

SEXUAL DIMORPHISM IN DINOSAURS

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ABSTRACT—Sexual dimorphism, reflected as size and/or shape differences between the sexes, is very common but quite variable among the various tetrapod groups. Consequently, we should expect to find it well established among the Dinosauria. Sexual dimorphism in its arbitrarily defined standard form occurs when males are larger and/or exhibit more extreme morphologies. Reversed sexual dimorphism is the opposite. Archosaurian patterns of sexual dimorphism show the standard form to be predominant but with the potentially significant exception among the predatory birds. In the dinosaurs, excellent examples of apparently standard sexual dimorphism occur in the lambeosaurine hadrosaurs, pachycephalosaurs and ceratopsians. Potential reverse dimorphism may predominate in the theropods, although only *Syntarsus* and possibly *Tyrannosaurus rex* are relatively well studied. Sex specific characters provide potential for identifying and analyzing sexual dimorphism in taxa where the number of specimens are too few to otherwise approach it such as sauropods and the Thyreophora.

INTRODUCTION

SEXUAL DIMORPHISM is the phenomenon in which the males and females of a single species look different from one another. This difference can be manifested solely in the genitalia, which by necessity will differ in their shapes in some way or level, or can also be expressed in other organs or parts of the organism. The latter is the most common context discussed in evolutionary studies and typically refers to variation in: overall size; shape differences associated with structures such as horns, teeth, crests, etc.; or both.

Zoologists studying living taxa have an advantage over paleontologists in that usually they can determine the sex of their animals directly, although this can be difficult and/or require dissection in some species. Once the sexes are known, however, determining and documenting how they differ in size and shape, if at all, is a relatively straight-forward procedure.

Paleontologists, on the other hand, start with a bunch of fossils and have to figure out, first, if any dimorphism is present that cannot be explained to evolutionary, systematic, or taphonomic causes. Then, they can go about building a case for sexual dimorphism and identifying which morph they believe represents which sex. It is not easy to do. Even when a potential sexual dimorphism is identified, there is always the possibility that it may be due to preservational differences. The dimorphism described for the early Triassic therapsid *Diademodon* by Grine and coworkers (Grine and Hahn 1978; Grine et al. 1978) might also be explained as preservational differences, with specimens crushed dorso-ventrally and others crushed laterally.

MODELS AND PROCEDURES

Figure 1-1 illustrates the general models used to characterize and recognize sexual dimorphism. In general, sexual dimorphism may be expressed as only a difference in size, as only a shape difference, or as a combination of the two. In reality, the distinctions are not as simple as this because shape frequently changes automatically with changes in size (allometry). This will make many species appear to exhibit both size and shape dimorphism when the underlying mechanism is only size-based; if the smaller morph were to increase in size, the larger morph shape would be attained. Sexual dimorphism based on shape differences generally should be recognized as such only if the shape differences are independent of size. For example, the sexes recognized by Chapman et al. (1981) for the pachycephalo-

saurid *Stegoceras* exhibited different morphologies across the same general size range.

The conventional wisdom about sexual dimorphism is based on models developed while studying primates, a few other mammals, and passerine birds (see Ralls, 1976, 1977 for a discussion). Here, males tend to be larger and show the more extreme morphologies (e.g., horns, caniniform teeth, crests). This pattern is summarized in Figure 1-2 where adult female growth is shown to be an extension of the general growth curve observed for juveniles. Adult male growth often takes off at some point in the ontogeny, sometimes quite early, and produces an overall shape different from that predicted from the juvenile growth patterns. Typically, the male also extends into a considerably larger size. For this paper, this will be taken, quite arbitrarily we might add, as the default pattern. Reversed sexual dimorphism will then indicate when females are larger or more extreme in their morphologies, which is much more common in both mammals and birds than typically is realized by most evolutionary scientists (see Ralls, 1976, 1977).

