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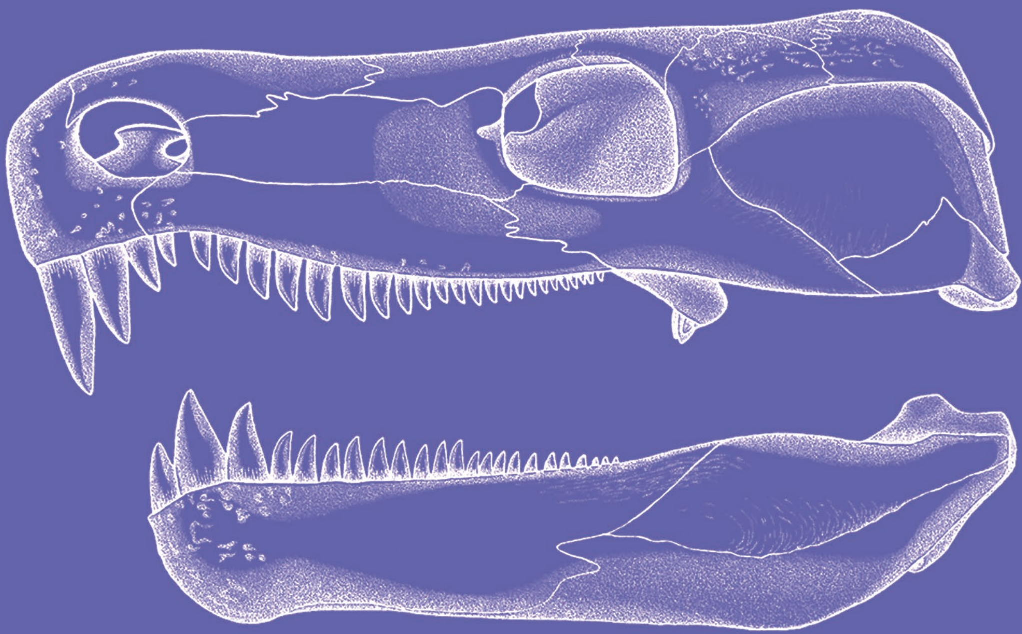

THE IMPORTANCE OF SCIENTIFIC ILLUSTRATIONS IN PALEONTOLOGY: A TRIBUTE TO DIANE SCOTT
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A methodology for skull reconstruction

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ABSTRACT
The reconstruction process of the skull and skeleton represents a critical step in the study of fossil vertebrates and is often responsible for how the evolutionary history of a taxon is interpreted. It is also an important step in any test of the researcher's understanding of the anatomy of the fossil. Even so, there is no recognized method for its completion, leaving the actual process to the individual undertaking the investigation. While this is often accomplished in an appropriate manner, there remains extensive room for error. With the onset of cladistic methodology dating back to the 1980s, character state description has become ever more critical in establishing phylogenetic histories, and over a period of 40 years, character state interpretation has often relied on specimen drawings and reconstructions. Based on a career dedicated to the detailed skeletal reconstruction of tetrapods, the content presented here highlights a stepwise approach that is designed to minimize error and increase the value of fossil reconstructions. We describe the skull reconstruction of the Palaeozoic tetrapod *Limnoscelis paludis* Williston, 1911 and highlight some of the more critical strategies that are necessary to maximize accuracy and hence increase phylogenetic reliability as well as support opportunities for testing anatomical interpretations as well as functional and ultimately behavioural interpretations. We also take the opportunity to highlight the extensive career contributions made to the field of palaeontology by Diane Scott, who for over 40 years has represented the *nec plus ultra* of fossil preparation, illustration, and reconstruction.

KEY WORDS
Skeletal reconstruction,
specimen drawings,
reconstruction
techniques.

RÉSUMÉ
Une méthodologie pour la reconstruction du crâne.
Le processus de reconstruction représente une étape critique dans l'étude du matériel fossile et est souvent responsable de la façon dont l'histoire évolutive d'un taxon est interprétée. Il s'agit également d'une étape importante pour vérifier la compréhension de l'anatomie du fossile par le chercheur. Malgré cela, il n'existe aucune méthode reconnue pour son achèvement, laissant le processus réel à la personne qui entreprend l'enquête. Bien que cela soit généralement accompli de manière appropriée, il reste une marge d'erreur. Avec l'apparition de la méthodologie cladistique remontant aux années 1980, la description des états de caractères est devenue de plus en plus critique dans l'établissement des histoires phylogénétiques, et sur une période de 40 ans, l'interprétation des états de caractères s'est souvent appuyée sur des dessins de spécimens, y compris des reconstructions. Basé sur une carrière consacrée à la reconstruction détaillée des tétrapodes, le contenu présenté ici met en évidence une approche par étapes conçue pour minimiser les erreurs et augmenter la valeur des reconstructions de fossiles. Nous décrivons la reconstruction du crâne du tétrapode paléozoïque *Limnoscelis paludis* Williston, 1911 et mettons en évidence certaines des stratégies les plus critiques qui sont nécessaires pour maximiser la précision et donc augmenter la fiabilité phylogénétique, ainsi que les opportunités de soutien pour les interprétations fonctionnelles et finalement comportementales. Nous profitons également de l'occasion pour souligner l'importante contribution de Diane Scott au domaine de la paléontologie, qui, pendant plus de 40 ans, a représenté l'avant-garde de l'illustration et de la reconstruction fossile.

MOTS CLÉS
Reconstruction squelettique, dessins de spécimens, techniques de reconstruction.

