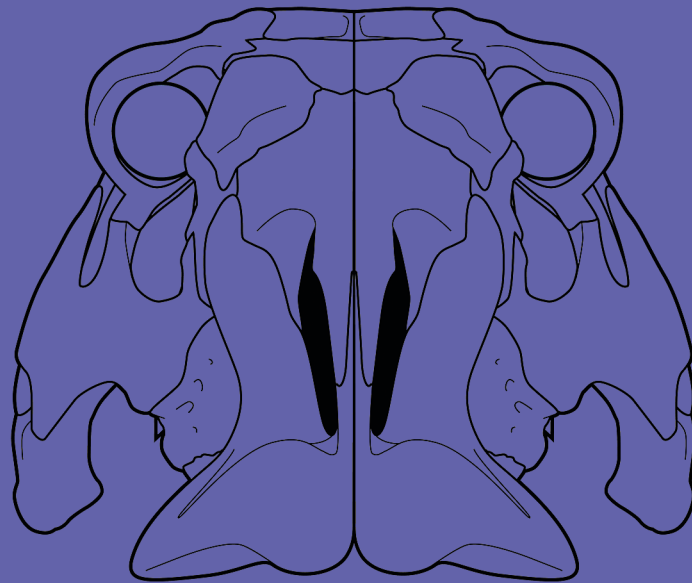# Skeletal reconstruction of fossil vertebrates as a process of hypothesis testing and a source of anatomical and palaeobiological inferences

Corwin SULLIVAN, Robin SISSONS, Henry SHARPE,
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THE IMPORTANCE OF SCIENTIFIC ILLUSTRATIONS
IN PALEONTOLOGY: A TRIBUTE TO DIANE SCOTT

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Skeletal reconstruction of fossil vertebrates as a process of hypothesis testing and a source of anatomical and palaeobiological inferences

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ABSTRACT

Reconstructions of extinct animals play an important role in vertebrate palaeontology. Such reconstructions represent visual hypotheses regarding the original morphology of the vertebrates they depict, which are amenable to future testing as additional information comes to light through discoveries of new specimens and re-examination of specimens that have already been collected. In this contribution, we argue that the scientific value of reconstructing a fossil vertebrate extends beyond simple presentation of a visual hypothesis, because the process of creating a reconstruction is itself analytical and hypothetico-deductive. Successive drafts of the reconstruction represent provisional visual hypotheses that can be tested on the basis of their internal consistency and their congruence with empirical evidence about the extinct taxon that is the reconstruction's subject. Iterative refinement of the reconstruction over successive rounds of testing and modification is likely to lead to discoveries about the subject's anatomy, as certain anatomical possibilities are rejected and others found to be plausible. These anatomical discoveries, here termed first-order inferences, may in turn lead to second-order inferences about functional morphology or other aspects of palaeobiology. Three case studies from dinosaur palaeontology, respectively involving the skull of the hadrosaurid *Edmontosaurus* Lambe, 1917, the forelimb of the ceratopsid *Pachyrhinosaurus* Sternberg, 1950, and the hindlimb of an indeterminate ceratopsid, are provided to illustrate how the process of reconstruction can be a fertile source of discoveries.

KEY WORDS
Reconstruction,
visual hypothesis,
illustration,
Ceratopsidae,
Hadrosauridae,
orthographic rendering.

RÉSUMÉ
La reconstitution squelettique des vertébrés fossiles en tant que processus de vérification des hypothèses et source d'inférences anatomiques et paléobiologiques.
Les reconstitutions d'animaux disparus jouent un rôle important dans la paléontologie des vertébrés. Ces reconstitutions représentent des hypothèses visuelles concernant la morphologie originale des vertébrés qu'elles représentent, qui peuvent être testées à l'avenir au fur et à mesure que des informations supplémentaires deviennent disponibles grâce à la découverte de nouveaux spécimens et au réexamen de spécimens déjà collectés. Dans cette contribution, nous soutenons que la valeur scientifique de la reconstitution d'un vertébré fossile va au-delà de la simple présentation d'une hypothèse visuelle, car le processus de création d'une reconstitution est lui-même analytique et hypothético-déductif. Des ébauches successives de la reconstitution représentent des hypothèses visuelles provisoires qui peuvent être testées sur la base de leur cohérence interne et de leur concordance avec les preuves empiriques concernant le taxon éteint qui fait l'objet de la reconstitution. L'affinement itératif de la reconstitution au cours de séries successives de tests et de modifications est susceptible de conduire à des découvertes sur l'anatomie du sujet, certaines possibilités anatomiques étant rejetées et d'autres jugées plausibles. Ces découvertes anatomiques, appelées ici inférences de premier ordre, peuvent à leur tour conduire à des inférences de second ordre sur la morphologie fonctionnelle, ou d'autres aspects de la paléobiologie. Trois études de cas de la paléontologie des dinosaures, concernant respectivement le crâne de l'hadrosauridé *Edmontosaurus* Lambe, 1917, le membre antérieur du cératopsidé *Pachyrhinosaurus* Sternberg, 1950 et le membre postérieur d'un cératopsidé indéterminé, sont présentées pour illustrer comment le processus de reconstitution peut être une source fertile de découvertes.

MOTS CLÉS
Reconstruction,
hypothèse visuelle,
illustration,
Ceratopsidae,
Hadrosauridae,
rendu orthographique.

INTRODUCTION

Humans are a highly visual species, with sight as arguably our primary means of acquiring data from the world around us (Kass 2013). Illustrations of various kinds can accordingly be a powerful medium for conveying both information and concepts in vertebrate palaeontology, as in other sciences. In the majority of cases, palaeontological researchers cannot personally examine all specimens that might be relevant to their work, and must rely to some extent on information available in the scientific literature in the form of written descriptions and visual representations. The latter may take the form of photos, drawings, X-ray images, surface renderings or cross-sectional views of 3D computer models, or animations, among other possibilities.

Although visual transmission of information has always been of the highest importance in vertebrate palaeontology (Davidson 2008), the techniques used to produce images have evolved over time, and much of this evolution has taken place comparatively recently. When the first author of this contribution was an undergraduate in the 1990s, he once heard vertebrate palaeontologist Bob Carroll of McGill University jokingly complain about having been repeatedly accused of running a drawing school rather than a scientific laboratory. The remark reflected both the considerable effort needed to train students to become good technical artists and the relatively central role that ink drawings retained in vertebrate palaeontology even towards the close of the 20th century. Currie's (1995) paper on the skull anatomy of the Cretaceous theropod *Dromaeosaurus* Matthew & Brown, 1922, for example, was illustrated entirely with drawings rather than photos.

Palaeontologists and the scientific illustrators who worked with them traditionally used pen and ink to create both specimen drawings, which were realistic renderings of vertebrate fossils as they were actually preserved, and reconstructions, which depicted the complete or partial skeleton of a fossil vertebrate as it might have appeared when fully intact and articulated. Throughout her long and prolific career, Diane Scott was a masterful creator of both types of palaeontological drawing, and her work characteristically combines scientific informativeness with incidental but very real aesthetic beauty.