Greg Paul (1988) has discussed sexual dimorphism and its possible manifestations in dinosaurs. He correctly states that in many living mammals the females of two different but closely related species can look more similar than the males and females of a single species. He notes the difficulties that this might produce for paleontologists trying to sort out the different taxa and sexes from a collection of material. He further suggests that size differences may more often be an indicator of sexual dimorphism, and shape differences more often an indicator of different taxa. We agree that size frequently reflects dimorphism but for continuously-growing reptiles the relationships can be more complex than this and that sexual dimorphism in dinosaurs will show up as either a size or shape difference, or both. Shape analyses of reptile taxa, including analyses of sexual dimorphism, are still all too rare for skeletal material. For another discussion synthesizing sexual dimorphism in social behavior in dinosaurs and other fossil tetrapods, see Bakker (1986).

Demonstrating sexual dimorphism for fossil taxa is very difficult because of the many other factors affecting variability in fossil taxa (see Rasskin-Gutman et al., this volume). Studies attempting to do so have taken approaches ranging from; 1) simple observation (e.g., Nopcsa, 1929) that there seems to be two morphs in a sample; 2) detailed morphometric analyses documenting differences in the size and shape of possible dimorphs

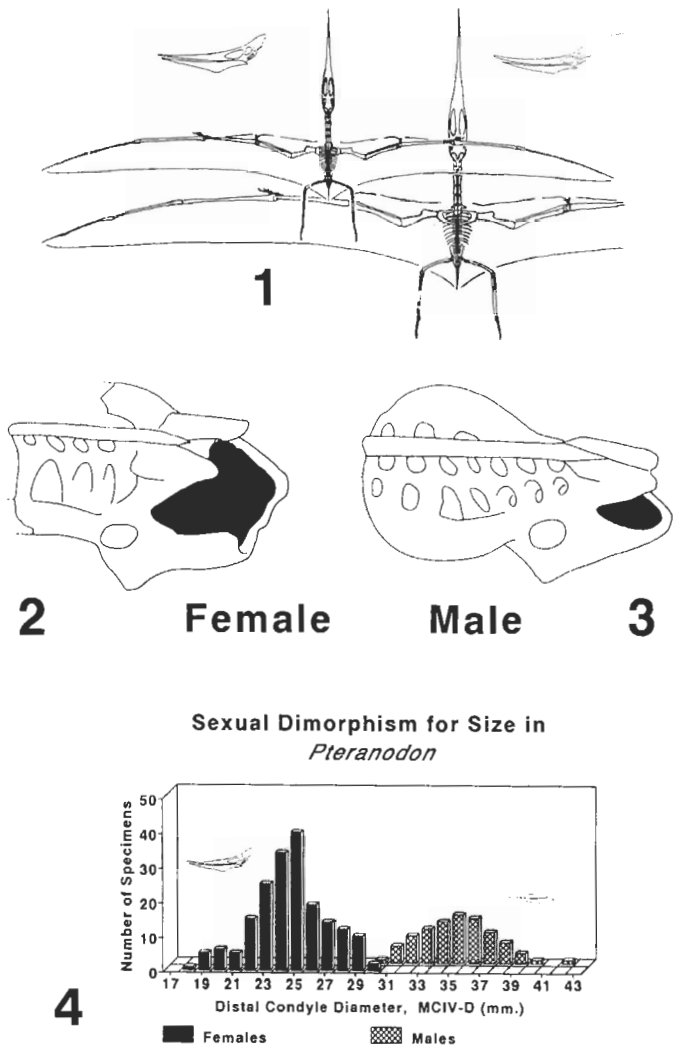
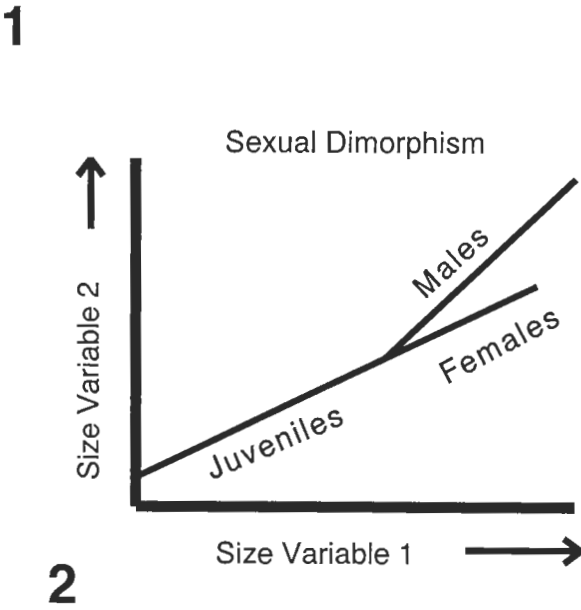
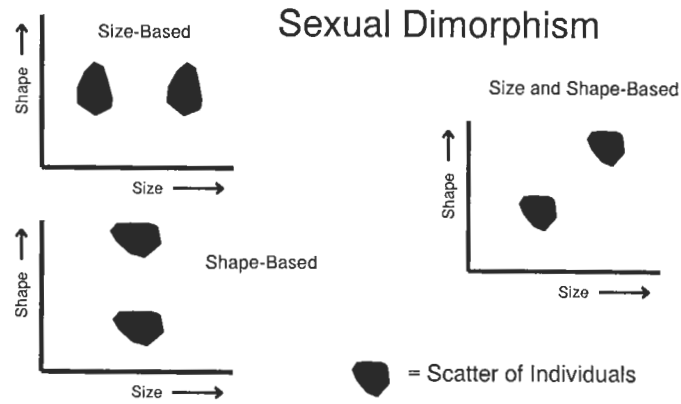


