pubes abducted), il – ilium, ipm – (hypothetical) iliopubic muscle, is – ischium, pu – pubis.

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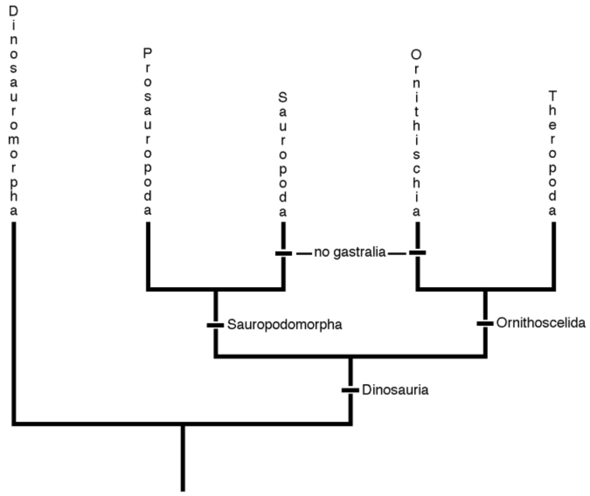

FIGURE 24 - ONE COLUMN WIDTH

Figure 24. Highly simplified phylogeny of dinosaurs. Note that gastralia are lost independently in sauropods and ornithischians but retained in all other clades (being also lost independently in the derivative avialan Theropoda [=birds]).

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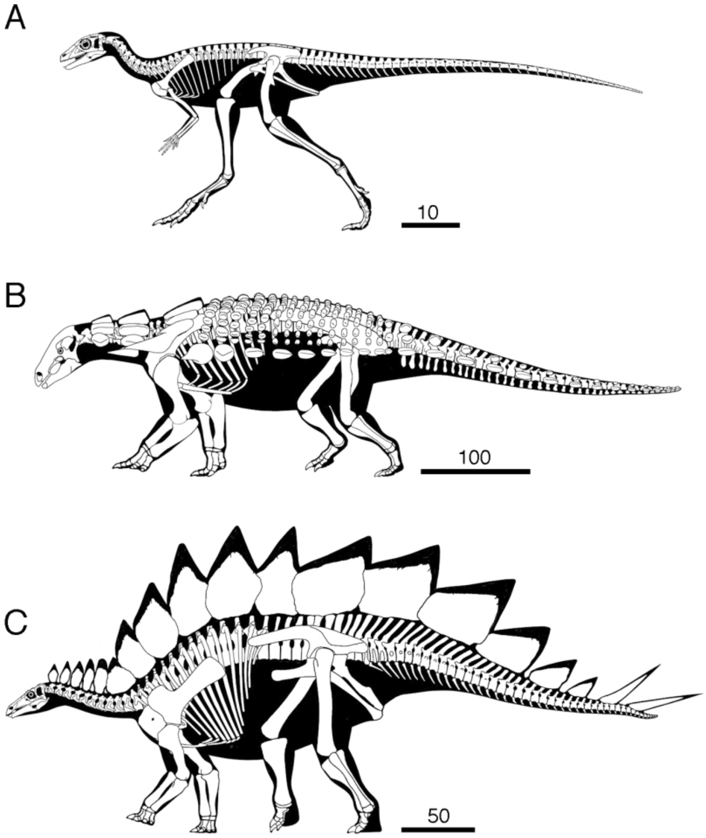

FIGURE 25 - ONE COLUMN WIDTH IFIT WORKS

Figure 25. Ornithischian skeletal forms. A. Eocursor. B. Edmontonia. C. Stegosaurus. No gastralia are present in these or any other known ornithischians.

Images kindly provided by Scott Hartman who retains the copyright of each. Scale bars in centimetres.

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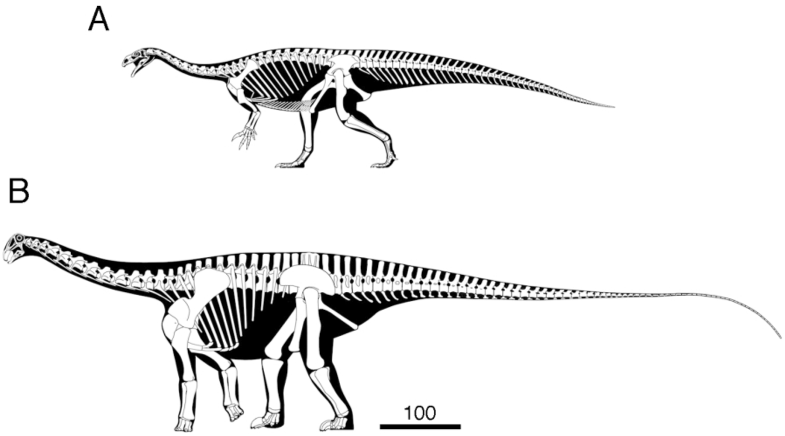