INTRODUCTION

The discipline of palaeontology has undergone major changes over the last four decades, not the least of which is the methodology applied to 2D (i.e., illustrations and other renderings) and 3D (mounted skeletons and life restorations) skeletal reconstruction. For much of the first two centuries, dating back to the early 19th century, skeletal reconstructions were primarily limited to the mounting of skeletons for museum displays. This traditional approach to mounting skeletons for display continued well into the 20th century and in many ways continues to this day; anyone from the middle of the 20th century into the 1980s could probably recall seeing a tripod mounted skeleton of *Tyrannosaurus rex* Osborn, 1905. While the limits imposed on skeletal mounts were a by-product of the iron frameworks that were required to support the heavy fossil skeletons and plaster casts before the advent of lightweight resin casts, they did not necessarily reflect the understanding of late 19th century and early 20th century palaeontlologists. It is necessary to keep in mind that these skeletal reconstructions were primarily for display purposes and did not necessarily serve as a basis for further palaeontological study. While illustrative reconstructions were produced, such as Marsh's (1896) Dinosaurs of North America, these attempts were rather subjective and generated more as creative or artistic perspectives that were not meant to lead to formal hypotheses testing. In Sullivan *et al.* (2024), a very convincing argument as to the value of a formal reconstruction is presented, which stands in sharp contrast to the more artistically inclined approach exemplified by Marsh and his contemporaries.

Skeletal reconstructions can serve multiple scientific purposes, including as a basis for biomechanical studies and also phylogenetic analyses. The biomechanical value of accurate reconstructions is detailed in the work included in this issue (Sullivan *et al.* 2024), but more critically, a reconstruction based on a comprehensive methodology is an integral part associated with the examination of the entire biology of extinct taxa, and a reliable and accurate reconstruction is, therefore, a necessary step in reconstructing the life of the past. While we acknowledge that both biomechanical and phylogenetically relevant information can be gleamed from accurate reconstructions, we do not suggest that these are the only benefits to its use, but will instead focus on the necessary steps that are essential for a comprehensive reconstruction.

Phylogenetically, it was during the latter part of the 20th century that the application of cladistic methodology was in full bloom, as evidenced in vertebrate palaentology by such major works on phylogenetic systematics as Gaffney 1980; Benton 1985, 1991; Heaton & Reisz 1986; Benton & Clark 1988; Estes & Pregill 1988; Gaffney & Meylan 1988; Panchen & Smithson 1988; Gauthier *et al.* 1988; Hopson 1990; Laurin 1991; Sereno 1991; Wible 1991; Carroll & deBraga 1992; Modesto & Reisz 1992; and Norell & Novachek 1992. At this time, with the ever-increasing need for larger phylogenetic matrices, investigators often turned to published specimen illustrations and reconstructions as a basis for coding morphological characters. The issue that arose was that not all of the illustrations being used to glean the characters were sufficiently accurate for the purpose of correctly inferring morphological character states. A cursory review of the literature reveals a wide range of accuracy in the quality of reconstructions. For example, it would not be unusual for the total length of a reconstructed skull to appear different in palatal and lateral views. For example, Carroll (1969) based the different views of the skull reconstruction of *Palaeothyris* Carroll, 1969 on different specimens resulting in discordance between each of the reconstructed views. Such errors may have been the result of a poor understanding of the fossil material, of drafting principles, or both.

Technological innovations can help with some aspects of reconstruction, but they don't solve everything. The early 1990s saw the appearance of digital software such as Adobe Photoshop© and Adobe Illustrator©, to name but two, which effectively sped up the drafting process. However, the process of ensuring accurate reconstructions, where there is concordance with all views, required a level of commitment to detail that was often limited. Computed tomography (CT) provides a new approach for investigating morphology, providing advantages of an X-ray view of the material. Yet even segmentation of fossil material using digitized data from CT scans, which presumably eliminates the potential subjectivity of the examiner and thus effectively reduces possible misinterpretation of fossil material, may inadvertently contribute to a false degree of confidence regarding anatomical information, as the nature of the CT scan is not immune to potential errors in anatomical interpretation, which can result from resolution-based limits associated with how the various densities of the scanned material (i.e., bone vs matrix) are rendered by the software. Even in the absence of resolution-based caveats, accurate fossil reconstructions must still undergo a comprehensive step-by-step reconstructive process in order to ensure an accurate restoration. However, unless the fossil material has been preserved entirely without distortion, relying exclusively on the digitized scanning of the fossil material to establish an accurate restoration is problematic, and the investigator could be led to false conclusions regarding a given character state, which could in turn hinder an accurate interpretation of the material and lead to errors in the resulting functional and/or phylogenetic conclusions.

Given the uneven quality of published reconstructions many palaeontologists insist on examining original material so that they can interpret the fossil characters directly and not through the lens of another investigator. This does serve to raise one very important question: if original reconstructions cannot be fully trusted, then what is the point of creating fossil reconstructions? We would argue that skeletal reconstructions are a necessary component of descriptive paleontology and it is only through accurate reconstructions that viable interpretations of functional morphology and characters for phylogenetic hypothesis testing can be fully realized. As such, in this paper, we have endeavoured to describe what we believe are the critical steps in ensuring the accuracy of a fossil reconstruction, whether traditionally or digitally rendered.

The approach described here is primarily derived from Diane Scott who worked at what was originally Erindale College, a satellite campus of the University of Toronto where she was a fomer student of Robert Reisz, who had personally gained an appreciation for the value of reconstructions when he had been a student of Dr Robert L. Carroll at McGill University. Reisz's experience with Carroll's scientific illustrator Pamela Gaskill, who had championed the orthographic process in fossil reconstructions, ultimately influenced the central theme of the Reisz and Scott reconstructive methodology that would evolve in the 1980s. Since then, and over a period that spanned nearly four decades, Diane Scott's critical attention to the method spawned its own unique approach that combined her skills as a preparator and comparative anatomist, attributes not shared by Carroll's illustrator Pamela Gaskill, and led Scott to establishing the vanguard for palaeontological reconstruction techniques, which in turn resulted in some of the most scientifically accurate and informative illustrations and reconstructions in the discipline.