FIGURE 1—General and bivariate models for sexual dimorphism. Figure 1-1 demonstrates sexual dimorphism based on size alone (top left), shape alone (bottom left) and size and shape (top right). Figure 1-2 demonstrates general bivariate model where juveniles and females show similar growth trajectories and males bifurcate from this trajectory and grow faster and to a larger size in sex-related structures, especially those related to sexual display or combat.

FIGURE 2—Pterosaur model (*Pteranodon*) for sexual dimorphism in archosaurs. Sexual dimorphism is assumed to be conventional and not reversed. Data and illustrations redrawn from Bennett (1992). Figure 2-1, the two morphotypes of *Pteranodon*, with smaller-crested and smaller female morph at upper left and larger, bigger-crested male at bottom right. Figure 2-2 and Figure 2-3, Female and Male pelvises of *Pteranodon*. Pelvic canal is black showing the relatively larger canal in the female in Figure 2-2. Figure 2-4, size dimorphism in *Pteranodon* as indicated in metacarpal IV dorsal distal condyle. Measurements in mm. Smaller female morph is to the front left and the larger male behind and to the right.

(e.g., Chapman et al. 1981; Dodson, 1975, 1976); finding sex-specific characters related either to the genitalia (e.g., the first chevron in the tails of crocodiles or, possibly tyrannosaurids; Larson, 1994), the act of copulation (e.g., fused vertebrae in sauropods; Rothschild and Berman, 1991), or sexual display (e.g., the domes of pachycephalosaurids or crests of lambeosaurines; Chapman et al. 1981; Dodson, 1975; Hopson, 1975) that can be used to identify the sex of an individual. Sex-specific characters allow paleontologists to approach the documentation of sexual dimorphism in much the same way zoologists can when they know the sex of their animals. The robustness of a single study increases as more and more of independent lines of evidence support the case for sexual dimorphism.

An excellent model for the documentation of sexual dimorphism in fossil taxa is provided by Chris Bennett's (1992) study of sexual dimorphism in *Pteranodon*. In that study, summarized in Figure 2, Bennett was able to document two morphs, one larger with a very enlarged crest, and a smaller one with a reduced crest. With these data alone, *Pteranodon* exhibits classic

patterns indicating that the larger morph is probably the male, unless sexual dimorphism is reversed in that taxon. However, an independent line of evidence supports the conventional model. Pelvis (puboischiadic plate) shape and size suggests that the smaller morph is the female because the pelvises of that morphotype are relatively larger and deeper than in the larger morph. This morphology would provide a relatively much larger pelvic canal, required by the egg-laying females. Additional analyses aimed at supporting this example even further would include an allometric analysis of the development of the crest. Support would result if such an analysis showed either: 1) different crests for the two morphs at equivalent size ranges; or, 2) that the male crest is even more developed than would be predicted by extending the allometric curve for the crests of the females into the male size range. Otherwise, the dimorphism in the crest

