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Hone, DW; Farke, AA; Wedel, MJ

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Complete List of Authors:	Hone, David; Queen Mary, University of London, Farke, Andrew; Raymond M. Alf Museum of Paleontology, Wedel, Mathew; Western University of Health Sciences, Department of Anatomy and College of Podiatric Medicine
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Ontogeny and the fossil record: What, if anything, is an adult dinosaur?

*David W. E. Hone[1], Andrew A. Farke[2], and Mathew J. Wedel[3]

1. School of Biological and Chemical Sciences, Queen Mary University of London, London, UK.

2. Raymond M. Alf Museum of Paleontology, Claremont, California, USA.

3. Department of Anatomy, College of Osteopathic Medicine of the Pacific and College of Podiatric Medicine, Western University of Health Sciences, Pomona, California, USA.

*d.hone@qmul.ac.uk

Abstract:

Identification of the ontogenetic status of an extinct organism is complex, and yet this underpins major areas of research, from taxonomy and systematics to ecology and evolution. In the case of the non-avialan dinosaurs, at least some were reproductively mature before they were skeletally mature, and a lack of consensus on how to define an 'adult' animal causes problems for even basic scientific investigations. Here we review the current methods available to determine the age of non-avialian dinosaurs, discuss the definitions of different ontogenetic stages, and summarize the implications of these disparate definitions for dinosaur palaeontology. Most critically, a growing body of evidence suggests that many dinosaurs that would be considered "adults" in a modern-day field study are considered "juveniles" or "subadults" in paleontological contexts.

Keywords: Dinosauria, growth, adult, subadult, juvenile, histology

Introduction:

The non-avialan members of the Dinosauria (hereafter simply 'dinosaurs') were a diverse group of terrestrial archosaurian tetrapods that dominated global terrestrial environments during most of the Mesozoic Era. In recent decades, major research advances have reframed our understanding of these animals, including their evolution, ecology, development, functional morphology and behaviour. Nonetheless, fundamentals about their biology remain problematic: most notably, the question of "what is an adult dinosaur?". Within extant sauropsids, an adult or mature individual is usually implicitly or explicitly defined as one that has reached sexual maturity (i.e., it is capable of reproduction). This is sometimes assessed directly, but frequently is inferred from proxies such as body size, coloration, or skeletal characteristics [e.g., 1, 2]. Because sexual maturity can only be indirectly inferred for a handful of specimens in most extinct dinosaurs, numerous other morphological criteria have been used (Table 1, Figure 1). Yet, due to discordances in the timing of life events, an adult under one definition may be juvenile under another. Additionally, it is rarely practical or even possible to evaluate a fossil individual under all potential criteria for adulthood.

Reconciling these contradictions is critical to advancing understanding of dinosaur palaeobiology. Many studies presume to sample individuals that are adult or close to adult status, representing the "adult" (typically an idealised "final" ontogenetic stage) of a taxon. As commonly implied by dinosaur palaeontologists (although rarely outright stated), fully adult animals are those that display the "ultimate" derived morphology for a taxon, with the complete development of autapomorphies and unique character combinations that define a taxon [e.g., 3]. A violation of this assumption has potentially enormous implications - juveniles and adults of the same taxon may be misidentified as adults of different species, affecting taxonomic and phylogenetic hypotheses [e.g.

4, 5]. The work built on these assumptions, such as assessments of evolutionary rates of anatomical traits, in turn becomes questionable. Similarly, our ability to use data from extant taxa and ecosystems to reconstruct the biology of ancient animals relies upon identification of age classes that are meaningfully equivalent.

Here we assess diverse concepts of ontogenetic status in dinosaurs and the associated problems with determining the life stage of a given specimen. We provide suggested definitions of different classes of ontogeny that attempt to align multiple current concepts and permit easier comparisons between disparate ideas about dinosaur growth. Importantly, and as part of a growing consensus in the field, we posit that a clear statement of criteria used for determining ontogenetic stage (already done in many studies) is necessary at all times. This not only enables unambiguous communication, but also allows discussion of the implications of the range of ages in dinosaurs and how this affects current ideas about their biology.

Institutional Abbreviations:

AMNH, American Museum of Natural History, New York, New York; BYU, Brigham Young University, Salt Lake City, Utah; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; GMNH, Gunma Museum of Natural History, Gunma; MBR, Museum für Naturkunde, Humboldt Universität, Berlin; NMST, Division of Vertebrate Paleontology, National Science Museum, Tokyo, Japan; YPM, Yale Peabody Museum of Natural History, New Haven; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw.