Scott leveraged her skills as a preparator and illustrator to emphasize the importance of drafting reconstructions that were based on careful fossil preparation and specimen illustration. In doing so, she explored possible disconnects between what the fossil material exhibited and what she as the specimen illustrator was interpreting. This process provided her with ample opportunity to test the accuracy of the reconstruction and informed her interpretation of the individual reconstructive views and thus ensuring that there would be concordance between all views, thereby improving the reliability of the phylogenetic and functional (i.e., biomechanical) skeletal information that could be hewn from that reconstruction. Often, this meant that Scott would go back to the specimen and carefully do more preparation without weakening the fossil in order to check and measure particular parts of the specimen for the purpose of reconstruction. While the greatest impact to the field by Scott began in the 1980s and became much more relevant in the 1990s, the methodological approach was one that would continue to pay dividends even with the growth of the 21st century technologies that are the basis for fossil skeletal reconstructions in use today. In this paper, we use the holotype (Yale Peabody Museum – YPM 811) skull of the diadectomorph *Limnoscelis paludis* Williston, 1911 (Figs 1-4) most recently described by Fracasso (1983) and Berman *et al.* 2010; as a case study, and walk the reader through Scott's original reconstruction methodology.

METHODS

The reconstructive process comprises three-steps. The first step outlines the specimen illustrative process, which is now often accomplished through the digital segmentation of CT scanning. The second step details a conceptual framework for the reconstruction process, which applies even with the use of digital segmentation; and the third step outlines the techniques applied in reconstructing the skull along three primary axes.

The specimen illustration

Historically, before the advent of digital software applications such as Photoshop©, drawings would be completed on drafting grid vellum (ten squares to the inch) using a 2H drafting pencil. A light table would be recommended for redrawing and comparing views. Most present-day drawings skip this light table stage entirely and either rely on programs such as Photoshop© to help render high resolution photographs of the fossil or are accomplished using the latest CT scan technology and then rendered and/or segmented using a program such as Avizo© (Lautenschlager 2017). While this last approach is frequently applied in present-day illustrations of fossil material, and has the added benefit of significantly reducing or entirely eliminating the need to mechanically prepare a fossil before it is drawn, it also suffers from challenges which are a by-product of the perception that any computerized rendering of information is somehow objectively superior to a human-based effort. The perceived accuracy of a computerized rendering may be true in theory, but is often not well understood in practice nor does it take into account the possible gaps and inaccuracies that may be the result of limits to scan resolution or the quality of the rendering software. Regardless of which method is applied to illustrate the fossil, the illustration or representation of the fossil specimen represents the first step in the fossil reconstructive process and while a specimen drawing is not an essential step to render a reconstruction, it does provide additional opportunity for the illustrator to develop a more complete and critical view of the material. However, this step is ultimately influenced by the skill of the individual undertaking the segmentation and/or the illustration. This skill represents an artistic ability that emphasizes an awareness of scale and perspective and while this approach can certainly be mastered by almost anyone who is committed to the craft, it fails to address one critical difference between a fossil reconstruction and an artistic rendering – the fact that perspective must be handled entirely differently in a formal specimen reconstruction. This caveat is further complicated by the ability of the illustrator (i.e., the individual interpreting the material) to ensure that the information being illustrated is complete and has been interpreted correctly.

For example, in either of the more traditional approaches (i.e., pencil or Photoshop©), the illustrator must decide how to interpret the information on the fossil and ensure that noise, such as cracks and other potentially distracting elements (i.e., variation in surface texture associated with the matrix) not relevant to the material are eliminated from the specimen being drawn. While the digitized CT scan may initially appear to eliminate this concern, there are issues with the segmentation process, not the least of which is the thickness of the CT scan slices (ranging from a few microns up to 1 mm in thickness) and how these slices are rendered by the individual undertaking the study. For example, given the sheer number of slices in a scan, often 2000 or more slices, it is not uncommon for the segmentation process to be based on every third slice instead of every single slice. This is due to the amount of time required for the segmentation of a specimen. As such, in what might at first appear to be a much more accurate approach to fossil illustration, may still result in information being accidentally lost due to the number of slices being segmented. Now this is not to suggest that a traditional specimen illustration is significantly faster. While the drawing may be much faster, the time required to prepare the fossil, to expose it from the matrix for study, may exceed even the 200 to 300 hrs. necessary to segment every slice from a typical CT scan. Furthermore, the fact that a CT scan effectively leaves the fossil fully intact and hence prevents damage that ultimately may result from even the most careful fossil preparation suggests that the CT scan segmentation for fossil illustration may be the preferred method. In particular, this approach may protect the fossil material for future investigators, allowing them to examine an undamaged pristine fossil. It must be emphasized that a relatively small proportion of fossil materials can be effectively CT scanned, regardless of the energy source (Schwarz *et al.* 2005; Sutton 2008; Schambach *et al.* 2010; Mays *et al.* 2017). However, regardless of the initial form applied to the specimen illustration, the reconstructive process still requires the same commitment to concordance that ensures the most accurate and, therefore, most informative reconstruction.

Specimen reconstruction

This next step requires that accurate measurements of the specimen be undertaken. This is not normally an issue if the fossil is directly available, but could pose a serious source of error if only a photograph of the specimen is available as even the best photographs will result in some parallax resulting from camera optical distortion; as such, only the actual specimens should ever be used to establish accurate measurements. This may not be an issue for a specimen that has been CT scanned and segmented slice by slice if the data are of good quality. Furthermore, care should be taken to ensure that as many measurements as possible are taken from a single specimen. This is primarily to avoid problems arising from ontogeny or from variation between individuals, which can creep into a reconstruction. This is particularly relevant if additional specimens increase the potential to accentuate ontogenetic differences. If other skulls are used, correction factors for size and age affects may have to be introduced. In general, any additional specimens, actual or photographed, should only be used to establish the shapes, and relationships of the skull elements. However, given the general incompleteness of fossil material, it is quite likely, except in rare instances, that multiple specimens will need to be examined in order to fully complete a reconstruction.