FIGURE 26 - TWO COLUMNS WIDTH

Figure 26. Sauropodomorph skeletal forms. A. Plateosaurus (a prosauropod). B. Nigersaurus (a sauropod). Gastralia are present in the prosauropod, but no sauropods possess gastralia.

Images kindly provided by Scott Hartman who retains the copyright of each. Scale bars in centimetres.

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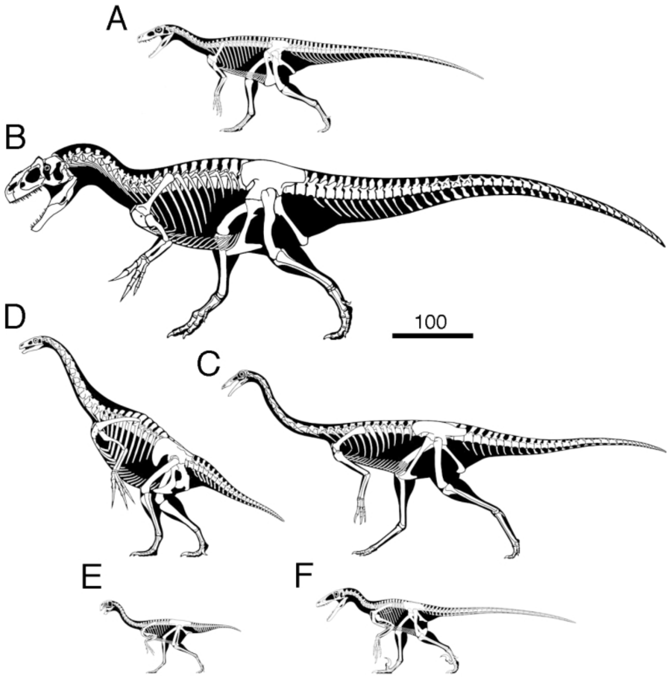

FIGURE 27 - TWO COLUMNS WIDTH

Figure 27. Theropod skeletal forms. A. Herrerasaurus (either a stem lineage pre-dinosaurian, a basal dinosaurian or a basal theropod, according to various analyses). B. Allosaurus a tetanuran theropod – see Figure 28). C. Ornithomimus a coelurosaur. D. Nothronychus, a coelurosaur. E. Oviraptor, a maniraptoran. F. Deinonychus, a paravian. Herrerasaurus and all other theropods possess gastralia.

Images kindly provided by Scott Hartman who retains the copyright of each. Scale bars in centimetres.

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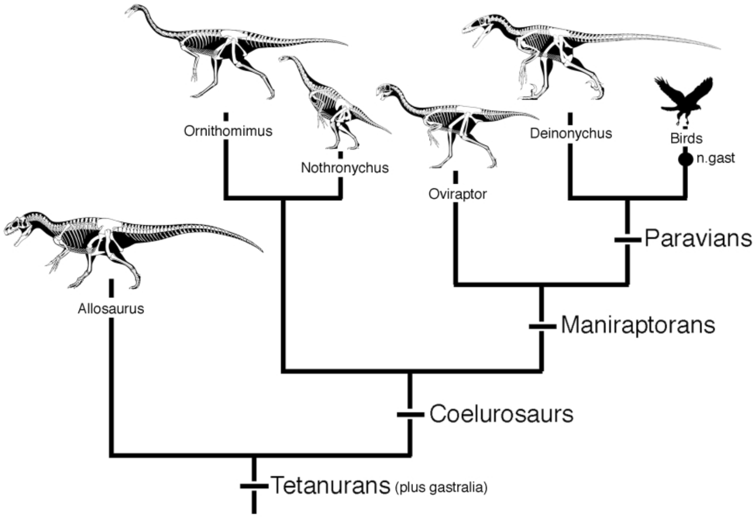

FIGURE 28 - TWO COLUMNS WIDTH

Figure 28. Simplified theropod phylogeny. All tetanuran theropods have gastralia; these are only lost in true birds (n.gast). The orientation of the pubis varies across these clades and is dependent upon multiple factors: dietary preference (herbivory, omnivory, carnivory); body proportions (notably the reduction in length and mass of the tail); and more specific locomotor adaptations and habits of individual theropods within each subclade. There is no simple and unambiguous correspondence between pelvic structure and posture, habit, locomotor style, or putative diet and respiratory mechanics.