Methods of assessing ontogenetic status:

The first key distinction in dinosaur ontogeny is that between adults and non-adults (Figure 2). Fully adult animals are ideally the basic unit of alpha taxonomy (and by extension, systematic work), and presumed adult morphology is also often the ideal basis of most functional and ecological analyses. For example, non-adult animals often have traits that match the presumed ancestral condition [6], and thus the inclusion of non-adult animals in an analysis may lead to the recovery of an incorrect position for such a taxon [7]. Therefore perhaps the most fundamental question with respect to ontogeny is: at what point does an animal become an adult?

Note that hereafter we use the term 'mature' or 'maturity' simply to mean that the animal has reached adult status under a particular criterion, and 'immature' that it has not reached this threshold. We do not mean to imply that maturity based on histology is, for example, the same as that based on skeletal fusion. In particular, 'maturity' does not necessarily imply that the animal is capable of reproducing, although this is a standard use of the term in extant animals (further complicating comparisons).

Body size:

Although the youngest individuals are undoubtedly smaller than the oldest individuals in a population, absolute body size generally is a poor indicator of adult status in most taxa [e.g., 8] although it has been used [e.g., 9] for some dinosaurs, and is often a (sometimes unreliable) proxy for maturity in studies of extant reptiles [e.g., 1; 10]. Indeed, at least some specimens are extremely large by any standard yet do not appear to have stopped growing or reached osteological maturity (see also below). Even within extant animals with determinate growth, maximum sized individuals may be considerably larger than a more typical animal (e.g. the Savannah elephant *Loxodonta africana* has a male height at adult recorded for between 3.2 and 4.0 m [11]). Thus, large size in one individual is not necessarily an indication of immaturity in another smaller one. Even if an adult has been diagnosed by multiple different criteria, a similarly sized animal from the same species may not be mature. Perhaps the best-case scenarios are represented by large samples of the hadrosaur dinosaurs *Maiasaura* and *Shantungosaurus* which apparently represent standing populations for a wide size range of individuals [12, 13]. The size distribution suggests that the largest individuals are indeed adults, corroborated by histology for *Maiasaura* [12].

Osteological fusion:

The fusion of major skeletal elements is often cited as a key indicator of adult status in dinosaurs (“skeletal maturity”; [14]). For instance fusion of the sacral vertebrae to each other and to the ilia are seen across many lineages as ontogeny progresses. Other elements show similar co-ossification, such as the fusion of cranial ossifications to the underlying skull bones in some dinosaurs [3, 15].

A widely-cited criterion of maturity in dinosaurs concerns fusion between the neural arches of the vertebrae with their respective centra. This process often begins posteriorly such that the posterior-most vertebrae will become fused before those that are more anterior. ‘Adult’ animals are presumed to have fully obliterated synchondroses in all vertebrae. Although this pattern of vertebral fusion in seen in extant crocodilians [16, 17] and at least appears to generally follow in dinosaurs, the situation is complex (see Table 2). As with the example above, animals may fuse their vertebrae and be considered adult even while considerably smaller than other known individuals of the genus. In extant lizards [18] homologous elements show extensive interspecific variation in fusion relative to sexual maturity, and dinosaurs were likely similarly variable.

Osteohistology:

At a microscopic level, bone tissue undergoes considerable modeling and remodeling through the course of development. This phenomenon is increasingly well-documented in modern species, permitting applications in extinct dinosaurs [7, 19-21].

The smallest, and presumed youngest, individuals have limb bones characterized by unmodified primary bone. As an individual grows, this primary bone is replaced and remodeled as secondary bone, with clear differences visible in thin-section. Appositional growth occurs around the circumference of a given element; pauses in this growth (often over an annual cycle) produce visible Lines of Arrested Growth (LAGs – also 'annuli' or 'resting lines'). As growth slows over the course of a lifetime, the spacing between LAGs becomes closer when LAGs are closely spaced within avascular bone of the peripheral cortex, these are termed an external fundamental system (EFS; [21-22]). An EFS is presumed to indicate cessation of overall growth and an unambiguous adult (even if it would already have been adult by other criteria), or even a senescent adult [12].

In some dinosaurs, mechanically important parts of the skeleton are cartilaginous, only ossifying late in ontogeny or not at all [23]. A prime example is the olecranon process of the stegosaur *Kentrosaurus*, which is only ossified in the largest individuals [24] and where smaller individuals lack an olecranon entirely.