Scaling of the measurements is often necessary either because the specimen is too small or too large for the eventual scale of the illustration. In traditional pencil and paper scaling, proportional dividers should be used to ensure accuracy. In the case of digital sources such as Photoshop© or CT scanned images using Avizo©, scaling is effectively automatic using the software and while this does represent a handy tool, with respect to the amount of time required to complete the rendering of a given specimen, the number of slices that are incorporated into the digital reconstruction are a factor, as the thickness of each slice can result in sutural misinterpretation and either underestimate or overestimate the point of contact between adjacent elements. In more traditional methods, proportional dividers are used to transfer the information from the specimen to the drafted

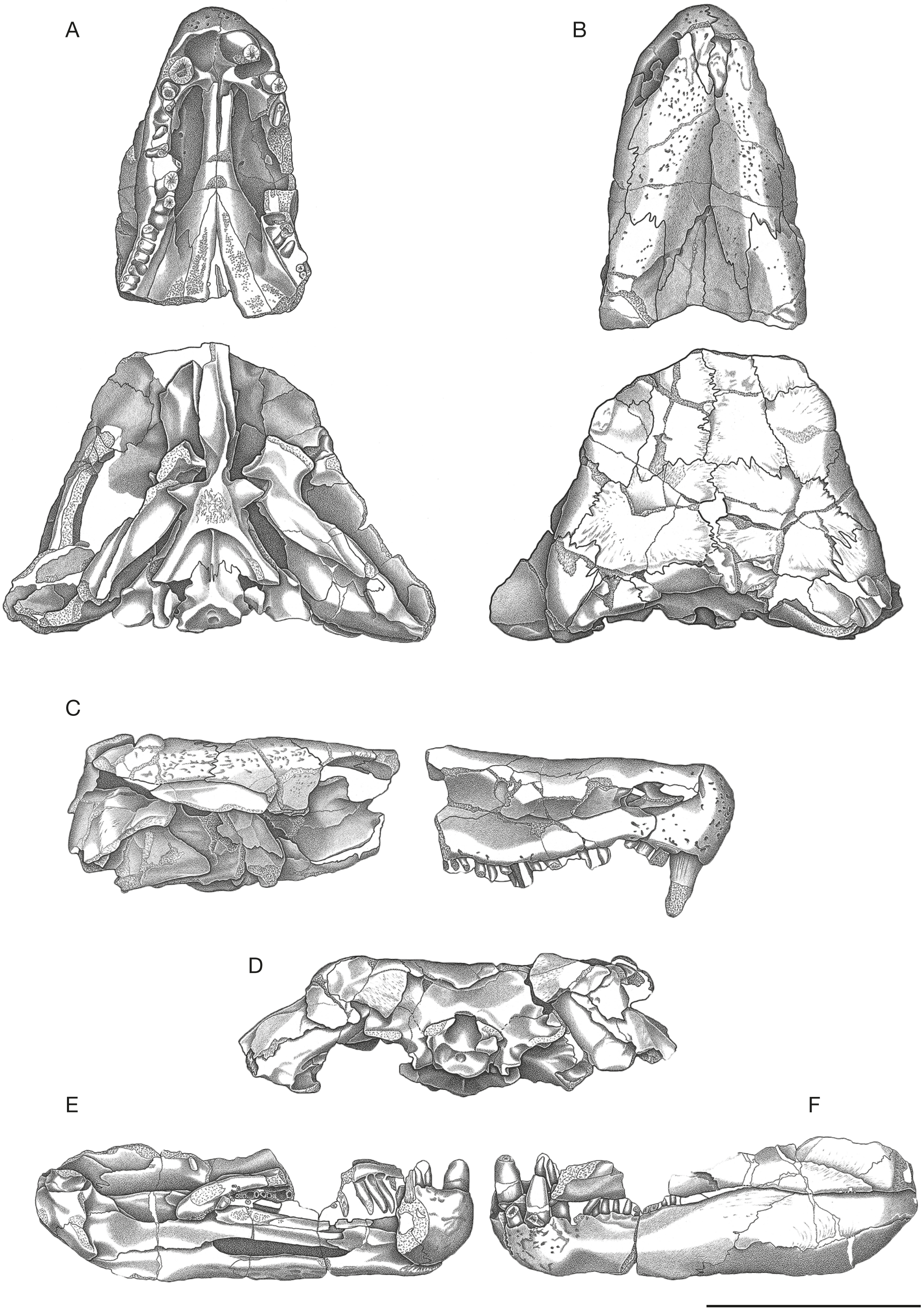

Fig. 1. — Specimen drawings of the skull of *Limnoscelis paludis* Williston, 1911 (Yale Peabody Musuem – YPM 811): **A**, palatal view; **B**, dorsal view; **C**, lateral view; **D**, occipital view; **E**, jaw in medial view; **F**, jaw in lateral view. Scale bar: 10 cm.

reconstruction and while this is not completed automatically, resulting in reconstructions that usually take several weeks, and likely take more time than digital reconstructions, they do benefit from a decreased likelihood of misinterpreting the direct sutural relationships. However, even with the use of this traditional approach, the proportional dividers should be checked periodically to ensure that they are at the correct scaling position. If the skull is very large, measurements will have to be taken using calipers and scaled accordingly.

RENDERING THREE-DIMENSIONAL INFORMATION

Although a skull reconstruction conveys three-dimensional information, it does not employ perspective techniques. We pointed this out as one of the major caveats of fossil reconstruction. The reason is that when using a reconstruction for anatomically and by extension phylogenetically informative reasons, all views must match up exactly. Notably the lateral view of an artistic illustration will often represent a slightly angled view, which addresses perspective, in that the slightly angled "pseudo-lateral view" are likely to all be approximately equidistant from the viewer, but which distorts the relationship of the elements of the skull to one another and hence any proportions or interpretations of the relationships of individual elements of the skull will be distorted. Eliminating perspective will result in structures that would be in "life" closer to the viewer, and hence would normally appear larger in a traditional artistic drawing, instead will not appear any larger in a formal reconstructive drawing than those that are farther away. Skull reconstruction, therefore, involves a process where landmarks distributed in three dimensions are projected onto a single plane, much like an architectural plan for a house or building. Each reconstructed view represents a different plane of mapping. In other words, a reconstruction is effectively an orthographic projection of the reconstructed specimen. Consequently, a measurement taken from any view will be represented as a true scaled measurement in the reconstruction.