As vertebrate palaeontologists shifted towards publishing almost all their research electronically, the increasing ease of including high-resolution colour photos in papers ensured that such images increasingly replaced specimen drawings. The latter still offer some benefits, notably an artist's ability to exclude distracting and palaeontologically irrelevant features such as minor cracks and mineral stains while emphasising important ones such as cranial sutures. Comparing a photo of the skull of the varanopid synapsid *Varanosaurus acutirostris* Broili, 1904 FMNH PR 1760 in left lateral view (Fig. 1A) with a corresponding high-quality specimen drawing (Fig. 1B), for example, shows that the drawing is much easier to visually decode. In the drawing, suture lines can be more readily discerned than in the photo, areas of breakage are clearly marked, and many cracks have been omitted for the sake of clarity. The 3D topography of the lateral side of the skull is more apparent in the drawing than in the photo as well. However, the advantages of specimen drawings over photos no longer seem to prove compelling to most researchers, perhaps because good drawings take much longer to produce and require the viewer to trust the illustrator's interpretation

A

B

C
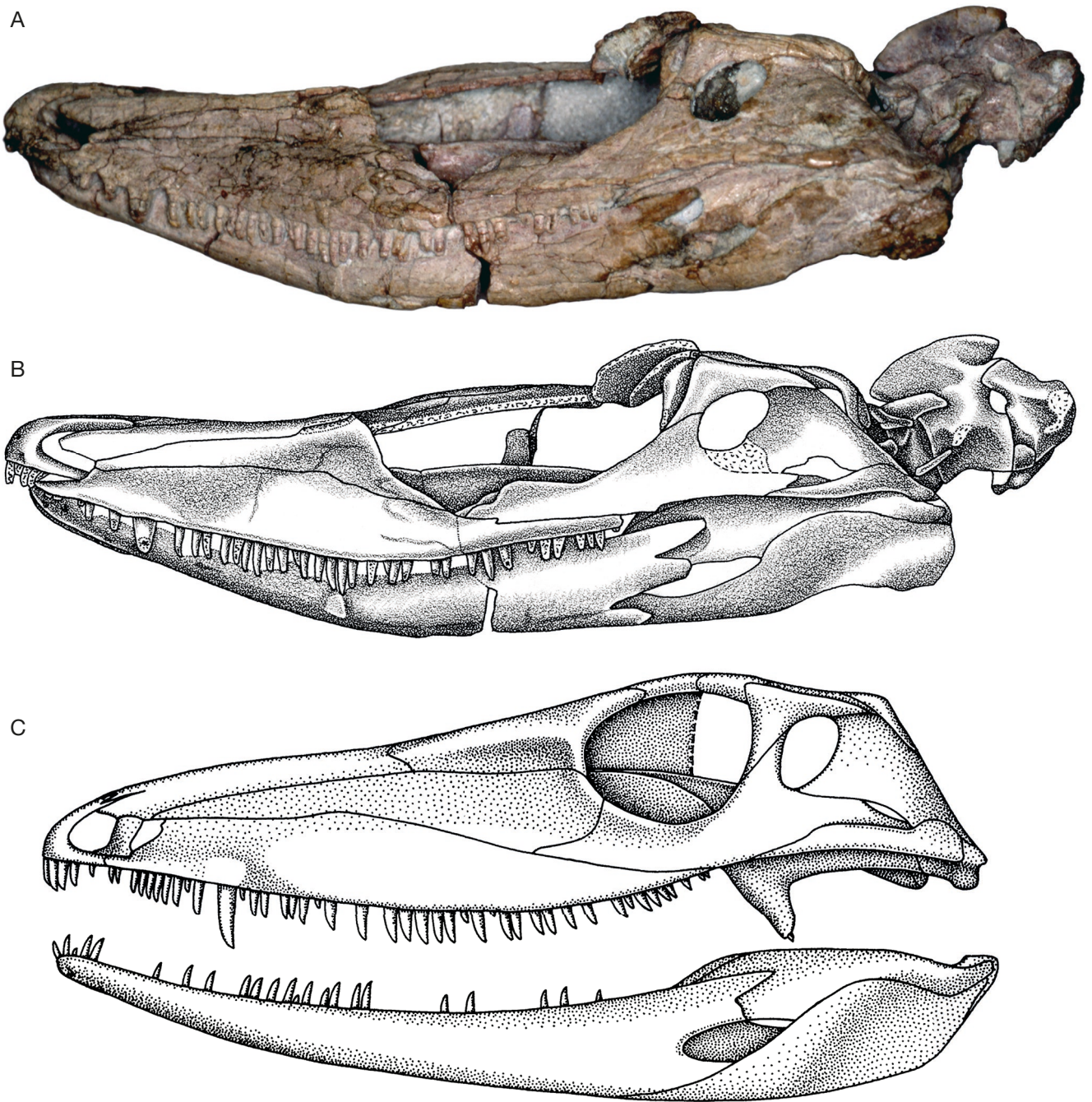
FIG. 1. — Skull and mandible of Permian synapsid *Varanosaurus acutirostris* Broili, 1904 FMNH PR 1760 in left lateral view: **A**, photo; **B**, specimen drawing; **C**, orthographic reconstruction. Scale bar: 1 cm. Credits: A, Diane Scott; B, C, Berman *et al.* (1995).

of the specimen. In the most recent issue of the *Journal of Vertebrate Paleontology* as of this writing (Volume 42, Issue 1), for example, only six (Buffa *et al.* 2022; Duque *et al.* 2022; Jiangzuo & Spassov 2022; Murray *et al.* 2022; Nam & Nazarkin 2022; Olroyd & Sidor 2022) out of 18 papers contained specimen drawings, whereas 16 contained photos of fossils.

Reconstructions, by contrast, continue to play a more substantial part in vertebrate palaeontology (Mateus & Tschopp 2017; deBraga *et al.* this issue) and may exert influence for a century or longer; for example, Mayr (2022: fig. 4.5) presented

a skeletal reconstruction of the giant anseriform bird *Gastornis gigantea* (Cope, 1876) that was redrawn from Matthew & Granger (1917). Unless a skeletal structure is preserved almost perfectly, a reconstruction showing a researcher's conception of its original appearance will differ substantially from any scan or photo of the specimen that could possibly be produced, and will portray its postulated morphology prior to taphonomic changes (Fig. 1C). Furthermore, a reconstruction can extend beyond the realm of pure skeletal morphology by incorporating soft tissues and/or depicting one or more hypothetical life

postures (Fig. 2), potentially as an animated sequence. Some kinds of biomechanical analysis require a reconstruction, often in the form of a 3D digital model, in order to yield accurate results (Herbst *et al.* 2022).

Any reconstruction represents a visual hypothesis pertaining to the structure and/or functionality of an extinct taxon's body (Kemp 1999), and such a hypothesis can be readily tested as new, better-preserved specimens are discovered and functional modelling techniques evolve. We argue, moreover, that the utility of any rigorously crafted reconstruction extends beyond simply communicating a visual hypothesis, in that the process of generating such a reconstruction is essentially analytical and already includes an element of hypothesis testing. In producing a reconstruction that is consistent across different views, and congruent with empirical evidence about the available fossil material, investigators must work within significant constraints, an operation that can –and often does– lead to fresh inferences regarding the structure and function of the taxon in question. In this contribution we briefly explore how anatomical reconstruction can be viewed as a hypothetico-deductive process from whose results important inferences may be drawn, and subsequently present three case studies that show how the making of reconstructions can generate such insights.

CONVENTIONS, DEFINITIONS AND SCOPE

We consider a reconstruction of a fossil vertebrate to be any visual representation of a vertebrate's body, in whole or in part, as it is thought by the illustrator to have appeared prior to death and taphonomic alteration. This definition allows the concept of a reconstruction to encompass depictions of whole animals, complete skeletons, detached skeletal components such as skulls and limbs, and non-skeletal body parts such as vascular networks. Furthermore, the reconstruction may be limited to a single view, include views from multiple directions, or constitute a 3D model, and may show the illustrated body part(s) either in an arbitrary pose or in a realistic pose or series of poses intended to represent a specific behaviour. For our purposes, an animated video clip of a pterosaur executing a complicated series of aerial manoeuvres and a single drawing of one of the pterosaur's wing bones as it might have appeared when intact are both reconstructions, albeit ones differing vastly in purpose and complexity. Most palaeontological reconstructions are intended to show the anatomy of a typical member of an extinct species, but some instead show the anatomy of individuals represented by particular specimens (e.g. Hutchinson *et al.* 2011).

For ease of discussion, the scope of this contribution is limited to reconstructions that pertain to species rather than individuals, and which are osteological in nature. We refer to the species whose skeletal anatomy is depicted by a given reconstruction as the "subject" of that reconstruction. However, the arguments outlined in this paper regarding the hypothetico-deductive character of the process of preparing a reconstruction, and the potential for that process to lead

to structural and functional inferences, can also be applied with appropriate modification to reconstructions that include renderings of soft tissue structures and/or pertain to individual fossil vertebrates.