Dinosaur images kindly provided by Scott Hartman, who retains the copyright of each. The raptor silhouette was made available through the following website: http://clipart-library.com/bird-silhouette.html

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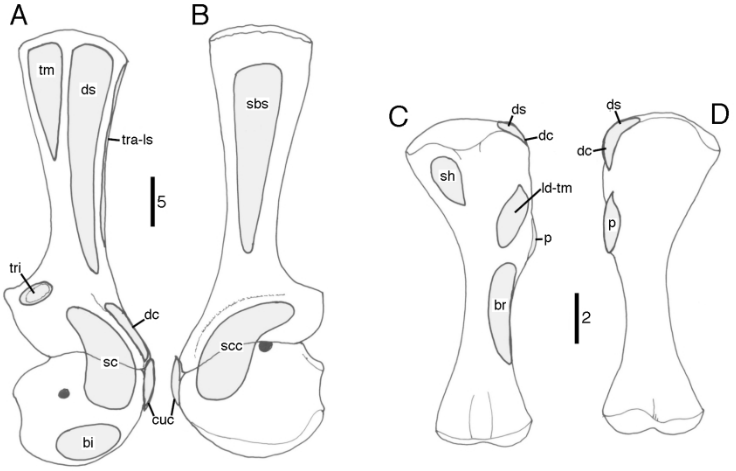

FIGURE 29 - TWO COLUMNS WIDTH

Figure 29. Scelidosaurus. Myological mapping of scapula and coracoid based on the lectotype NHMUK R1111 (A, lateral. B, medial) and humerus, based on the referred specimen BRSMG LEGL 0005 (C, posterior. D, anterior). After Norman (2019b: figs 56, 58, 63).

Abbreviations: bi – m. biceps, cuc – m. cucullaris, br – m. brachialis, dc – clavicular deltoid, ds, scapular deltoid, ld-tm – mm. latissimus dorsi-teres major, p – m. pectoralis, sbs – m. subscapularis, sh – m. scapulohumeralis, sc – m. supracoracoideus, scc – m. subcoracoideus, tra-ls – mm. trapezius-levator scapulae. Scale bars in centimetres.

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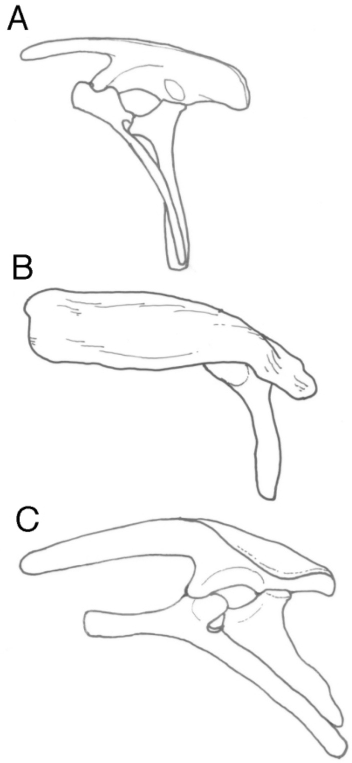

FIGURE 31 - ONE COLUMN WIDTH

Figure 31. Pelvic reconstructions in left lateral view. A. Scelidosaurus (after Norman 2019b: fig. 77). B. Euoplocephalus (after Coombs 1978a). C. Stegosaurus (after Gilmore 1914).