Usually, four views of the skull are reconstructed: 1) palatal; 2) dorsal; 3) lateral; and 4) occipital. Sometimes, an additional anterior view is also rendered. However, this view is not usually a common representation of the specimen reconstruction process and will not be considered further here. Generally, it is recommended that the palatal view be drafted first. This is because the palate tends to be more conservative in form, is usually fairly flat, and is composed of robust elements that tend to preserve well and with less distortion than might be present for other elements of the skull. Even if the palate is distorted, it can be more easily corrected than other parts of the skull. When the elements are disarticulated or distorted, it may take several attempts before all the elements can be drafted. It is important to continually recheck your measurements and to keep in mind that this re-checking of measurements is necessary regardless of what the original source of the specimen illustration might have been. In other words, the reconstruction requires the same careful verification of measurements whether it was originally drawn directly from the fossil, high resolution photograph (i.e., illustrated using Photoshop©), or digitally segmented (Avizo©). Always keep old versions of the reconstruction, whether these are on drafting paper or digitally rendered using some computer graphic software to refer back to, and note areas of difficulty which may be introducing uncertainty into the reconstruction.

Assuming sufficient quality and completeness of the material, the palatal reconstruction will then serve to direct the reconstruction of the total skull length as well as some width dimensions. The outline of the palatal view can then be used when drafting the dorsal view. It is essential that discrepancies in the width of the skull table with respect to the width of the palate be considered and any correction applied where the evidence is more supportive. In other words, if once the dorsal view is completed and it does not correctly align with the palatal view, it will be necessary to re-examine the palatal reconstruction in order to assess where the misalignment might be.

Reconstruction of lateral view of skull (a detailed example)

The lateral view is constructed by projecting landmarks onto a parasagittal plane. The component of palatal view measurements that occur parallel to the midline can be used as a framework for starting the lateral view reconstruction. Keep in mind that this reconstruction does not apply perspective in the drafting process and as such it is this aspect of the reconstruction that is most often mis-represented in fossil skull reconstructions. The approach presented here precludes any chance of producing a false lateral view (see Fig. 2). In the false lateral view, the plane of mapping is parallel to the lateral margin of the skull. Because the outer surface of the skull is at an angle to the midline, a false lateral view reconstruction results in an overestimation of the true skull length. In a proper lateral view, some structures will appear foreshortened.

To illustrate the effect of foreshortening, Figure 3 (shaded rectangle) shows the difference in orbit length between the dorsal and lateral view. Note also in the case of *Limnoscelis*, the anterior margin of the orbit is not actually visible in dorsal view due to overhanging of the prefrontal bone; as a result the anterior margin of the orbits don't appear to precisely match in dorsal and lateral view. The difference in the anterior position of the orbit between the dorsal and lateral view is shown with a blue shaded box. A consequence of this overhanging bone is that the true orbital length is not discernable in any of the views. In this case, if the author wants to highlight the true length of the orbit, they could do so using an arrow in dorsal view to indicate the obscured location of the anterior margin of the orbit (Fig. 3). Other elements may also be foreshortened. For example, the maxilla will appear shorter in an orthographic representation of the element in lateral view than it would be if measured along its entire marginal length (Fig. 3). Note that the actual length of the maxilla marked by the line B – A is 2.5% longer than the apparent length marked at B – C.