Measurements taken on *Stegoceras*

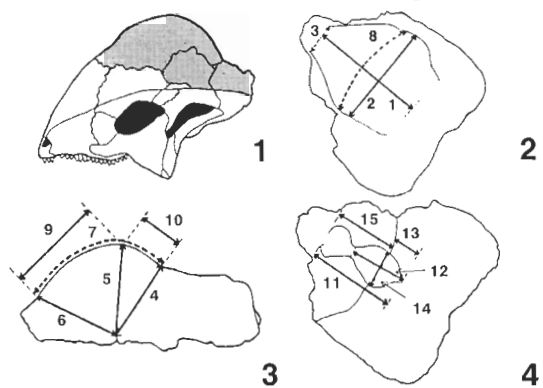


FIGURE 3—Measurements taken on the domes of the pachycephalosaurid dinosaur *Stegoceras* and used in the study by Chapman et al. (1981). 1-1 is a lateral view of a skull with the commonly-preserved dome shaded. 1-2 Dorsal view, 1-3 lateral view, and 1-4 ventral view of dome with 15 measurements indicated.

shape could just be size-related. Figure 1 shows a reconstruction of the morphs, Figure 2 and Figure 3 the pelvis of the male and female morph, respectively. Figure 4 shows a histogram of metacarpal IV (d condyle) size, showing a well-defined bimodal size distribution.

A similar example can be made from the Dinosauria. Chapman et al. (1981) studied sexual dimorphism in the pachycephalosaurid *Stegoceras*. Figure 3 shows a series of 15 measurements taken on the domes of 29 specimens assigned to a number of different species of that genus. These included dome, skull, and braincase measurements studied in detail using bivariate and multivariate methods (principal components analysis and discriminant analysis). The results are summarized in Figure 4-1 as an ordination of the specimens on the first two principal components (X-axis is PC1 and Y-axis is PC2). The results showed one specimen to be totally different from the others and it was referred to a new genus, *Gravitholus*. The other specimens all plotted in a single cloud representing the genus *Stegoceras*. Five of these exhibited characters that would not show up in the measurements taken, which suggested they be relegated to different species of that genus (one was later shifted to another new genus, *Ornatolitholus*). The rest are considered to be a single species that exhibits a distinct dimorphism with both morphs covering a similar size distribution (both are similarly scattered across the X-axis). The second axis, reflecting the dimorphism, shows a very distinct gap between the values for the two morphs (see Figure 4-2).

SEXUAL DIMORPHISM IN NON-ARCHOSAURIAN GROUPS

One way to infer the patterns for sexual dimorphism to be expected for the Dinosauria is to examine patterns observed in groups bracketing that taxon. For living taxa, this will include other archosaurs such as birds and crocodiles. Fossil taxa would include other groups such as the pterosaurs. These will be discussed in detail below. First, however, we will add some quick comments from a broader phylogenetic context that includes the whole Tetrapoda. A large scale phylogeny is shown in Figure 5-1 and includes labels showing the position of the groups to be discussed. It is important to note that this phylogenetic reconstruction, and the others used in this paper, are intended to be illustrative and not rigorous representations of the phylogeny of the groups involved. Groups not discussed, including many basal taxa, have been left out for graphical clarity.

Using Figure 5-1, the groups to be discussed here include: the start of the tetrapod line, the Amphibia; reptile groups including turtles, snakes and lizards; and members of the synapsid lineage (pelycosaur, therapsids, and mammals). This latter lineage can provide useful insight because it contains taxa living and evolving in situations ecologically analogous to those of dinosaurs. Consequently, they may show similar morphological trends and are valuable as a second grand experiment of a tetrapod lineage achieving ecological and body-size diversity. We will not discuss many aquatic, especially marine, taxa (e.g., ichthyosaurs) because their ecological context is so different from the terrestrial dinosaurs.

Amphibia.—Known patterns for amphibians show mixed trends relative to the standard model. Males frequently exhibit extreme morphologies such as brightly colored inflatable pouches but also tend to be smaller than the females in most frog and salamander taxa. This reversed size dimorphism probably reflects the strong correlation between body size and egg production in those groups. There are exceptions known for all these trends, however (Zug, 1993 and personal communications). Shape trends are not well-studied. Sexual dimorphism in shape was not apparent even in a taxon with extreme morphology such as the Permian amphibian *Diplocaulus* (Olson, 1951, 1969).