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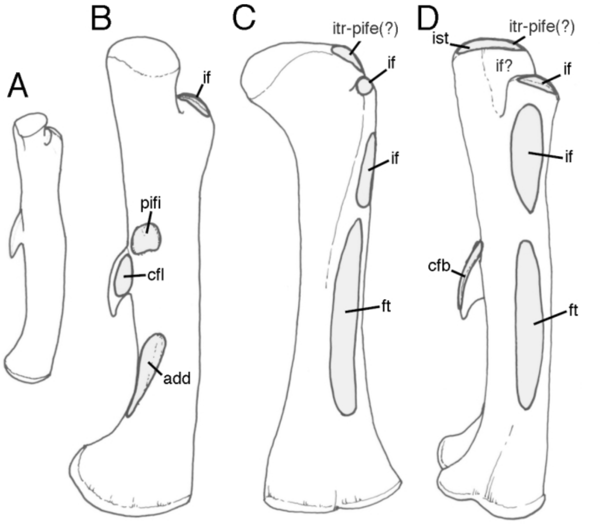

FIGURE 32 - TWO COLUMN WIDTH/ONE COLUMN IF IT WORKS VISUALLY

Figure 32. Scelidosaurus. Femoral muscle maps. Includes small and large femora to show the change of curvature of shaft that occurs during ontogeny. A. 'Juvenile' (NHMUK R6704 – after Norman, 2019b: fig. 79). B-D. 'Adult' (NHMUK R1111 – the lectotype, after Norman, 2019b: fig. 78) in medial (B), anterior (C) and lateral (D).

Abbreviations: add – adductor, cfb – m. caudifemoralis brevis, cfl – m. caudifemoralis longus, ft – m. femorotibialis, if – m. iliofemoralis, if? – possible area for attachment of a slip of the m. iliofemoralis; itr-pife? – area available for insertion of the m. iliotrochantericus (m. iliofemoralis) and perhaps the m. puboischiofemoralis externus (site of origin uncertain), ist – m. ischiotrochantericus, pifi – m. puboischiofemoralis internus.

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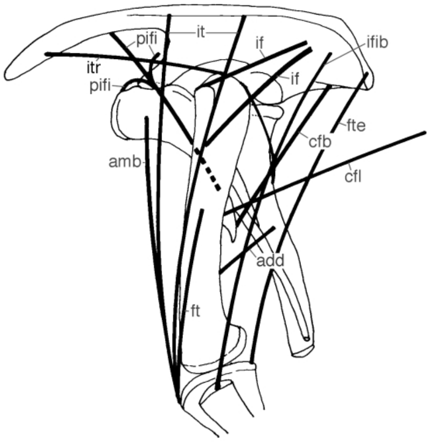

FIGURE 33 - ONE COLUMN WIDTH
IF RESOLUTION IS OK.

Figure 33. Scelidosaurus. Myology of the principal pelvis and hindlimb reconstructed as lines of action.

Abbreviations: add – adductor, amb – m. ambiens, cfb – m. caudifemoralis brevis, cfl – m. caudifemoralis longus, ft – m. femorotibialis, fte – m. flexor tibialis externus, if – m. iliofemoralis, ifib – m. iliofibularis, ist – m. ischiotrochantericus, it – m. iliotibialis, itr – m. iliotrochantericus (avian-equivalent subdivision of the iliofemoralis), pifi – m. puboischiofemoralis internus.

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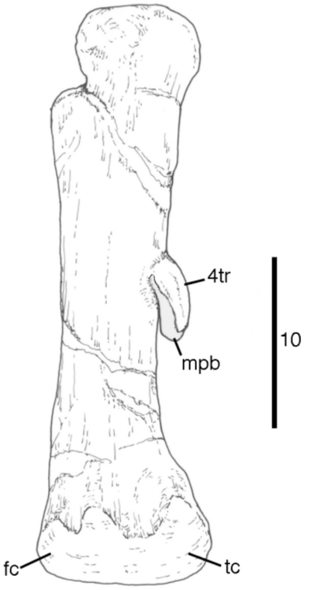

FIGURE 34 - SINGLE COLUMN WIDTH

Figure 34. Scelidosaurus cf. harrisonii. Femur (NHMUK OR41322) crushed proximally, but showing a well-developed 4th trochanter that is secondarily thickened by the addition of a layer of metaplastic bone over its surface. The metaplastic bone derives from calcification of the caudifemoral tendons where they attach to the trochanter.

Abbreviations: 4tr – fourth trochanter, fc – fibular condyle, mpb – metaplastic bone, tc – tibial condyle. Scale bar in centimetres.