RECONSTRUCTIONS AS TESTABLE HYPOTHESES

If a reconstruction is accepted as a hypothesis regarding the appearance of some part of the subject's anatomy, then there are two criteria by which that hypothesis can be tested and potentially falsified in a classic Popperian manner (Popper 1968): internal consistency, and congruence with whatever relevant direct and circumstantial empirical evidence might be available regarding the subject. A reconstruction that is subjected to such testing, and avoids falsification, may be recognised as a plausible and scientifically acceptable representation of an extinct vertebrate's anatomy.

The criterion of internal consistency is an intuitive one, and is unambiguous in the sense that the presence of any inconsistency falsifies the reconstruction in its current form, and implies a need for modification to remove the inconsistency. In the case of a reconstruction that presents one static view, internal consistency is merely the absence of any geometries that would make the depicted anatomical entity into an impossible object such as those considered and classified by Sugihara (1982). For reconstructions that present multiple, usually mutually perpendicular, views, internal consistency is a more substantive consideration, involving not only absence of impossible geometries but also uniformity of dimensions across the different views. Uniformity of dimensions can be most easily checked for reconstructions that are orthographic in nature, meaning that rules of perspective drawing are *not* applied, and each view is instead treated as a 2D projection of the reconstructed 3D morphology (Baartmans & Sorby 1996). In an orthographic image, an anatomical structure's proximity to the viewer has no bearing on its apparent size. Orthographic dorsal, ventral and lateral views of a tetrapod skull, for example, should all show the jugal or any other bone visible in all three images as being the same length, allowing for differences in exposure due to overlapping contacts with adjoining elements, and orthographic opposite views (e.g. dorsal and ventral) of the skull should have precise mirror-image outlines. Orthographic reconstructions are standard (deBraga *et al.* this issue), but in principle the test of uniformity of dimensions could also be applied to a reconstruction drawn according to the rules of perspective. This would entail checking whether the dimensions of each bone
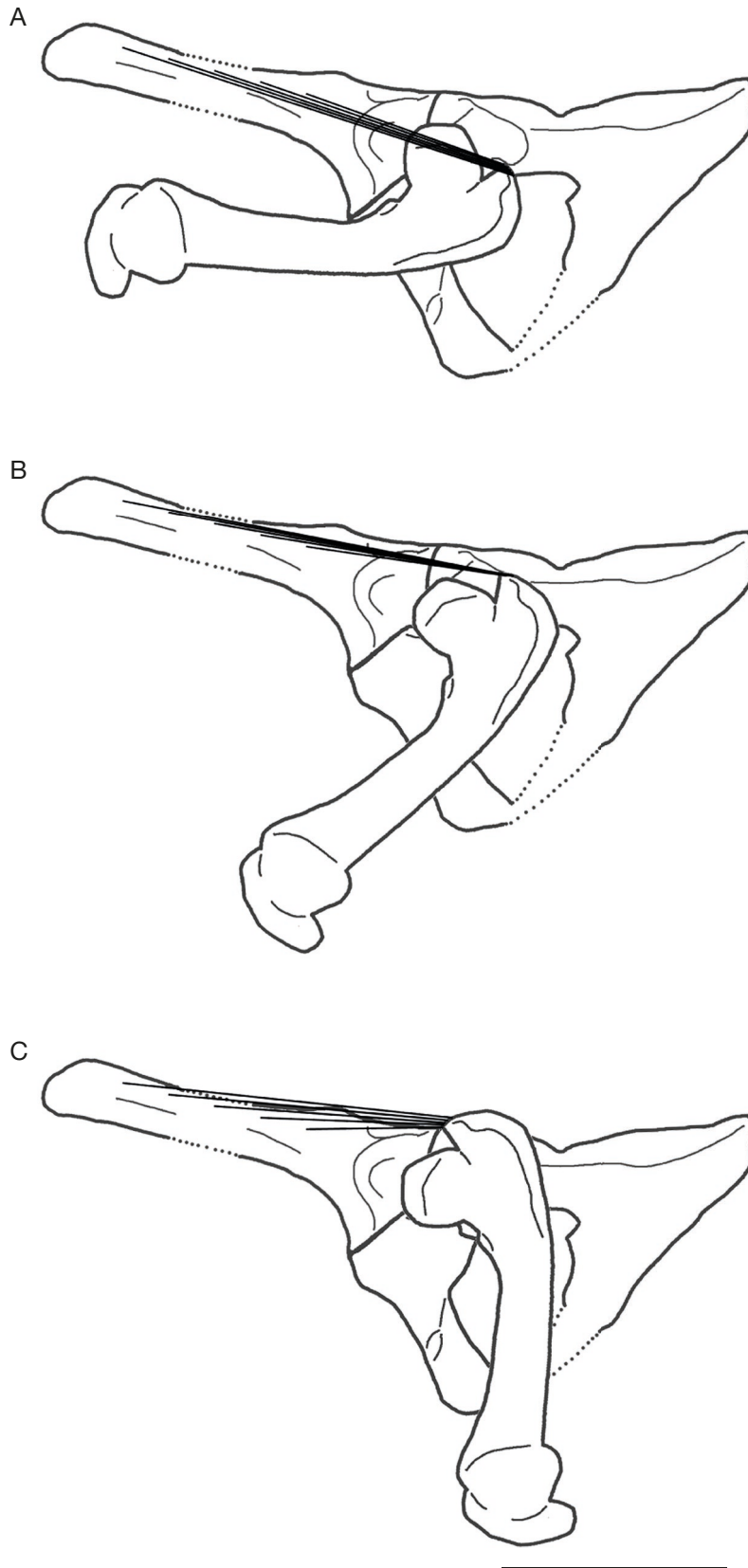
Fig. 2. — Reconstructed femur and pelvis of indeterminate Jurassic tritylodontid synapsid, with femur in different hypothetical positions: **A**, femur protracted; **B**, femur partially retracted; **C**, femur fully retracted. **Straight lines** between ilium and femur form schematic representation of gluteus musculature, thought to have contributed to femoral retraction (Sullivan *et al.* 2013). Scale bar: 4 cm. Credits: Sullivan *et al.* (2013).

in each view were consistent with its proximity to the viewer, assuming an underlying 3D geometry in which the positions and dimensions of the bones were fixed. For a reconstructed sequence of postures, uniformity of dimensions should be maintained not only across different views, but also across the frames that make up the sequence, taking into account that any given skeletal element will appear foreshortened to varying degrees in a particular viewing plane if its angular relationship to that plane changes from frame to frame. This more geometrically complex situation requires either basic knowledge of artistic conventions pertaining to perspective or particularly scrupulous attention to the rules of orthographic projection, depending on whether perspective or orthographic views are being presented, together with careful construction.

The criterion of congruence with empirical evidence is more complex and nuanced than the criterion of internal consistency, given that empirical evidence may take many different forms and may vary both in strength and scope. The most direct form of empirical evidence is, of course, fossil material referable to the subject. If the available material comprises a single relatively complete and undistorted example of the skeleton, preserved in a lifelike pose, then the task of preparing a full static osteological reconstruction asymptotically approaches that of simply drawing the specimen in whatever orthographic views are desired (Fig. 3). The overwhelmingly more common situation, however, involves specimens that are both distorted and incomplete (Fig. 1A, B), with the subject potentially represented by a hypodigm (*sensu* Simpson 1940) comprising multiple specimens that display substantial anatomical variation. A particular specimen or combination of specimens must then be chosen to provide the basis for the reconstruction, and any distortion affecting these specimens must somehow be compensated for, a task that may be doable in part by applying an algorithmic retrodeformation methodology (e.g. Schlager *et al.* 2018) to 3D scans of the selected specimens. However, the potential complexities of taphonomic distortion are great enough that no general retrodeformation algorithm can be defined (Demuth *et al.* 2022; Herbst *et al.* 2022), so that removal of distortion is ultimately likely to require an ad hoc, at least partly manual approach guided by anatomical knowledge and tailored to the unique set of problems posed by the specimen(s) at hand. Finally, any parts of the reconstruction that are not represented in the hypodigm must be filled in using other evidence. This additional evidence is likely to come predominantly from anatomical information about related taxa, but a second potential source is functional analysis, in that a hypothetical osteological configuration that is obviously maladaptive is unlikely to have existed as the normal condition in any extinct vertebrate species. Taking these lines of evidence into account, a reconstruction can be falsified if parts that can be checked against preserved specimens of the subject are substantively inconsistent with the typical morphology of those specimens, or if parts that are not represented in the hypodigm are too divergent from the corresponding parts of closely related taxa and/or appear grossly inadequate from a biomechanical perspective. The element of vagueness in the phrases "substan-

tively inconsistent", "too divergent" and "grossly inadequate" reflects the fact that testing a reconstruction against empirical evidence inescapably involves some degree of subjective judgement. However, such evidence clearly can be used to constrain reconstructions within certain boundaries of plausibility, despite the potential for disagreement as to precisely where those boundaries may lie.