Bone Surface Texture:

Gross texture of the bone surface changes through ontogeny, mirroring microscopic remodeling [25]. Perhaps the best example within dinosaurs concerns the skulls of horned dinosaurs, which change surface texture from lightly striated to deeply rugose during ontogeny [3, 26].

Growth Curves:

Because LAGs and similar features are often assumed to be annual in deposition, they have been used to create growth curves for an individual [27]. The shapes of the growth curves (which illustrate changes in growth rate), through comparison with extant taxa, are in turn used to mark ontogenetic milestones such as reproductive maturity (associated with the initial slow-down of growth) and the effective cessation of growth during full adulthood [28]. These sorts of analyses and observations have been important for recognizing individuals that were reproductively mature but not skeletally mature [e.g., 29, 30].

Reproductive maturity:

Reproductive (i.e. sexual) maturity is the ability to produce offspring and could be indicated by the presence of eggs inside the body cavity of an animal [31] or the possession of medullary bone [32], either of which indicate a female that is able to lay eggs. Additional support could come from an animal preserved brooding on a nest or in the company of small conspecifics. The latter indicators are based on the assumption that the larger animal in question is a parent or of similar age, and other interpretations are possible. For example, species where juveniles assist adults in rearing the young (e.g. 'helper at the nest') could lead to immature animals that are not parents preserving with nests or younger animals. Mixed age class aggregations also are also known for many dinosaurs, and there seems to be bias in some aggregations that favours sampling of smaller individuals [33]. It is therefore possible that in some contexts, apparent aggregations of juveniles with 'adults' may in fact be two sizes of juveniles. Importantly, some studies have identified individuals that are reproductively mature but not skeletally or histologically mature, nor at full "adult" size [29, 30].

Development of sociosexual dominance characteristics:

In association with reproductive maturity comes the full development of additional sociosexual characteristics that are linked to reproduction. Animals that are not yet capable of reproducing are unlikely to need these often large and costly ornaments and weapons. Thus, the allometric growth of such features likely indicates that they are used, at least as one function, in sexual or social dominance contests and that the animals are capable of reproducing [34]. For growth series within a single taxon, adults are identified as the individuals with full development of ornamentation. Noted examples in dinosaurs include the facial horns and frills of ceratopsids [e.g., 3, 35] or the cranial crests of hadrosaurids [36]. Because structures involved with sociosexual dominance tend to be exaggerated, they will typically form part of the package of autoapomorphies and synapomorphies by which specimens are both identified and sorted by phylogenetic analysis. This measure of ontogeny has the potential to confound our understanding more than any other, since juveniles and subadults that lack 'extreme' display structures can be difficult to even recognize as members of the same taxon

Reconciliation of definitions:

Clearly, there are both contradictions and overlap for various definitions of maturity (Table 1), and these create problems for researchers. A specimen that is mature on the basis of cranial ornamentation may be immature on the basis of osteohistology or skeletal fusion, for instance. This is further complicated if the basis of assigning maturity within a particular research paper is not noted, and complicated still further by a lack of comparability with sometimes conflicting definitions of maturity (usually reproductive) in extant taxa.

In addition, many fossils simply cannot be compared to one another. Histological samples cannot be taken from every specimen due to preservation, fragility or equipment availability and such detailed studies are not practical for large and wide-ranging studies that may cover hundreds of specimens. Thus definitions must be flexible enough to cover the variation seen not just in the growth of dinosaurs, but also the available information. Here we create a set of definitions for the fundamental life stages of dinosaurs that will be broadly applicable in most situations. We consider these only a starting point and encourage different definitions to be used as appropriate to the situation. However, we caution that terms even as simple as 'adult' or 'juvenile' be accompanied by a definition (and/or appropriate citation) or description of the characteristics used to define such life stages.

Within a given genus or species, the relative ages of specimens may be somewhat simple to determine, with different animals exhibiting different sizes, or differing levels of acquisition of adult characteristics and histological thin sections may show simply different LAG counts. However, such comparisons are of little value between species (including close relatives), and may even vary greatly within a species, hence the suggestions here for reconciliation of definitions.

Additional subdivisions can be identified in some cases [e.g., 37], and should not be automatically subsumed. However, because the intention here is to provide simple definitions that can work across multiple taxa with different biology and differing types of evidence, we restrict ourselves to broad definitions of largely unambiguous life stages that are common across all dinosaurs.