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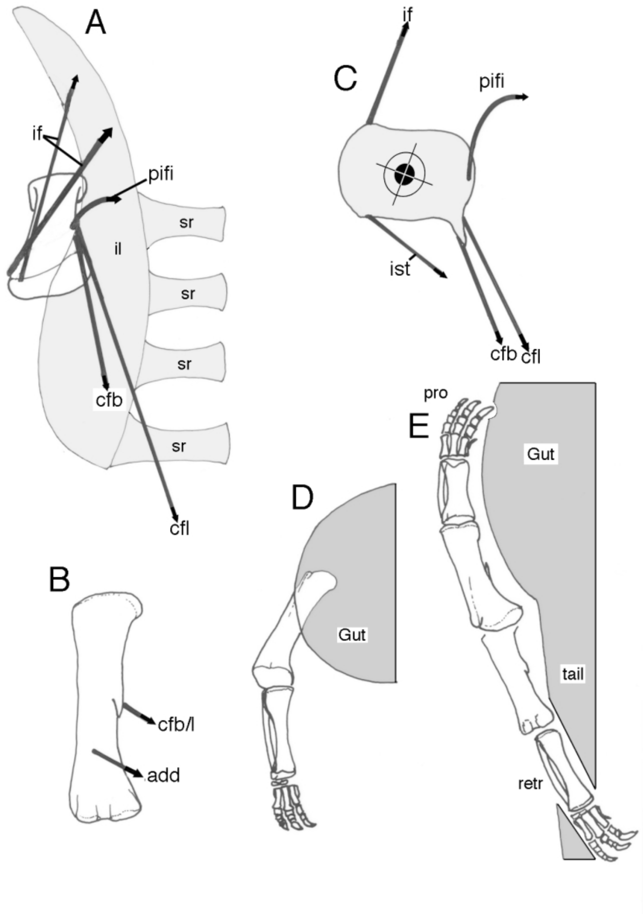

FIGURE 35 - SINGLE COLUMN - BUT MAY NEED TO BE DOUBLE COLUMN WIDTH

Figure 35. Scelidosaurus. Femur and hindlimb motion examined. The principal lines of action of retractor muscles and their influence upon the femur and hindlimb poses have been reconstructed as a series of cartoons. A. Dorsal view of the femur in 'neutral' pose with lines of action of main muscles: note in particular the lateral or medial attachment of these muscles on the femoral shaft. B. Vertical pose of the femur with an indication of the posteromedial lines of action of the powerful limb retractors (m. caudifemoralis – cfb/l, and m. adductor – add). C. Cross-section through the femoral shaft at the level of the fourth trochanter showing the torsion inducing lines of action of the principal protractors (pifi, ist) and retractors (if, cfb, cfl). D. Mechanical influence on hindlimb protraction resulting from the breadth of the gut. E. Oblique-to-parasagittal hindlimb excursion during the protraction-retraction cycle.

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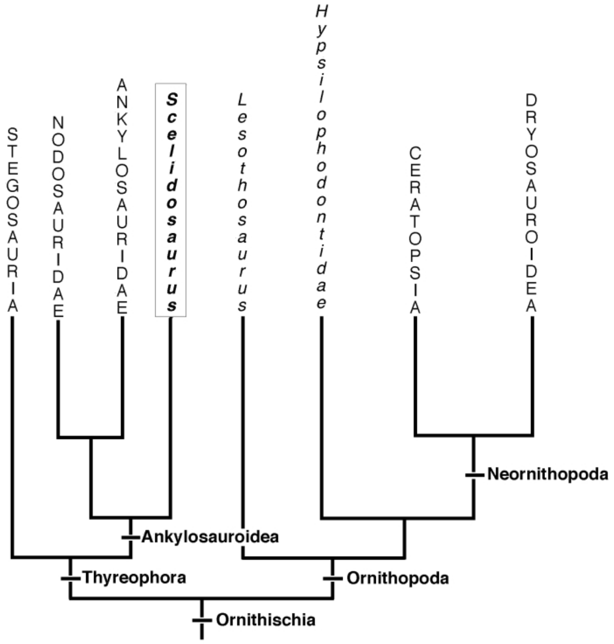

FIGURE 36 - ONE COLUMN WIDTH

Figure 36. Early cladistics-based attempts to establish a topology for armoured dinosaurs within the clade Ornithischia. The topology created by Norman (1984b: fig. 2).