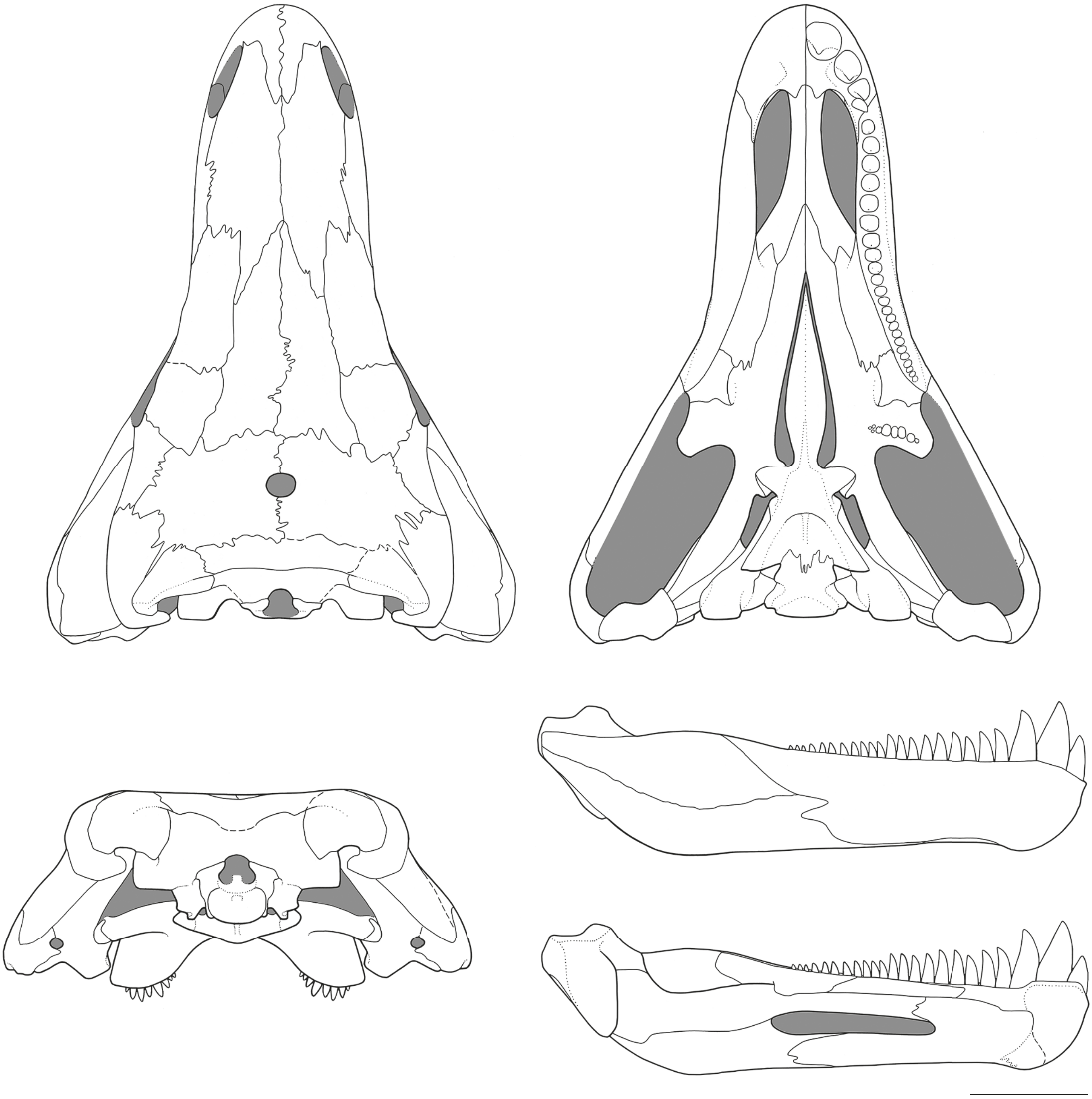

Fig. 2. — Line drawings of the reconstructed skull of *Limnoscelis paludis* Williston, 1911 (YPM 811). **Grayed areas** represent areas that are deeper than those of the exposed surface (i.e., white regions). Scale bar: 5 cm.

Let's consider these steps as a means of ensuring concordance with the dorsal and lateral views of the reconstructed specimen.

Begin by choosing a landmark at each end of the foreshortened structure on the specimen. The anterior landmark (Fig. 3A or C) is your fixed landmark. For this example, its position is located at the anterior-most point of the maxilla as viewed in the lateral reconstruction on Figure 3. The posterior landmark (Fig. 3B), can be determined by the posterior-most limit of the maxilla where it contacts the jugal. The resulting lateral reconstruction will obscure, to a degree the true direction of the long axis of the maxilla. The curvature of the skull in this region, therefore, not only foreshortens the length of the maxilla but also impacts on the orientation of the orbit, For example, from a biological interpretation perspective, the angle thus formed will help to determine the degree to which binocular vision might have been possible for the specimen in question.

To check the accuracy of the lateral reconstruction, superimpose it over the dorsal rendering of the skull and examine the relative position of the anterior (Fig. 3A or C) and posterior (Fig. 3B) margins of the maxilla or orbits (Fig.3). This superimposition can be accomplished using velum paper as it would be accomplished in traditional paper and pencil