RECONSTRUCTIONS AS SOURCES OF ANATOMICAL AND PALAEOBIOLOGICAL INFERENCES

In practice, preparing a reconstruction is likely to involve an iterative process that begins with gathering together at least some of the available empirical evidence, a procedure referred to by Ghilardi & Ribeiro (2010) as "briefing". The illustrator is then in a position to make a first attempt at drafting one or more views of the subject, creating an initial version of the visual hypothesis represented by the reconstruction. This was traditionally done based on careful measurements of one or more fully prepared specimens, to avoid the optical distortion that would be introduced by simply tracing photos, but unprepared material can also potentially be used as a starting point for a reconstruction if a high-quality CT (computed tomography) scan is available (deBraga *et al.* this issue). While CT scans are not guaranteed to lack artefacts (Kidoh *et al.* 2014), they provide spatial information that is not subject to optical distortion, and software such as Dragonfly ORS can be used to produce a 3D model from CT data and generate an orthographic image of that model in any desired view. Similarly, the surface morphology of a fully prepared specimen can be captured without systematic distortion using photogrammetry (Falkingham 2012; Díez Díaz *et al.* 2021), laser scanning (Sellers *et al.* 2012) or structured light scanning (Díez Díaz *et al.* 2021), and orthographic views of the resulting 3D model can be used as a basis for drafting a reconstruction. If neither creating scans nor taking an extensive set of measurements is feasible, another option is to work from pictures taken with a telephoto lens. No photo is entirely free of distortion, but telephoto images more closely approach orthographic projections of objects than do other photos (Mobasseri 1993). Whatever approach is used, taphonomic distortion and incompleteness must still be corrected for on a case-by-case basis, as noted above.

Once drafted, the different views can be rigorously checked against each other and against whatever empirical evidence was collected during the briefing stage or can be subsequently gleaned (see deBraga *et al.* this issue for discussion of the practicalities of such checking in the case of orthographic views of a reconstructed skull), and can then be modified to remove whatever inconsistencies and incongruities have been identified. This step amounts to rejecting the visual hypothesis in its earlier form, and postulating a new, refined version of the hypothesis that can then be subjected to a fresh round of checking and modification. Additional rounds may follow until no further internal inconsistencies or meaning-
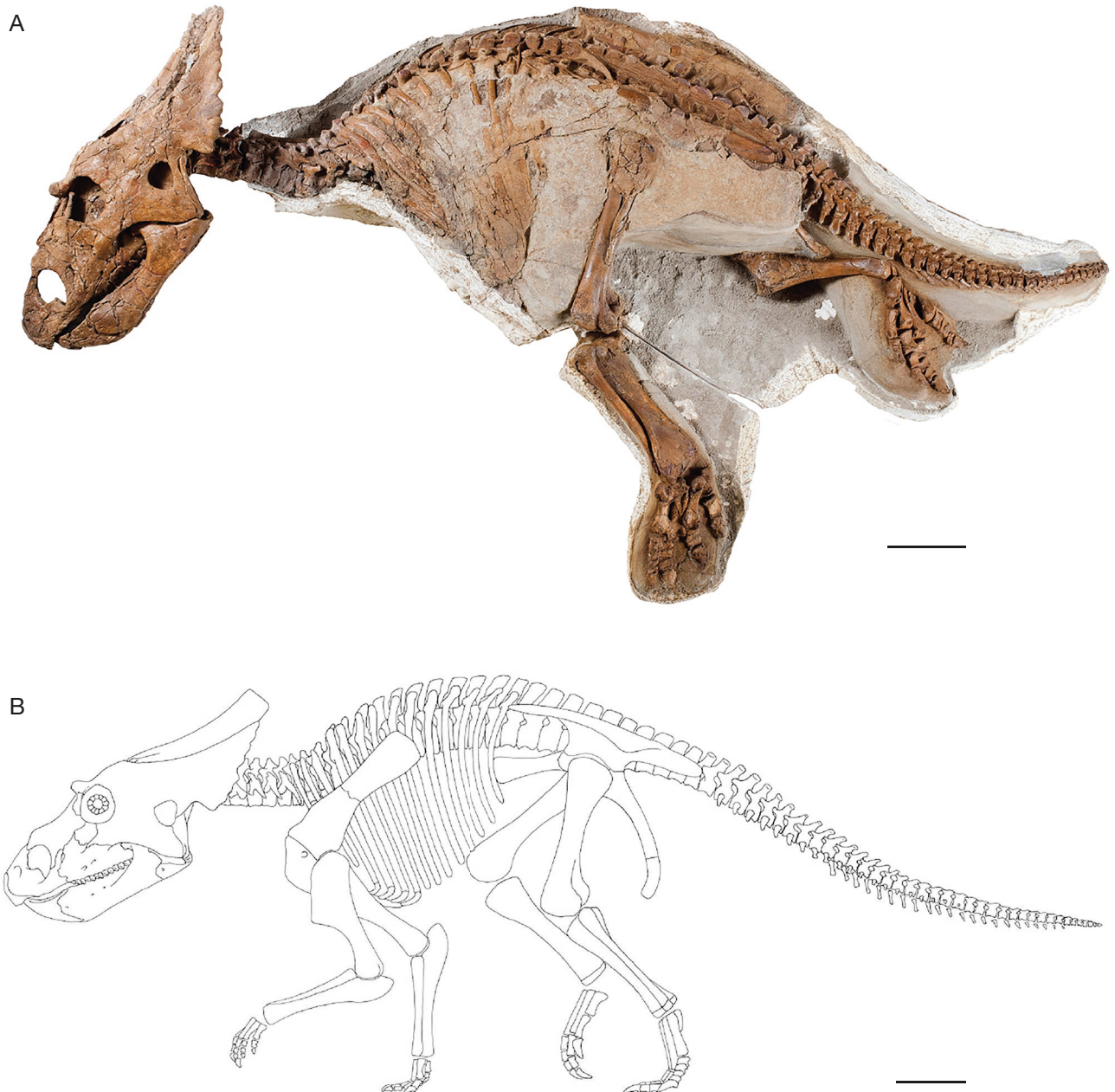
Fig. 3. — **A**, **B**, Photo (**A**) and reconstruction (**B**) of juvenile individual of ceratopsid dinosaur *Chasmosaurus belli* Lambe, 1902 (UALVP 52613). Scale bars: 10 cm. Credits: Currie *et al.* (2016).

ful incongruities with empirical evidence can be identified, implying that the reconstruction has reached a final state that should be judged acceptable.

As hypotheses (drafts) are formulated, tested, and reformulated, the illustrator will perforce draw what we term first-order inferences regarding what the skeletal anatomy of the subject must have been like. Some such inferences may arise from the process of preparing the initial drafts, particularly if information from multiple disarticulated skeletal parts is being integrated in a single set of drawings: if the hypodigm includes several highly incomplete skulls, for example, but none retains a preserved frontal bone, the illustrator's first attempt to reconstruct the skull in dorsal view by combin-ing information from the available specimens may allow the frontal's shape to be inferred in large part from the outlines of the surrounding elements. This initial impression of the subject's frontal morphology may be further refined as the reconstruction is improved over multiple rounds of checking and modification, leading to additional first-order inferences. The finished reconstruction will then offer more information than would have been available from the specimens composing the hypodigm, had they not been visually integrated in a rigorous and orthographic manner. As a final step, the first-order inferences drawn while preparing the reconstruction may then provide a basis for second-order inferences pertaining to function, or potentially to soft-tissue anatomy.