Turtles.—Turtles also show a variable pattern but sexual dimorphism again tends to be reversed and size related, again possibly due to the need to produce as many eggs as possible. There are taxa, however, where the males are larger (Gibbons and Lovich, 1990; Fitch, 1981). Shape trends in sexual dimorphism are, especially in skeletal elements, little studied.

Snakes and Lizards.—Snakes also tend to display reversed size dimorphism, although conventional size relationships are also common. Relatively little quantitative study has been done on shape trends related to sexual dimorphism. Lizards, on the other hand, most frequently exhibit standard patterns of size dimorphism, although many examples of reversed size sexual dimorphism also are known. Shape differences are better studied but still all too rare (for reviews, see Fitch, 1981; Zug, 1993). Myers (1996) recently has suggested that sexual dimorphism is better expressed in some lizards by their hind limbs and not apparent in their fore limbs.

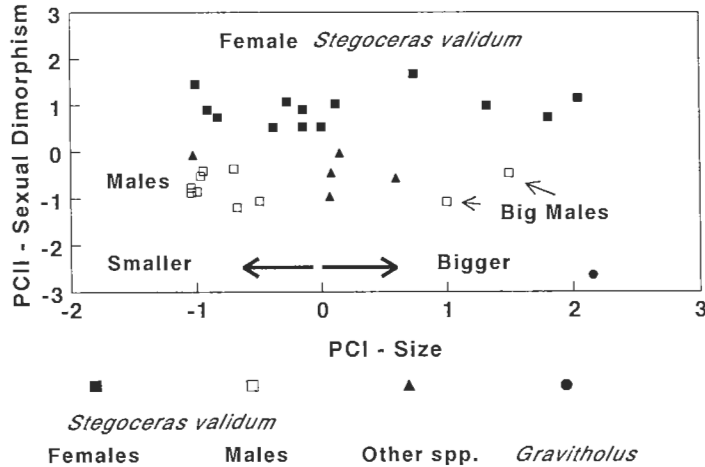
Synapsids.—Taxa within the synapsid line exhibit many different trends but when sexual dimorphism is present it tends to follow conventional patterns; larger males, many exhibiting extreme morphologies (Kurten, 1969). Many taxa are known to exhibit reversed sexual dimorphism, however (see Ralls, 1975, 1976). Among the pelycosaur, dimorphism appears to be more size-related, although little quantitative work has been done. Examples include Romer and Price (1940) on *Dimetrodon* and Stovall, et al.'s (1966) study of *Cotylorhynchus romeri*. Therapsids, especially dicynodonts, have been observed to add shape variation to the size differences. An example is the study by Broili and Schroeder (1937) on *Dicynodon broomi*, which exhibits a strong sexual dimorphism in tusk size and shape. Some therapsids have developed extreme morphologies used possibly for sexual combat (e.g., Barghusen, 1975). Mammal patterns are varied but tend to follow conventional patterns (see Kurten, 1969; Wright 1993) but reversed taxa also are common (Ralls, 1975, 1976).

SEXUAL DIMORPHISM IN OTHER ARCHOSAUR GROUPS

The more relevant comparisons are with taxa included within the Archosauria. These groups serve to bracket the non-avian Dinosauria and may provide the ability to infer expected patterns for the dinosaurs based on their phylogenetic position alone and independent of other lines of evidence. A phylogenetic reconstruction, again not intended to be comprehensive, is given in



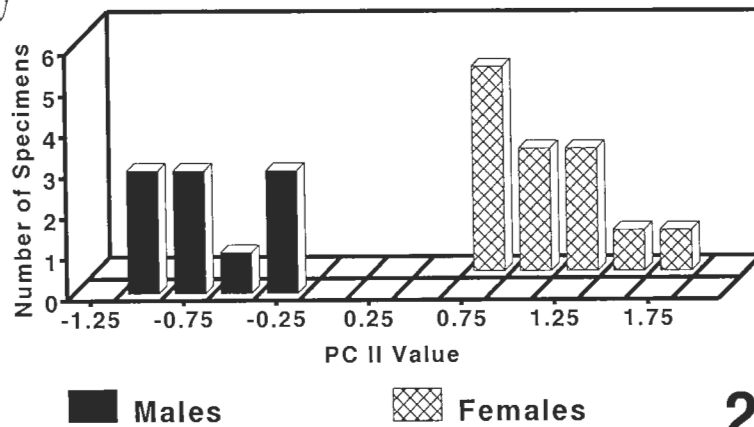
Principal Components Analysis of *Stegoceras*