Adult: The identity of this age class is critical because definitions of other classes often rely on it [e.g., 9]. Adult animals may be diagnosed through any of the above described criteria (size, asymptote of growth, osteological fusion, etc.), but may also be confounded by conflicting signals (e.g., sexually mature animals that have not yet acquired all morphological features that characterise a taxon). Ideally therefore, multiple overlapping criteria should be used, and researchers should explicitly state which regime they employ (histological, fusion etc.). A definition of an adult dinosaur is therefore: *An animal that has reached a point in life commensurate with the cessation of rapid growth as indicated by osteological and histological features, in addition to reproductive maturity.* Animals that fall *primarily* under this definition may be considered adult.

Subadult: Those individuals that are transitioning between juvenile and adult status are subadult, and thus any definition should encompass this shift. Therefore we define subadults as: *An animal that combines features of juveniles and adults, lacking definitive adult characteristics (e.g. an EFS, final form of ornamentation) but possessing features that do not correspond to the juvenile condition (e.g. numerous fused elements, large body size)*. Because sexual maturity can occur well before adult status under some criteria (e.g., an EFS), this is one area where a given individual might be considered both reproductively mature and yet still osteologically subadult.

Juvenile: These may be considered as: *Any animal that does not show any signs of impending maturity that would place it as an adult or subadult animal (i.e., little or no skeletal fusion, poorly developed ornamentation, few or no LAGS, no medullary bone , etc.)*. Note that some characters do appear very early in the ontogeny of some taxa (e.g., the incipient frill present in even very young ceratopsians [38]. We subsume the oft-used categories of 'hatchling', 'neonate,' and 'nestling' into 'juvenile'. Although they are useful descriptors from a behavioural and taphonomic perspective, they represent a very limited stretch of life for most animals (and for precocial animals, potentially only a matter of minutes).

Embryo: An embryo is here considered: *Any specimen preserved within the confines of an egg or likely to have been so, representing an individual prior to hatching*. An egg is not required as part of this definition becuase examples of embryos apparently preserved without an egg [39, p 211] are known. Note that we also consider Horner et al.'s [40] 'perinate' a useful alternative, because it is not always possible to distinguish between an embryo and a newly hatched animal.

Discussion and Implications:

Many of the ways by which 'adult' dinosaurs have previously been recognised imply that numerous individual dinosaurs had not actually reached maturity when they died. Even very large animals may exhibit a lack of fusion across multiple elements or lack an EFS, indicating potential for considerable growth. This is true even for some specimens exhibiting fully developed sociosexual characteristics, occurrence within normal population distributions, or the presence of medullary bone implying that they are reproductively mature.

As a result, studies of dinosaurs may make assumptions about the ontogenetic status of a given specimen without regard to the variations known. Although ontogenetic trajectories have been studied in detail for a handful of taxa, allowing solid interpretations of the likely intersection of features such as size, asymptote of growth and fusion of various sutures (thus allowing maturity to be judged in other specimens from limited data [4, 28, 32] for *Tyrannosaurus*), most are not. Reasonable assumptions can be made in many cases about the likely age of various specimens, but nevertheless we urge researchers to be more explicit in stating under which criteria they are defining specimens as various ontogenetic stages, particularly adults. A lack of explicit information about such identifications does not inherently mark an assignment incorrect, but does potentially limit confidence in the referral and the repeatability of any analysis or use of the data. Ontogenetic sequence analysis holds some promise in this regard, particularly in formalizing definitions of ontogenetic stages and documentation of individual variation [41].

Correct identification of the ontogenetic status of a specimen (or at least a clear statement on the basis for the assignment) is critical to ensuring that specimens and/or taxa are comparable in large analyses where body size is relevant to the data. For example studies on browsing height, giantism, and biomass of populations may all be profoundly influenced if specimens are identified as adult when they are not.

Similarly, given the ontogenetic changes that can occur to major characters, it is critical to both taxonomic and cladistic studies that the life stage of a given specimen is correctly identified.

This is not to suggest that non-adult specimens should be excluded from such assessments and analyses, or that single small changes or incongruencies in, for example, patterns of osteological fusion, should be used to assign a specimen to a particular life stage or rule out another. Many important taxa are known from only from definitively non-adult specimens [42]. Although caution is warranted in their identification and use in studies, they are often identifiable as distinct taxa and should not be *a priori* ignored.