CASE STUDIES

The following brief case studies, drawn from current work by the authors, are intended to illustrate the general principle that the process of anatomical reconstruction can be a source of scientific insights. Each of them offers an example of a research project in which important findings emerged as some sort of rigorous reconstruction of vertebrate anatomy was being prepared. The first case study pertains to the skull of the hadrosaurid dinosaur *Edmontosaurus regalis* Lambe, 1917, the second to the forelimb of the ceratopsid dinosaur *Pachyrhinosaurus lakustai* Currie, Langston & Tanke, 2008, and the third to the hindlimb of an indeterminate ceratopsid.

Case study I: skull of *Edmontosaurus*

Edmontosaurus is a relatively well-known genus of large hadrosaurid from the Upper Cretaceous of North America. One of the most striking synapomorphies of this genus is the presence of a large posterior excavation in the postorbital bone, termed the postorbital pocket, which is best developed in *Edmontosaurus regalis* (Campione & Evans 2011). *E. regalis* is a commonly occurring fossil in Alberta, known from numerous monodominant bonebeds (Evans *et al.* 2015). One of us (HS) recently described cranial material recovered from one such site, the Danek Bonebed in southwestern Edmonton, Canada (Bell & Campione 2014), for an undergraduate class project.

Part of this description involved drawing anterior, lateral, and dorsal orthographic views of a skull reconstruction of *E. regalis* to show the life positions of different skull elements recovered from the Danek Bonebed (Fig. 4). These reconstructions were based on 3D scans of the mostly-disarticulated paratype specimen (CMN 2289), the only *E. regalis* skull for which 3D scans were available (Rybczynski *et al.* 2008). The scans of individual bones were assembled in Autodesk Maya 2018 to produce a 3D rendering of the nearly complete skull (Fig. 4A, B), using complete *E. regalis* skulls (CMN 2288, ROM 801) for guidance in articulating elements and correcting taphonomic distortion. Drawings (Fig. 4C, D) were made by tracing rendered images of this re-articulated skull in Adobe Photoshop 2022. It was quickly noticed upon illustrating the orbits in anterior view that the postorbital pockets were not only deeply concave posteriorly, but also protruded laterally (Fig. 4D). This caused the posterior margin of the orbit to be positioned much further laterally than the anterior margin, suggesting a large degree of binocular overlap in this species (Sharpe *et al.* work in progress). Re-examination of the 3D scans confirmed the first-order inference regarding the orientation of the orbits, and by extension the second-order inference regarding the presence of binocular overlap: the orbits of *E. regalis* are shifted laterally, and attempting to distort the postorbitals to minimise this feature resulted in a 3D skull that did not fit together, falsifying the alternative hypothesis that the posterior margins of the orbits were not especially laterally prominent. The simple act of illustrating a skull in anterior view permitted important new structural and functional inferences about a species described over a century ago (Lambe 1917).

Case study II: forelimb of *Pachyrhinosaurus Lakustai*

This case study focusses on a reconstruction of the shoulder girdle and forelimb of an adult *Pachyrhinosaurus lakustai,* a centrosaurine ceratopsid from the Upper Cretaceous Wapiti Formation of northern Alberta (Fig. 5A, B), that was produced mainly by one of us (KN) for a forthcoming descriptive paper (Vice *et al.* work in progress). The reconstruction was partly based on a previously published illustration by Thompson & Holmes (2007), depicting the shoulder girdle and forelimb of the chasmosaurine *Vagaceratops irvinensis* (Holmes, Forster, Ryan & Shepherd, 2001) in what they considered to be a "neutral" semi-erect standing position (Fig. 5D). The *P. lakustai* reconstruction followed that of Thompson & Holmes (2007) in showing a right forelimb in a semi-erect standing pose, in anterior and lateral views, but differed from their reconstruction in being orthographic in nature.

One obstacle encountered during the reconstruction process was the limited availability of reference material. All known *P. lakustai* specimens are from the Pipestone Creek Bonebed south of Wembley, Alberta, in which juvenile to adult bones are preserved in a disarticulated condition with varying degrees of distortion (Ralrick & Tanke 2008). The consequent lack of a complete, undistorted, and articulated adult *P. lakustai* forelimb led to heavy reliance on other ceratopsids, including *Centrosaurus*, *Styracosaurus*, *Vagaceratops, Triceratops,* and *Pachyrhinosaurus* sp. from the Wapiti River Bonebed (WRB) locality (Fanti *et al.* 2015), to fill the gaps in the *P. lakustai* hypodigm. For example, several well preserved centrosaurine specimens of varying completeness, such as the *Centrosaurus* humerus UALVP 55164 and the *Styracosaurus* partial skeleton UALVP 55900, provided information on osteological details such as tubercles and ridges. Given the need to rely on observations from other ceratopsid taxa, even the final version of the reconstruction represents a more or less provisional hypothesis that could readily be tested further should an articulated pectoral girdle and forelimb of *P. lakustai* be found in the future.

The reconstruction used reference photos of *P. lakustai* bones as a starting point. The orthographic approach made it necessary to "flatten" many elements captured in the reference photos, removing the effects of perspective to keep the positions of key landmarks consistent across both views. To minimise the amount of perspective distortion in the original reference photos, a telephoto camera lens with a focal length from 50-75 mm was used whenever this was logistically feasible. Photos of complete and articulated ceratopsid forelimbs, primarily an articulated right *Centrosaurus apertus* forelimb (UALVP 55261) that was available for direct examination, and *Triceratops* (NSM PV 20379) and *Vagaceratops irvinensis* (CMN 41357) specimens described in the literature (Thompson & Holmes 2007; Fujiwara 2009), were used as a basis for scaling and orienting the elements in both views. Because most of the bones were steeply inclined either anteroventrally or posteroventrally, perspective had a strong impact on the anterior view, which was corrected by projecting multiple landmarks from the lateral view into the transverse plane as a guide to the proper proportions of each element. Perspec-
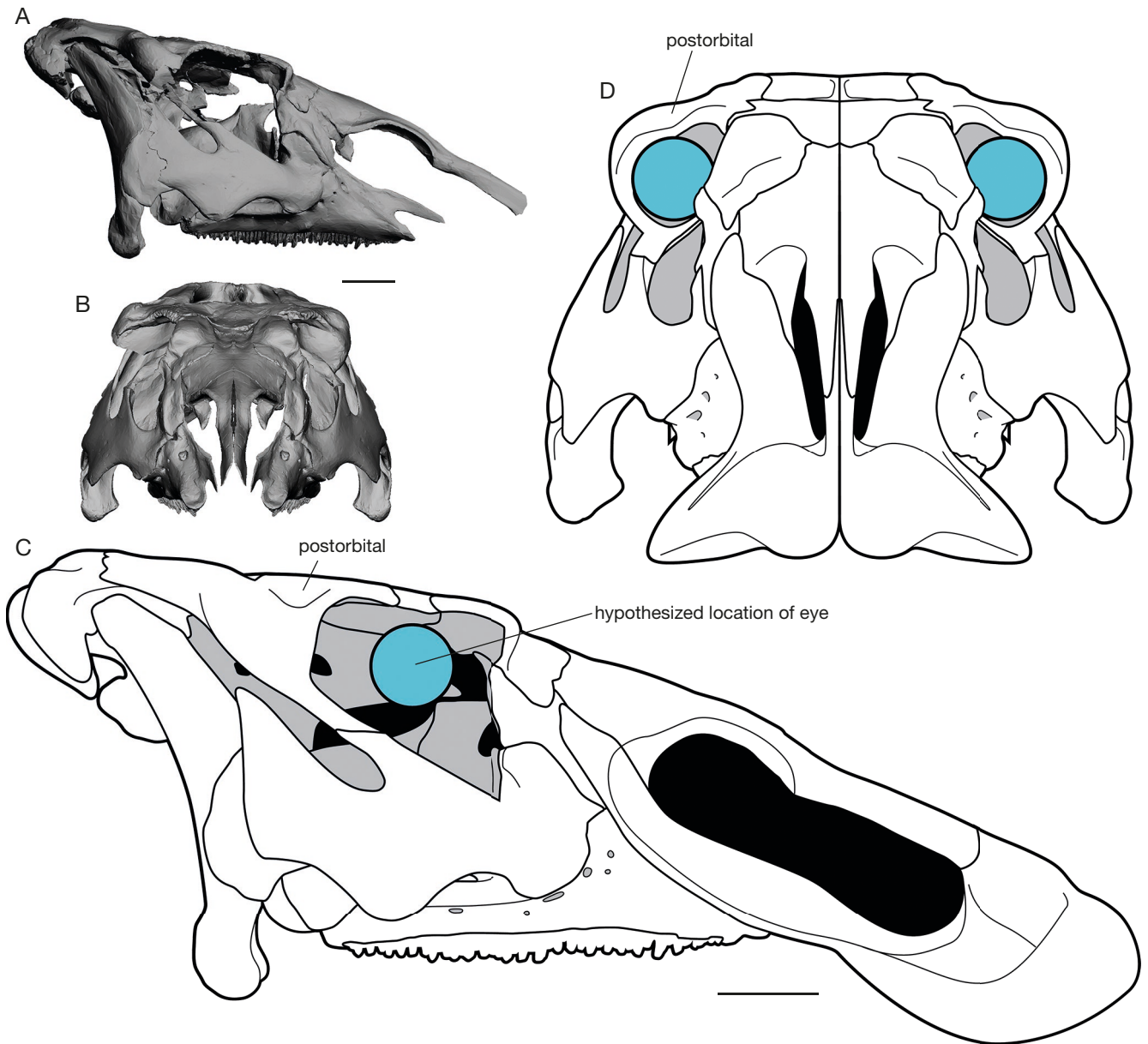
Fig. 4. — Cranial anatomy of the hadrosaurid dinosaur *Edmontosaurus regalis* Lambe, 1917: **A**, **B**, digital model of scanned, retrodeformed, and reassembled skull of *E. regalis* CMN 2289: **A**, right lateral view; **B**, anterior view; **C**, **D**, orthographic reconstructions of the skull of *E. regalis*: **C**, right lateral view; **D**, anterior view. Reconstruction based mainly on CMN 2289, with missing portions filled in using other specimens of *E. regalis* (NHMUK R8927 and ROM 801). Position of the eyeball inferred from a sclerotic ring preserved in a specimen of *E. annectens* (Marsh, 1892) (ROM 57100). Scale bars: 10 cm.