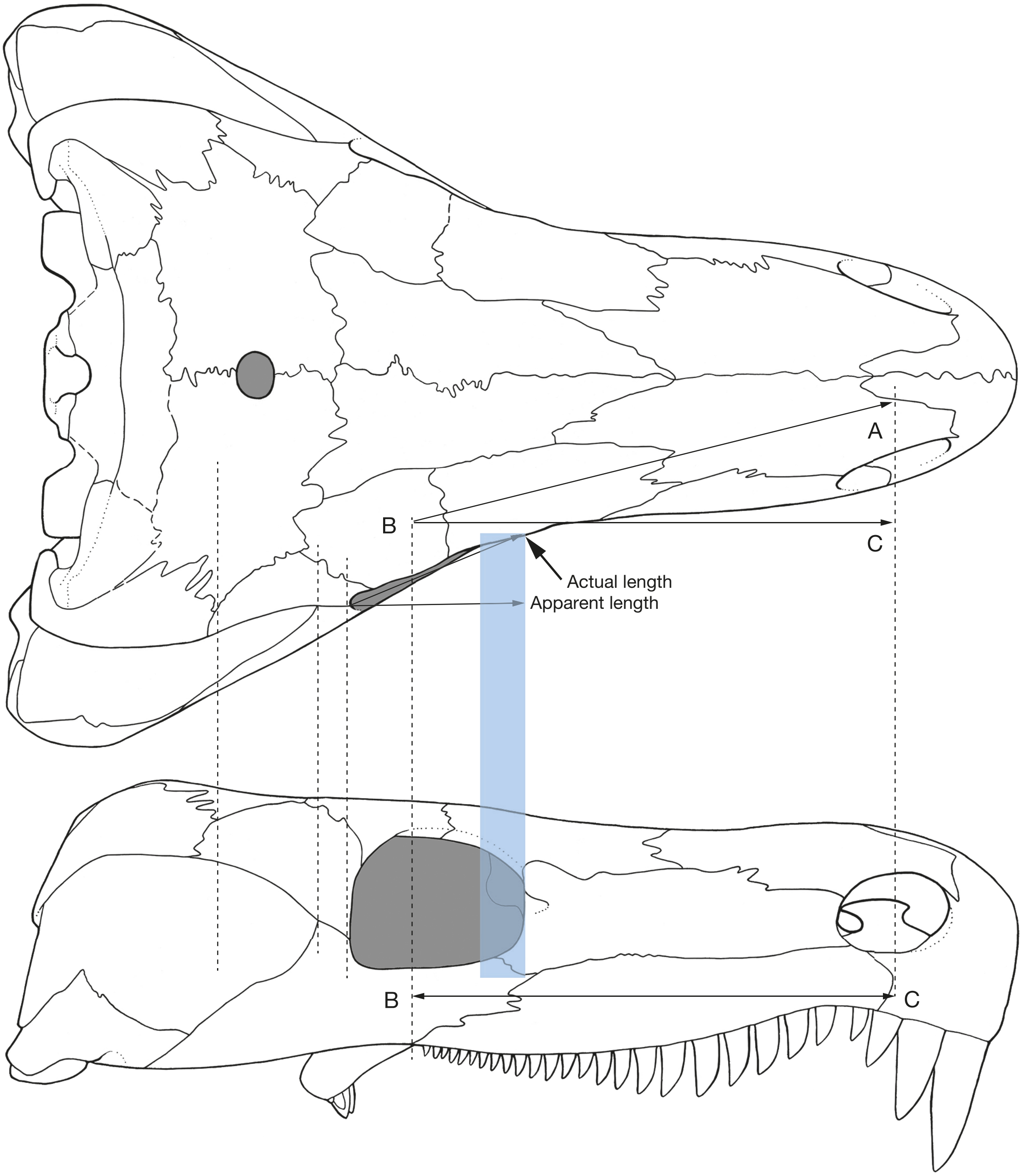

Fig. 3. — Line drawing reconstruction of the dorsal and lateral view of *Limnoscelis paludis* Williston, 1911 (YPM 811) depicting the manner in which concordance between alternative views are assessed. **Dashed lines** show points of concordance; **arrows** depict the lengths that result when examining the orthographic projection of the maxilla, as interpreted in the actual length (**B** to **A**) depicted in the dorsal reconstruction to how the length will be presented in lateral view (**B** to **C**). Note the large **bolded arrow** points to the anterior extent of the orbit which is hidden from view in dorsal aspect and **blue-shaded box** exposes the amount to which the orbit is effectively hidden in dorsal view.

reconstructions, or it can be accomplished using digital software such as Adobe Photoshop©. Note once again that given the orthographic nature of the lateral reconstruction, a direct parasagittal measure of the maxillary antero-posterior dimension will yield a measurement that is 2.5% actually shorter than the long axis of the entire maxilla.

The next step requires that the landmarks for the anterior and posterior margins of the elements being measured line up in both dorsal and lateral views. Note that in this step, the anterior or posterior limits of the orbital margin may be hidden in dorsal view (see shaded region highlighted in Figure 3). Any misalignment will require a reinterpretation of

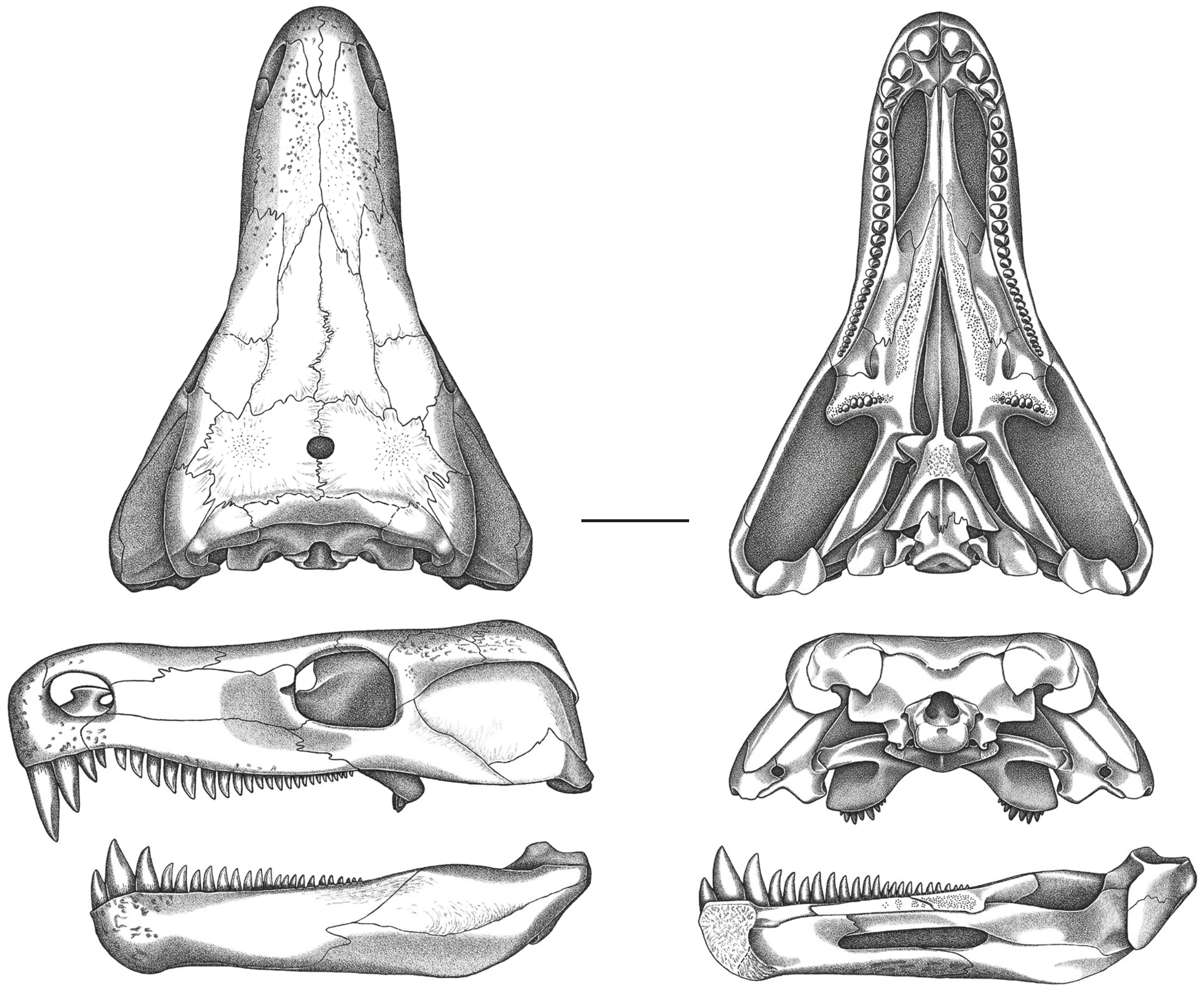

Fig. 4. — Full reconstruction of the entire skull and mandible of *Limnoscelis paludis* Williston, 1911 (YPM 811). These shaded illustrations were completed on coquille paper using a conté pencil and ink and then rendered digitally using Photoshop©. Scale bar: 5 cm.

the relationship of the relevant bones to the orbital margins, but with careful attention to this step, the exposure of the orbit in lateral view will accurately depict its natural appearance. In general, this approach should be applied to all openings in a skull, as they are presumably affected in a similar manner.