1



Sexual Dimorphism for *Stegoceras validum*



2

FIGURE 4—Results of principal components analysis of the 15 measurements for 29 available domes of *Stegoceras*. Figure 4-1, redrawn from Chapman et al. (1981), is a scatter diagram of specimens (factor loadings) for the first two principal components. The x-axis is the first component (PCI) and represents size; those specimens to the right are larger than those to the left. The y-axis is the component (PCII) that produced the presumed sexual dimorphism in *S. validum*. Those with small values (open boxes) have relatively large domes for their brain size and are presumed to be males. The closed boxes have relatively flat domes for their brain size. Other taxa of *Stegoceras* fit within the scatter for *S. validum*. Note the peripheral position of the specimen referred to *Gravitholus*. Figure 4-2 is a histogram of values for second component (PCII) from principal components analysis. Values are for *Stegoceras validum* specimens only, with presumed males at front separated widely from their presumed female counterparts.

Figure 5-2. We will discuss three groups here; crocodiles, pterosaurs, and birds.

Crocodiles.—Crocodiles exhibit relatively conventional trends. Males are larger in most forms studied (Fitch, 1981; Zug, 1993; Games, 1990). Also, at least one form, the gharial *Gavialis gangeticus*, develops a sexually dimorphic growth at the anterior tip of its snout (Martin and Bellairs, 1977).

Pterosaurs.—Pterosaurs exhibit a tremendous range of morphologies (see Wellnhofer, 1991) indicating a broad range of life habits. This should have allowed for the development and/or

expression of sexual dimorphism in many taxa and this appears to be the case. The patterns observed follow conventional lines with males being larger and more extreme in their morphologies. Examples include the study discussed above by Bennett (1992) on *Pteranodon*, Wellnhofer's (1975) study of *Rhamphorhynchus*, Mateer's (1976) study on *Pterodactylus*, and Wellnhofer's (1991) assertion of sexual dimorphism in *Anhanguera*.

Birds.—Birds exhibit conventional trends in sexual dimorphism in that the males tend to be larger and exhibit the more extreme morphologies (Gill, 1995; Amadon, 1975). There are a