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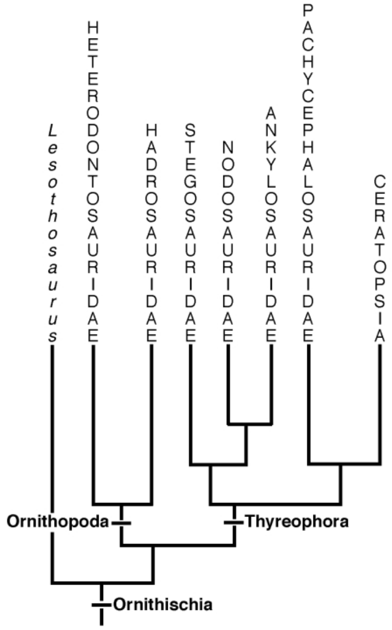

FIGURE 37 - ONE COLUMN WIDTH

Figure 37. Early cladistics-based attempts to establish a topology for armoured dinosaurs within the clade Ornithischia. The topology derived from Sereno (1984: fig. 1).

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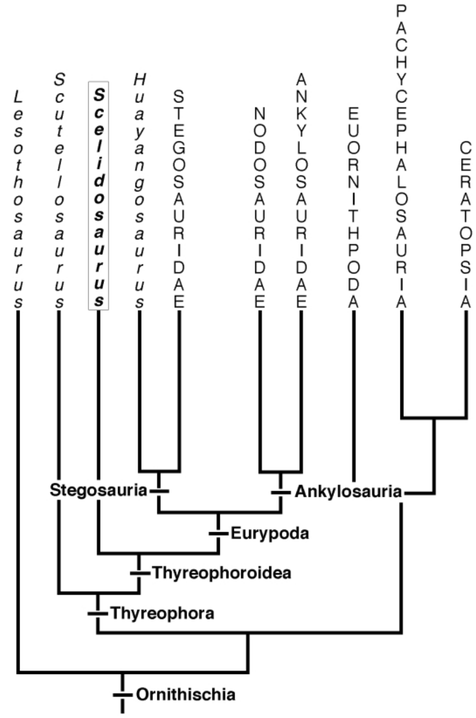

FIGURE 38 - ONE COLUMN WIDTH

Figure 38. Early cladistics-based attempts to establish a topology for armoured (thyreophoran) dinosaurs within the clade Ornithischia. The topology is derived from Sereno (1986: fig. 3).

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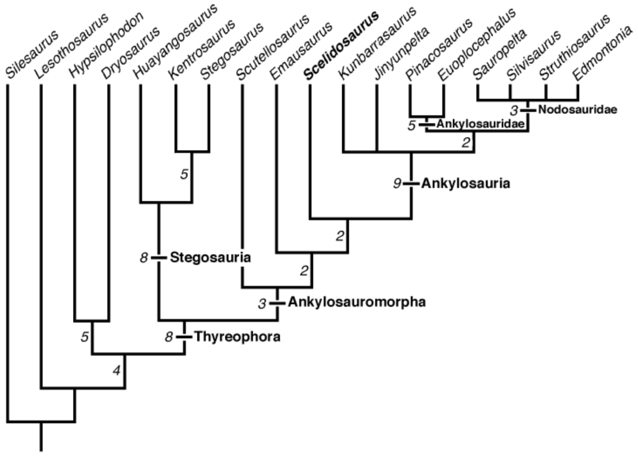

FIGURE 39 - TWO COLUMNS WIDTH

Figure 39. Strict Consensus Tree based on the 10 equally most parsimonious trees (MPTs) generated by the new analysis. The lack of resolution lies in the topographic ambiguity of Kunbarrasaurus, Jinyunpelta and that of the four nodosaurid taxa. Overall, the topology supports many aspects of previously published cladograms. However, and controversially, Scutellosaurus, Emausaurus and Scelidosaurus are positioned as successive out-groups on the branch leading to Ankylosauria. Convention places these taxa on the branch leading to Thyreophora. Kunbarrasaurus may well prove to be a stem ankylosaur once it has been fully described; furthermore, Jinyunpelta is positioned as a basal ankylosaurian. However, Zheng et al., (2018) propose that it is an ankylosaurine ankylosaur (despite the lack of resolution in their strict consensus tree) – see also Figure 41.
Numerical Decay Indices (Bremer support) for the individual clades are indicated in italics adjacent to the relevant branches.