The questions of “when in ontogeny can you recognize a species as distinct from closely related species?” and “when in ontogeny can you correctly place a species in its evolutionary position?” are separate, but related (and often conflated) points. This is exemplified by the case of hadrosaurid dinosaurs in which genus or species-diagnostic features are observable within juveniles of many taxa, despite major morphological changes through ontogeny [e.g., 43]. Nonetheless, the preponderance of “primitive” features in juveniles still renders them difficult to place “correctly” in a phylogeny [e.g., 44].

Correct identification of life stage also is relevant to fundamentals of evolution – if the onset of sexual reproduction substantially preceded cessation of growth in dinosaurs then the 'adult' phenotype may not have been the primary target of selection. In fact, once juveniles or subadults are capable of reproducing, it is conceivable a population could exist with potentially no individuals making it through the survivorship gauntlet into 'adulthood' and close to maximum body size. The occasional hints from the fossil record of anomalously large sauropods like *Bruhathkayosaurus* [45], and the Plagne trackmaker [46] might be explained if many sauropods were primarily ‘subadult’ reproducers, and thus extremely large adults were actually vanishingly rare. This is a rather extreme hypothesis, but not an impossible one, and it raises the issue that some well-known species may not actually be represented by fully adult individuals under any of the criteria suggested above. Similarly, the apparent lack of sexual dimorphism common in taxa with large ornaments could relate to mutual sexual selection [47] but might also be because few individuals reached a 'final' stage where dimorphism was clear between the two ornamented sexes.

Indeed, the whole concept of an "adult" may not be directly comparable in any meaningful sense between extant tetrapods and extinct dinosaurs. This issue is ripe for study, both in extant and extinct taxa.

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FIGURE 1. A tableau of *Tyrannosaurus rex* skeletal reconstructions, on display at the Natural History Museum of Los Angeles County. The largest individual represents typical adult size for the taxon - current mainstream scientific consensus considers them all different

ontogenetic stages of *T. rex* but the smaller specimens were originally referred to different genera. Photo: DWEH.

FIGURE 2. Various methods that may be used to determine the age / ontogenetic status of a given dinosaur specimen. Central image is a reconstruction of the skeleton of an adult ceratopsian *Zuniceratops* with surrounding indications of maturity (taken from multiple sources and do not necessarily relate to this taxon). A) development of sociosexual signals (adult left, juvenile right – modified from [48]), B) surface bone texture (traced from [26]), C) large size, represented here by an ilium of the same taxon that is considerably larger than that of a known adult specimen, D) reproductive maturity, here based on the presence of medullary bone (traced from [31]), E) fusion of the neurocentral arch – location of the obliterated suture indicated by black arrow (traced from [49]), F) asymptote of growth based on multiple species indicated by black arrow (based on [28]). Central image by Julius Csotonyi, used with permission.

TABLE 1. This is not an exhaustive list of terms used or definitions given. Age classes are given as used in the original sources and the definitions or reasoning for the assignment to this age class are direct quotes from the text, (an * indicates they have been compressed for brevity). Additional details are often provided in the respective sources for assigning age classes, but these quotes are intended to be representative and not overarching.

Age class	Definition	Source
Embryo	These occur both *in situ* and inside fragments of eggs exposed on erosional surfaces.	50
Perinate	We use the term "perinate" ("around birth").	40
Small nestling	The bone tissue that forms the shafts of the longer limb bones is…composed of vascular canals surrounded by an undifferentiated mineralized bone matrix.	37
Large nestling	In cross section, the shafts of the long bones generally have a cortex that is well differentiated from the marrow cavity	37
Young	*Numerous differences in cranial and postcranial morphology given between 'young' and 'adult' *Protoceratops*.	35
Juvenile	A bone that is less than one-half the size of that of a typical adult specimen.	13
Juvenile	those individuals ranging from hatchling to near full grown	17
Juvenile	Many of the sutures [are] not fused	48
Juvenile	histological section of the tibia shows well-vascularized, woven and parallel-fibered primary cortical bone typical of juvenile ornithopods	40
Subadult	individuals of adult or virtually adult size, with additional characters indicating pre-adult status… but individuals lack several adult characters	3