tive effects on the lateral view were less pronounced, because the limb segments were not strongly angled relative to the sagittal plane, and were considered to lie within the margin of acceptability given the use of the telephoto lens.

The reconstruction process led to novel insights into the forelimb anatomy of *P. lakustai*, particularly with respect to the structure of the metacarpus. The metacarpal configuration of centrosaurines is poorly known, so the reconstruction of the *P. lakustai* manus was informed by previous work on associated, and in some cases articulated, specimens of other neoceratopsians, mostly chasmosaurines (Thompson & Holmes 2007; Fujiwara 2009; Mallon & Holmes 2010). Thompson & Holmes (2007) reconstructed the manus of

V. irvinensis with only slight contact between the proximal heads of the metacarpals, which were all depicted as being in approximately the same plane (Fig. 5D). The metacarpus of *P. lakustai* was initially reconstructed in a similar configuration, but this resulted in a proximal articular surface that was substantially wider than the opposing articular surface formed by the distal ends of the ulna and radius, a clearly implausible arrangement even allowing for the likely presence of both ossified and cartilaginous carpal elements. Additionally, Holmes (2022 pers. comm.) indicated that Thompson & Holmes (2007) had deliberately flattened and spread out the metacarpus of *V. irvinensis* to better show the morphology of each element.
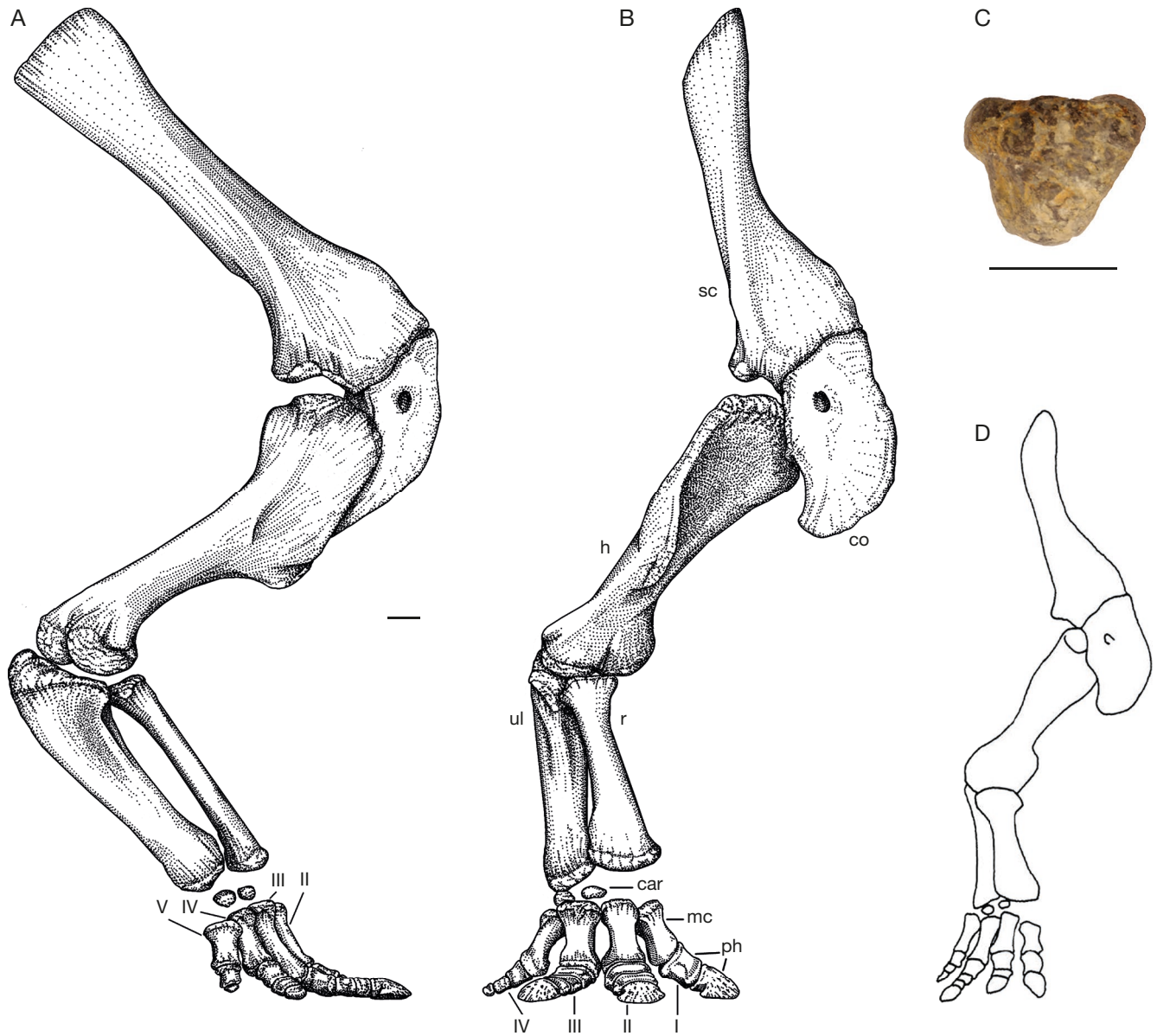
FIG. 5. — **A**, **B**, Reconstructed right shoulder girdle and forelimb of ceratopsid dinosaur *Pachyrhinosaurus lakustai* Currie, Langston & Tanke, 2008 in a hypothetical standing pose: **A**, lateral view; **B**, anterior view; **C**, proximal view of left metacarpal II of *Pachyrhinosaurus lakustai* (UALVP 54961), showing subtriangular outline of proximal articular surface; **D**, reconstructed forelimb of *Chasmosaurus irvinensis* Holmes, Forster, Ryan & Shepherd, 2001 in anterior view, posed in semi-erect stance as inferred by Thompson & Holmes (2007). Abbreviations: **car**, carpal; **co**, coracoid; **h**, humerus; **mc**; metacarpal; **ph**, phalanx; **r**, radius; **sc**, scapula; **ul**, ulna. Roman numerals identify digits. Scale bars: A-C, 5 cm; D, not to scale. Credits: C, Rebekah Vice; D, Thompson & Holmes (2007).