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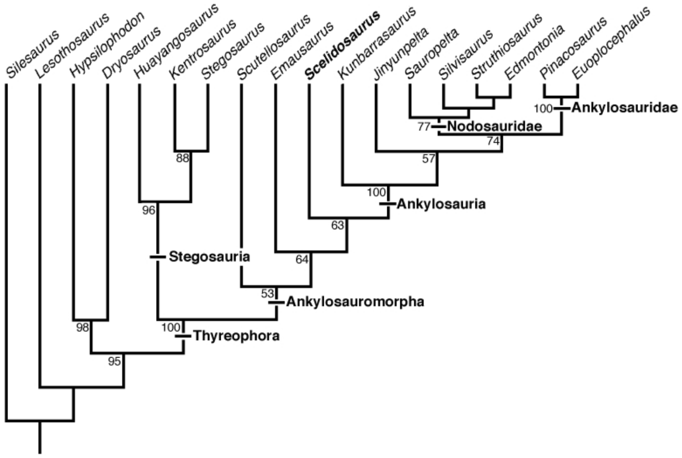

FIGURE 40 - TWO COLUMNS WIDTH

Figure 40. A bootstrap analysis (Heuristic) of the dataset using 10,000 replicates. Bootstrap support percentages are indicated on individual branches.

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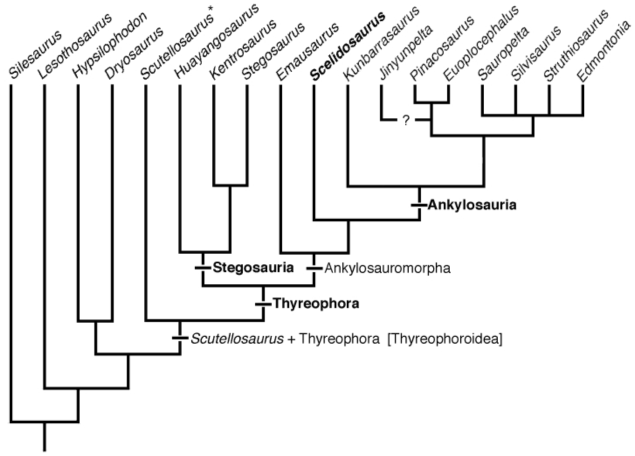

FIGURE 41 - TWO COLUMNS WIDTH

Figure 41. Cladogram manipulation using MacClade. In this example Scutellosaurus* has been positioned as the proximate sister taxon to the clade Thyreophora. Tree length is calculated to be 229 steps, which is three steps longer than the most parsimonious trees obtained by the analysis of this dataset. The re-positioning of Scutellosaurus, if it could be supported by additional data, might justify a redefinition of the taxon Thyreophoroidea, as indicated on this branch. Note: an additional adjustment, which involves a single step increase (230 steps) positions Jinyunpelta (albeit tentatively = ?) as a basal ankylosaurid on the basis of its possession of a tail club (in conformity with Coombs, 1978a).

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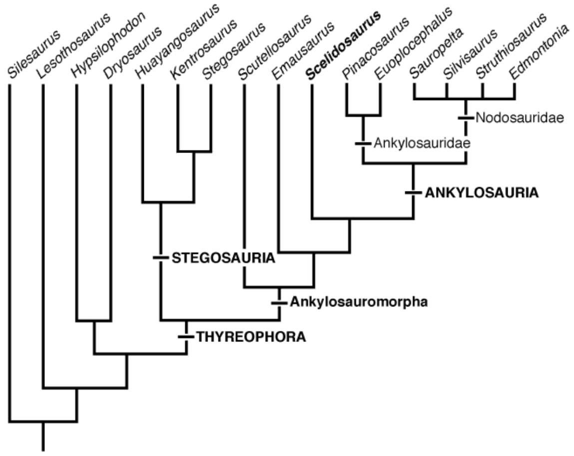

FIGURE 42 - TWO COLUMNS WIDTH

Figure 42. Taxon deletion tree. Kunbarrasaurus and Jinyunpelta have been deleted. Tree length (of the 6 MPTs) is 212 steps, 14 steps fewer than found in the MPTs of the original dataset (Fig. 39). The principal clades: THYREOPHORA, STEGOSAURIA, ANKYLOSAURIA, Nodosauridae and Ankylosauridae conform topographically with those established by previous analyses. However, the ankylosauromorph branch and its composition, if confirmed in subsequent analyses, implies that the way Sereno (1986, et seq.) envisioned Eurypoda and Thyreophoroidea are meaningless.

297x209mm (300 x 300 DPI)