Subadult	A bone between one-half and two-thirds the size of that of a typical adult specimen	9
Subadult	The individuals in this stage have both “Young” and “Adult” characters	52
Subadult or young adult	* Neurocentral sutures have closed, partial fusion of scapula and coracoid and of the ilium and ischium, fusion of some cranial elements	53
Adult	fully grown individuals with full expression of adult characters, often including fusion of skull elements	3
Adult	A bone that is approximately the size of that of a typical adult specimen.	9
Adult	This histology is typical of an external fundamental system (ESF), and indicates that the individual was fully grown	54
Old adult	Nearly all of the cranial sutures are obliterated by co-ossification.	55

TABLE 2. The timing of macroscopic changes in sauropod skeletons over ontogeny is not consistent among taxa. “YES” indicates fusion to the adjacent respective spines or centra “no” indicates lack of fusion, and a blank indicates that the relevant material is not preserved. Modified from Wedel and Taylor [8, table 1].

Taxon	Specimen	Sacral 1 spine	Sacral 4 spine	Sacral 1 centrum	Sacral 5 centrum	Sacral 1 rib	Sacral 5 rib	All cervical ribs fused	Scapula and coracoid fused
Apatosaurus ajax	YPM 1860			No	No	No	No	YES	No
Apatosaurus ajax	NMST-PV 20375	No	YES	YES	YES	YES	YES	YES	YES
Brontosaurus excelsus	YPM 1981			YES	No	YES	No		
Brontosaurus excelsus	YPM 1980	No	YES	YES	YES	YES	YES	YES	No
Diplodocus carnegii	CM 84/94	No	No	YES	YES	No	YES	YES	YES
Barosaurus lentus	AMNH 6341	No		No	YES			No	YES
Haplocanthosaurus delfsi	CM 879	YES	YES	No	No	No	No	No	No
Haplocanthosaurus delfsi	CM 572	YES	No	YES	YES	YES	YES	YES	
Camarasaurus grandis	GMNH-PV 101	No	No					No	No
Camarasaurus lewisi	BYU 9047	YES	No	YES	YES	YES	YES	YES	
Camarasaurus supremus	AMNH 5761	No	YES	No	YES	No	YES	No	No
Brachiosaurus altithorax	FMNH P 25107	No	No	YES	YES	YES	YES		No
Opistocoelocaudia skarzynskii	ZPAL MgD-I/48			YES	YES	YES	YES		YES

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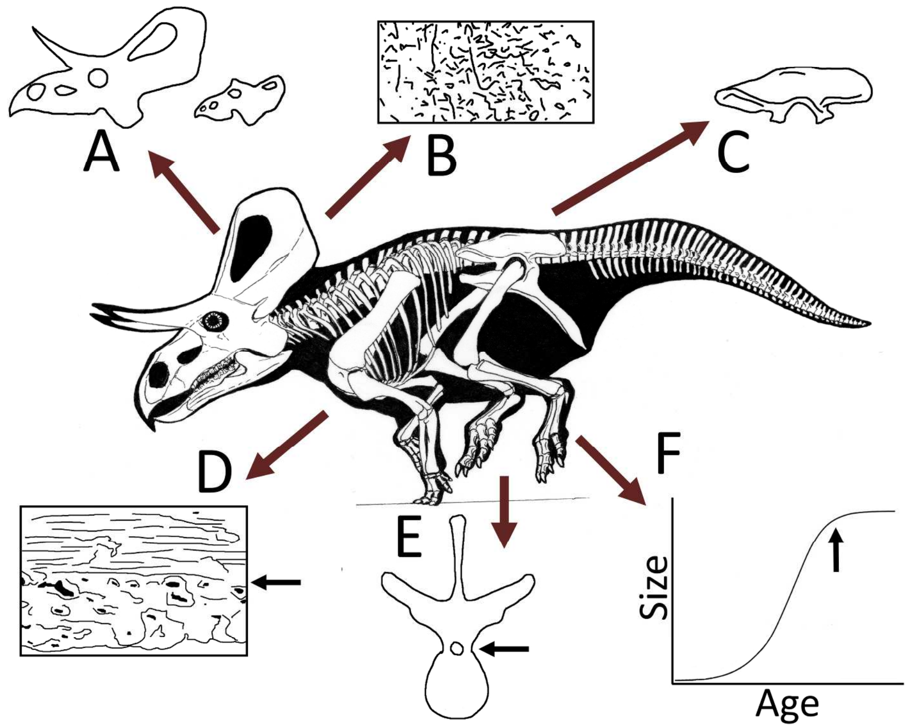
1341x811mm (72 x 72 DPI)



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225x171mm (300 x 300 DPI)