Accordingly, the reconstruction of *P. lakustai* was revised to show a more transversely arched metacarpus with the proximal heads of the metacarpals in closer contact (Fig. 5A, B). This resulted in a proximal articular surface that better fitted the distal articular surface of the antebrachium, and the arched metacarpus also resembled those of *Triceratops* (Fujiwara 2009) and the well articulated but indeterminate chasmosaurine CMN 8547 (Mallon & Holmes 2010). Moreover, transverse arching of the metacarpus is consistent with the fact that the proximal surface of metacarpal II strongly tapers ventrally (Fig. 5C), and the presence of rugosities indicates possible close intermetacarpal contacts near the proximal ends of some of the metacarpals known from the Pipestone Creek Bonebed. However, the proximal end of metacarpal III appears more medially expanded relative to the shaft in *P. lakustai* than in chasmosaurines, implying correspondingly greater separation between the shafts of MC II and MC III (Thompson & Holmes 2007; Fujiwara 2009; Mallon & Holmes 2010). For this reason, the shafts of these metacarpals are separated by a distinct gap in our reconstruction of the manus of *P. lakustai* (Fig. 5B), rather than closely adjacent as in Fujiwara's (2009: fig. 8B) reconstruction of the manus of *Triceratops* Marsh, 1889 and Thompson & Holmes' (2007) reconstruction of *V. irvinensis* (Fig. 5D). Verification of the arched configuration and the degree of separation between the shafts of MC II and MC III awaits a detailed description of the articulated manus of a centrosaurine, and ideally of *P. lakustai* specifically. However, the chasmosaurine condition,

Fig. 6. — Left tibia, fibula, and calcaneum of an indeterminate ceratopsid dinosaur (UALVP 42) as restored and articulated by George Sternberg for display of the distal part of the left hindlimb as a mount. The mount was dismantled in the late 1950s, but the bones shown here remain as positioned by Sternberg because the tibia and fibula are bolted together, and the calcaneum is firmly affixed to the fibula. Some areas have been retouched with plaster mixed with paint, which can be difficult to distinguish from the remaining original bone: **A**, elements in anterior (**left**) and posterior (**right**) views; **B**, elements in close-up anteromedial view, showing the gap (**red arrow**) introduced by Sternberg between the tibia medially and the calcaneum and distal part of the fibula laterally. Abbreviations: **c**, calcaneum; **fib**, fibula; **otc**, outer tibial condyle; **tib**, tibia. Scale bars: 10 cm.

the morphology of the proximal ends of the metacarpals of *P. lakustai*, and the geometric fit between the articular surfaces of the antebrachium and metacarpus all weigh against the hypothesis that the metacarpals were widely spaced and in a single plane, suggesting that the metacarpus of *P. lakustai* was indeed transversely arched.

CASE STUDY III:

HINDLIMB OF AN INDETERMINATE CERATOPSID DINOSAUR
One of us (BT) created a reconstruction of UALVP 42, an indeterminate ceratopsid left partial hindlimb comprising almost all the crural and pedal elements, to explore and illustrate the articular configuration of the lower hindlimb in Ceratopsidae for a future descriptive paper (Theurer *et al.* work in progress). The reconstruction was informed by published descriptions of ceratopsid hindlimbs (e.g. Brown 1917; Lull 1933; Currie *et al.* 2016: fig. 15) and a ceratopsid footprint (Gierlinski & Sabath 2008: fig. 10F), and to a lesser extent by descriptions of hindlimbs of other ornithischians (e.g. Forster 1990: fig. 21; Salgado *et al.* 1997: fig. 5). A model segmented from a CT scan of the juvenile *Chasmosaurus belli* Lambe, 1902 skeleton UALVP 52613 was also available for comparison.

UALVP 42 was collected by George F. Sternberg in 1920, from exposures of the Belly River Group (Campanian) on Sand Creek in southern Alberta. Sternberg subsequently created a mount of the specimen that was displayed from 1935 to the late 1950s, reconstructing the distal hindlimb skeleton in a physical sense. As well as positioning the bones, Sternberg restored some of them extensively with plaster to conceal damage (Fig. 6). The proximal and distal ends of the tibia, in particular, were heavily retouched. Having been mixed with brown paint, the plaster is difficult to distinguish from the original fossil bone. Therefore, the bones were CT scanned using a Siemens Somatom Definition Flash scanner at the University of Alberta Hospital (voltage: 120 kV; current: 300 mA; voxel size: 0.6 mm), and the genuine bone was segmented out using Dragonfly ORS. A defined range of intensities was used to create an initial "point and click" segmentation, which was then refined manually a few slices at a time. The scanned bones were imported into Autodesk Maya, an animation program that can be utilised to position digital models in 3D space and produce 2D orthographic and perspective renderings of them from arbitrary angles.

TABLE 1. — Ratio of the length of phalanx I-1 to the length of metatarsal I in several ceratopsids. Length measurements were made from images with metatarsal I and phalanx I-1 in the same focal plane, using ImageJ (Schneider *et al.* 2012). The median ratio was used to determine that the expected length of phalanx I-1 for UALVP 42 was approximately 88.45% the length of phalanx I-1 in UALVP 16248. The digital model was scaled accordingly for the reconstruction.

Specimen	Taxon	Ratio
AMNH 5351 cast (right foot)	*Centrosaurus apertus* (Lambe, 1905)	1.021
CMN 8547	Indeterminate chasmosaurine	0.986
TMP 2002.076.0001	Indeterminate pachyrinosaurin	0.893
CMN 41357	*Vagaceratops irvinensis* (Holmes Holmes, Forster, Ryan & Shepherd, 2001)	0.885
TMP 1989.097.0001	*Styracosaurus albertensis* Lambe, 1913	0.883
AMNH 5351 cast (left foot)	*Centrosaurus apertus*	0.859
Median	–	0.889

The only distal hindlimb bone missing from UALVP 42 is the proximal phalanx of digit I. The Sternberg mount included another bone in place of this element, but comparison with the left metacarpal IV of *Styracosaurus albertensis* CMN 344 (Holmes *et al.* 2005: pl. 30G-J), in particular, indicates that this substitute is actually a ceratopsid metacarpal. Sternberg may have borrowed the metacarpal, which has not been retouched with plaster in the same manner as the genuine hindlimb elements of UALVP 42, from another specimen, but this possibility is unsupported by any documentation. To complete our reconstruction of UALVP 42, a 3D model of phalanx I-1 from an associated skeleton of the ceratopsid *Centrosaurus apertus* (UALVP 16248) was created using photogrammetry and the program Agisoft Metashape, and a small piece missing from the anteromedial corner of the proximal end was reconstructed in Pixologic ZBrush. The resulting model was imported into Maya and scaled to an appropriate size for UALVP 42, based on the median ratio of phalanx I-1 length to metatarsal I length (0.889) in several other ceratopsid specimens in which both elements are preserved (Table 1). This procedure involved a tacit assumption, amenable to testing in future comparative studies, that the morphology of phalanx I-1 was unlikely to vary much across ceratopsid species.

Maya was used to reconstruct the articulation of the bones of UALVP 42, plus the rescaled phalanx I-1, and generate an image of the reconstructed configuration (Fig. 7A). Sternberg's restoration of the shape of each individual bone was provisionally accepted as a well-educated guess, with the obvious exception of phalanx I-1, but the digital reconstruction distinguished visually between bone and plaster based on the segmented models. One advantage of this method of reconstruction was that internal consistency among the resulting 2D images was guaranteed, given that they all depicted the same 3D model. Therefore, successive versions of the reconstruction always passed the test of internal consistency provided no two elements overlapped in 3D space. Furthermore, "versions" of the underlying 3D model could be quickly generated by rotating and translating individual bones to experiment with different possible configurations, and quickly evaluated by viewing the model from different angles. Accordingly, the iterative process outlined above, in which visual hypotheses are tested, rejected and refined over successive rounds, gave way to a more free-flowing approach in which generation, testing, rejection and refinement of "micro-hypotheses" pertaining to parts of the model took place more or less continuously.