Finally, it is important to note that this alignment step will also serve as a means of verifying the degree to which other elements of the skull have been correctly rendered. For example, the anterior and posterior limits of elements such as the lacrimal must align in both dorsal and lateral views. If using a drawing application, Photoshop© in this instance, one simple method for assessing the alignment of the remaining skull elements is to draw a perpendicular line through both dorsal and lateral reconstructions at various points along the extent of the skull (as shown in Figure 3 by the dashed lines). The more of these perpendicular lines that are drawn the greater the accuracy of the reconstruction.

While foreshortening is most apparent when examining the lateral view of the skull reconstruction, it would be present wherever any view of the skull is angled in a manner that would result in perspective influencing the actual appearance of the given element. Some views are more sensitive to distortion whereas others are less so. One view that is relatively free from the influence of perspective, in stem amniotes such as *Limnoscelis* Williston, 1911, is the occipital view, which is explored briefly in the next section.

Occipital view and testing for concordance

The occipital view can be partially drafted by referring to the three views thus far described. As this view is determined by its best fit to the rest of the measurements from the skull, it is essential that any significant differences be accounted for and it is critical that when describing character states that reflect the occiput, that these states be carefully considered as it is likely that there will be a tendency for increased error especially where proportions are being assessed. As such character states that are linked to proportions of occipital elements must be considered carefully and should be used with caution.

The skull reconstruction becomes most difficult when all four views are under construction at the same time. Be prepared to go through many drafts of each view before reaching a final product. Remember to recheck your measurements, and keep old versions of each view. The process is only complete when there is agreement between all four views, with the possible exception of the occipital view, which should be considered carefully as it is the most prone to misinterpretation. This key step is perhaps the most critical as it tests each view for concordance. If during this "quality control" stage of the rendering produces any inconsistencies, each view must be examined and measurements and interpretations of curvatures etc. must be reconsidered.

One additional point to consider in preparing for the reconstruction process, is whether the mandible is also available. Presence of the mandible will provide an additional opportunity to assess overall shape of the skull, notably the region of the snout. If the mandible is not available, the skull reconstruction can be used to estimate the general architecture of the mandible, even if the actual detail of the anatomy remains unknown. If only jaw fragments are present, it might be possible to project these onto an estimated shape that would be determined by the skull reconstruction. Here again the major point to consider is that any attempt at reconstructing the mandible ensure that concordance with the known elements of the skull remain in agreement. On the other hand, if the mandible is very well preserved, it would provide an excellent opportunity to verify the curvature of the skull element associated with the snout and hence should be consulted early in the reconstruction process of the skull, as it may provide such valuable information as the position of the jaw joint relative to the palate.

Ultimately, the order in which the reconstruction process is undertaken is at the behest of the investigator and while we recommend a specific order to the reconstructive process, the method to be applied is limited by the condition of the fossil material under evaluation. Once the skull reconstruction is fully rendered, one remaining step would be the illustration, where some attempt at rendering the reconstruction through shading and or stippling is accomplished. We will explore the illustrative process in the section that follows.

ILLUSTRATION

The last stage in the reconstruction process is its illustration (Fig. 4). This step can either be accomplished through traditional paper and pencil or ink as historically accomplished or through the use of digital software or a combination of these approaches. Although the development of a personal style of scientific illustration is inevitable it is important to keep in mind that the illustration will be most easily interpreted by the viewer if the use of symbols is consistent and specific. Reconstructions are usually presented as a combination of line and shading. Lines should only be used to represent the edges of the skull and the sutures between elements. Distinguishing between the skull edge lines and the suture lines may be accomplished by using two-line thicknesses; the thinner line defining a suture. Sutures should be drawn as completely as possible in every view, and the position of those sutures that pose uncertainty should be represented with dashed lines.

Once the general outline of the skull along with all of the necessary sutures are in place, the final stage is the shading of the reconstruction. Here again, the method being applied is based on the expertise of the illustrator and can either be fully manual, as in the traditional Conté pencil shading, or ink-based stippling, or can be digitally rendered, or a combination of all of these techniques. One important point to consider, is that regardless of the method being employed, the use of lines for shading the skull should be avoided as they may obscure the appearance of sutures. It is conventional to render a given view as if the shadows were produced by a light source located in the upper left-hand corner of the field of view. A major point to consider especially if using traditional pencil and or ink shading, is to start with the darkest areas first. This avoids darkening the whole image, and ensures that the lightest areas will remain white. The edges of overlapping structures should also appear white as can be seen in Figure 4 where the postorbital and supratemporal overalp the asquamosal in the upper left of the image.

CONCLUSION

The art of fossil reconstruction dates to the earliest foundations of palaeontology and over the roughly 200 years that have passed, the art of reconstruction has changed to the point where it now benefits from traditional approaches using pencil and paper to the use of digital software. Regardless of the preferred approach, to produce a good reconstruction requires time and patience. It must also ensure that the reconstruction is the servant of the science and not the determinant. In a world, where access to fanciful interpretations of the fossil past is subject to embellishment, the reconstructive process has never been more important. Significantly, the process of a reconstruction is not an exercise in the reaffirmation of preconceptions. Rather, it tends to result in re-evaluation of one's own assumptions, often challenging existing orthodoxy, but even in this instance some caution must be heeded. It is often a frustrating process, but the result is extremely valuable. A completed reconstruction is a demonstration that the presented interpretation of the skull's appearance has been thoroughly tested.

While we recognize that modern day digital segmentation is a method that helps to accurately represent fossil material in a manner not previously possible, we submit that a reconstructive application to fossil material remains an important and informative practice and one that highlights the value of the traditional methodology emphasized by Scott's work. In other words, even now in a nearly fully digitized approach to palaeontology, the established drafting principles should still be employed.

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