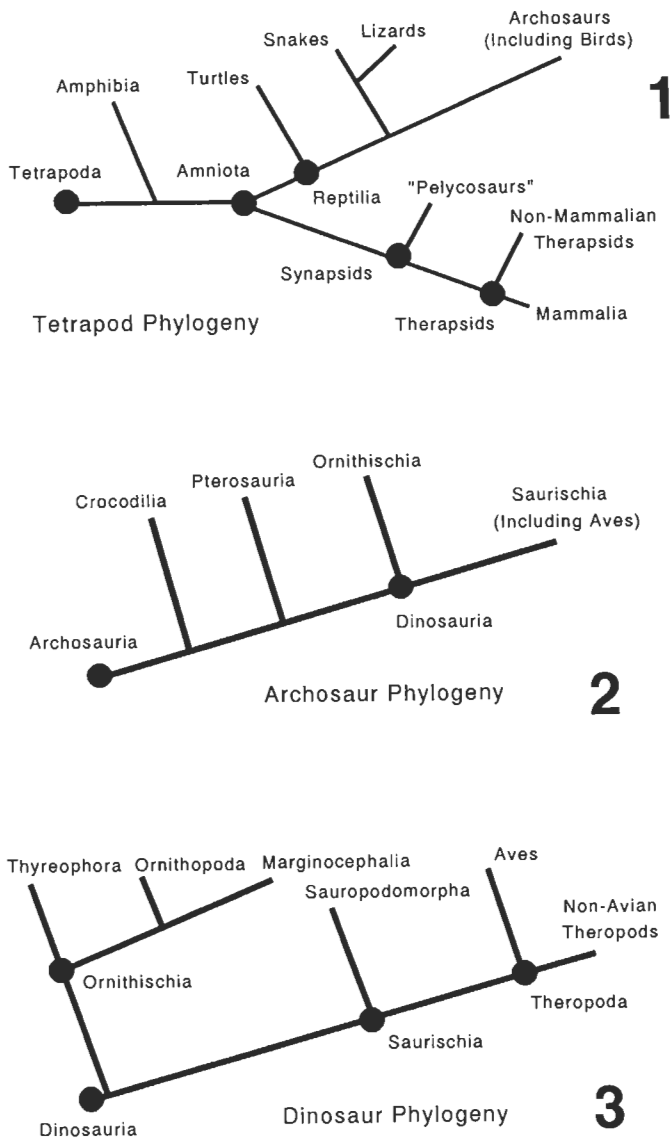


FIGURE 5—Illustrations of the general phylogenetic relationships of the groups being discussed. The trees are not intended to be exhaustive by any means but, instead, show the general positions of the groups being discussed. Figure 5-1, Tetrapod phylogeny. Figure 5-2, Archosaur phylogeny. Figure 5-3, Dinosaur phylogeny.

large number of exceptions, however, especially with size dimorphism. Two of these exceptions within the birds of prey are very interesting and have possible implications for some theropods. Two orders, the Falconiformes (hawks) and the Strigiformes (owls) have evolved, apparently independently, reversed sexual dimorphism that suggests that reversed sexual dimorphism is favored within some ecological contexts. In these groups the females are larger because they have to hunt down prey to provide to their offspring. The key appears to be the high level of predatory behavior necessary to kill their prey; the females are larger and more dimorphic in species that have to pursue, attack, kill and rend large, active prey (Amadon, 1975). The larger the prey, the greater the size of the female relative to the male. These patterns are supported further by yet another independent line of predatory birds which exhibit them, the Stercorariidae (skuas and jaegers).

SEXUAL DIMORPHISM IN DINOSAURS

The first impression gained from reading much of the dinosaur literature is that very little has ever been said about the topic. Most references have little or nothing about the subject and, at times, seem to go out of their way to avoid such discussions. In the earlier part of this century, Nopcsa (1929) suggested that the fancy crests of lambeosaurines only could be the result of sexual selection. He then made the fatal error of suggesting that lambeosaurines had to be male dimorphs to the female hadrosaurines. North American researchers reacted very strongly to this (e.g., Russell, 1946). They pointed out, quite correctly, that biostratigraphic separations between the presumed dimorphs made it highly unlikely that they could be members of the same species. The enthusiasm of their disagreement with Nopcsa closed the discussion of this topic almost completely for a while. This is unfortunate because many of Nopcsa's observations were, to a large extent, correct. The problem was revisited much later by both Hopson (1975) and Dodson (1975) who were able to show, conclusively, that the lambeosaurine crest was indeed a sexually dimorphic character. Other lambeosaurines, and not hadrosaurines, however, served as the corresponding dimorphs.

A second look in detail at the literature on dinosaurs shows there to be lots of references on sexual dimorphism, mostly inserted stealthily into larger papers on systematics and evolution. The discussions range from quick mentions of possible dimorphisms (e.g., Galton, 1974) to detailed studies (e.g., Dodson, 1975; Chapman et al. 1981). Major reviews and studies of the topic include Nopcsa (1929), Davitashvili (1961), Galton (1971, 1972), Dodson (1975, 1976), Molnar (1977), Chapman et al. (1981), Bakker (1986), and the various chapters in Weishampel, et al. (1990) and Carpenter and Currie (1990).

Sexual dimorphism in dinosaurs will be discussed within the context of five major taxa illustrated in Figure (5-3). These include the Sauropodomorpha and the Theropoda from within the Saurischia, and the Thyreophora, the Ornithopoda and the Marginocephalia from the Ornithischia.

Sauropodomorpha.—If dinosaurs are characterized as having a fossil record of taxa represented by one or a few incomplete specimens, then the sauropodomorphs are the most dinosaurian of the dinosaurs. Only a few prosauropods are represented by enough specimens to allow any sort of quantitative analysis. Consequently, at least for now, paleontologists will have to rely on sex-specific characters if they are to have any chance of identifying sexual dimorphs for almost all taxa.