Subjecting the proximal tarsal elements to this type of manipulation led to an unexpected arrangement of the astragalus relative to the calcaneum and to the outer condyle of the distal end of the tibia, which in ceratopsids combines with the two proximal tarsal elements to form the articular surface for the distal tarsals and the proximal ends of the metatarsals (Brown & Schlaikjer 1940). Sternberg's original mount placed the calcaneum lateral to the outer condyle of the tibia and only slightly anteriorly displaced (Fig. 6). This initially led us to likewise place the astragalus medial and slightly anterior to the outer condyle of the tibia in our digital reconstruction (Fig. 7B). However, it quickly became apparent that positioning the astragalus in this way, without creating an impossible geometry by impinging on the tibia, introduced a large gap between the lateral articular surface of the astragalus and the outer tibial condyle (Fig. 7C). Such a large gap seemed unrealistic, so the hypothesis of a near-linear arrangement of the astragalus, calcaneum and outer condyle was rejected and alternatives were investigated. Angling the astragalus so that the medial side was positioned more anteriorly than the lateral side eliminated the gap (Fig. 7D, E) and left the anterior part of the proximal surface of the astragalus resting against a relatively flat area on the anteromedial portion of the distal end of the tibia, and the lateral articular surface of the astragalus against the outer tibial condyle. The anterior margin of the distal articular surface formed by the astragalus, outer tibial condyle and calcaneum is then distinctly concave. It should be noted that acceptance of Sternberg's restoration of the missing portions of the tibia influences the exact position, but not the overall orientation, that appears optimal for the astragalus.

Sternberg's placement of the calcaneum almost directly lateral to the outer condyle of the tibia (Fig. 7B, C) was evaluated by comparison to UALVP 52613 and published descriptions of ceratopsid hindlimbs (e.g. Lull 1933), which indicated that the calcaneum should instead lie anterior to the outer tibial condyle. Repositioning of the calcaneum in accordance with this evidence further accentuated the anterior concavity of the articular surface for the distal tarsals and metatarsals (Fig. 7D). The articular relationship between the astragalus and tibia in UALVP 42, and the resulting concavity of the anterior margin of the distal articular surface formed by these elements and the calcaneum, are discoveries arising from the process of reconstruction and supported by comparison with published descriptions and UALVP 52613.
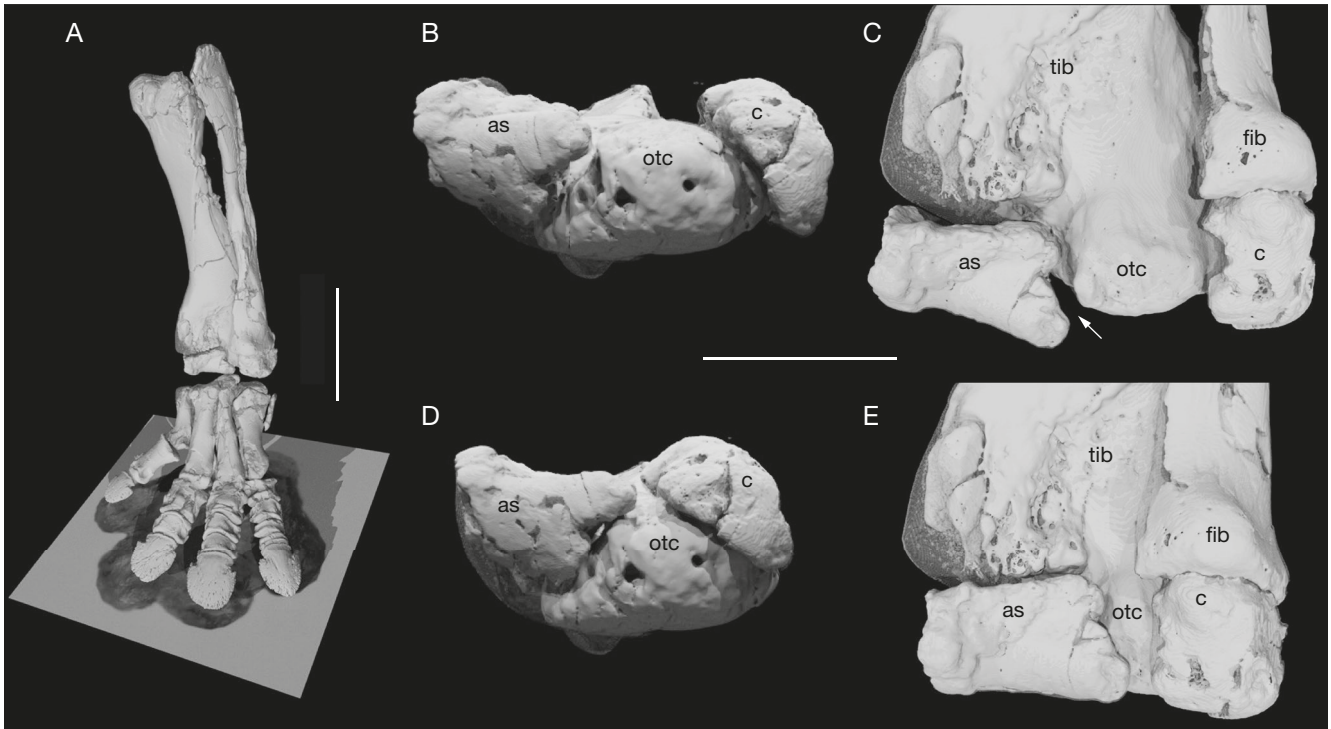
Fig. 7. — Reconstructed articular configuration of distal part of left hindlimb of an indeterminate ceratopsid dinosaur (UALVP 42): **A**, perspective view of entire reconstructed crus and pes standing on scaled ceratopsid footprint. Opaque areas represent original bone material, while transparent ones represent plaster. Phalanx I-1 from UALVP 16248, an associated *Centrosaurus apertus* (Lambe, 1905) skeleton from Dinosaur Provincial Park, with missing anteromedial corner of proximal end restored in Pixologic ZBrush but shown as transparent. Footprint adapted from Gierlinski & Sabath (2008: fig. 10F). **B-E**, two postulated articular configurations of the crus and proximal tarsals in distal (**B**, **D**) and anterior (**C**, **E**) orthographic views; **B**, **C**, astragalus, outer tibial condyle, and calcaneum aligned roughly along a mediolateral line; **white arrow** points to large gap between astragalus and outer tibial condyle; **D**, **E**, astragalus angled in order to eliminate the gap, with the medial side farther anterior than the lateral side, and the calcaneum placed anteriorly. Abbreviations: **as**, astragalus; **c**, calcaneum; **fib**, fibula; **otc**, outer tibial condyle; **tib**, tibia. Scale bars: A, 20 cm; B-E, 10 cm.

CONCLUSION

Visual information plays a crucial role in scientific exploration of the natural world, including in palaeontology. When specimens that are relevant to a particular research endeavour cannot be examined directly, published images of them become a key source of morphological information, together with descriptive text. Reconstructions, by contrast, convey visual hypotheses about the structure and potentially the functionality of extinct taxa, often generated by researchers and illustrators over painstaking hours of careful consideration.

The process of generating a rigorous reconstruction not only requires informed judgement, but represents a hypothetico-deductive undertaking in which versions of the reconstruction are iteratively tested, rejected and modified on the basis of internal consistency and congruence with empirical evidence about the reconstruction's subject. Over successive rounds of this procedure, rejection of some possibilities and acceptance of others is likely to lead to concrete first-order inferences about the subject's anatomy, which may in turn provide a basis for second-order inferences regarding its palaeobiology. The act of preparing a reconstruction is therefore an analytical operation, rather than a merely illustrative one, and can be an important part of a palaeontologist's research on a particular taxon.

The case studies in this contribution provide specific examples from dinosaur palaeontology, involving the skull of the hadrosaurid *Edmontosaurus,* the forelimb of the ceratopsid *Pachyrhinosaurus*, and the hindlimb of an indeterminate ceratopsid, of how reconstruction represents a process of hypothesis testing and a potential source of discoveries. They support the view that reconstruction of extinct taxa is a fruitful scientific methodology in its own right, and one that deserves more explicit consideration and discussion in the palaeontological literature than it has so far tended to receive.

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