Prosauropods include taxa that are much more common than any sauropod and, consequently, the only realistic possibilities for applying quantitative methods to document sexual dimorphism. One study of *Plateosaurus* by Weishampel and Chapman (1990) did just that. Using bivariate and multivariate methods, they studied femoral dimensions for specimens referred to at least six species from a single quarry, the Trossingen Quarry in Germany, as well as other key specimens from other localities. The results showed that all appeared to belong to a single species, with a very subtle dimorphism in femoral dimensions. Weishampel and Chapman interpreted this as a sexual dimorphism, reflecting small differences in the loading of the body weight on the back legs. No size differences between the two morphs was apparent from their data.

Sauropods would appear to be hopeless for the documentation of sexual dimorphism because there typically are only one or a few (generally headless) specimens per taxon, mostly represented by very incomplete material which is very difficult to study because of its size. However, Rothschild (1994, Rothschild and Berman, 1991) describes a fusion of the caudal vertebrae in the sauropods *Apatosaurus*, *Diplodocus*, and *Camarasaurus* that

might be related to the difficulties encountered during copulation in these massive animals. The fusion is not considered pathological and, instead, it is considered to be an adaptation in the females to keep the tail elevated. The phenomenon is found in about half of the known specimens, here assumed to be the females.

For sauropodomorphs therefore, there is a suggestion of subtle dimorphism in the prosauropod *Plateosaurus* and at least a potential for identifying females in sauropods. The latter would then allow for the documentation of possible differences between morphs with and without the vertebral fusion, if enough skeletons can be found for a single taxon.

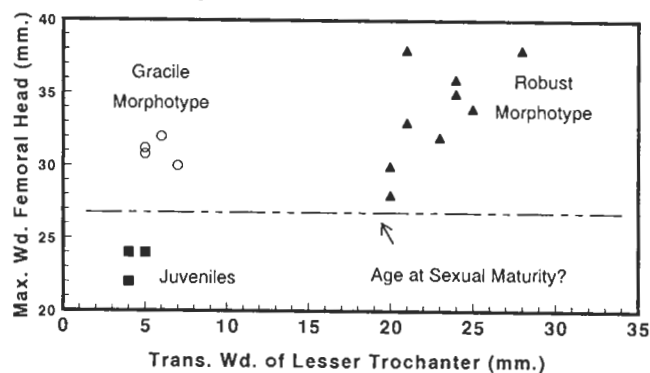
Theropoda.—These are among the most popular of dinosaurs and, consequently, have attracted a lot of attention from researchers. Suggestions of possible sexual dimorphism have followed three lines: 1) the presence of crests, rugosities, and horns in the nasal and postorbital portions of the skull; 2) the presence of possible gracile and robust dimorphs in a number of taxa; 3) the possibility of defining a sex-specific character, the presence/absence of the first caudal chevron, in some theropod species.

Cranial crests, rugosities and horns of any type frequently are associated with the phenomenon of sexual dimorphism and instances of sexual display and combat. Bakker (1986) has discussed this in detail and suggests the snout crests in *Allosaurus*, *Ceratosaurus*, and tyrannosaurs were dimorphic and used for intraspecific combat in males. He notes that these structures are less adequate for killing prey than the many other weapons these animals possessed and would serve better as dimorphic structures for display and combat. The larger, fragile crest in *Dilophosaurus* would serve only for display. Other recent finds of crests in new theropods, such as *Monolophosaurus* (Zhao and Currie, 1993) and *Cryolophosaurus* (Hammer and Hickerson, 1994), would seem to support this as well. However, no instances of dimorphism have been demonstrated. What is needed is to document multiple specimens of a single taxon where differences in crest morphology are studied within the context of allometry, ontogeny, and sexual dimorphism. Most theropods will never be represented in sufficient numbers to allow this.

There appears to be a phenomenon in many theropods where robust and gracile morphs are present for what appears to be a single taxon. This pattern has been described in taxa such as *Coelophysis* (Colbert, 1989, 1990), *Syntarsus* (Raath, 1990), and *Tyrannosaurus rex* (Carpenter, 1990A; Larson, 1994). *Coelophysis* would appear to provide the perfect test case but the returns for the studies done so far are mixed (Colbert, 1989, 1990; Covey, 1993) and adequate morphometric analyses have yet to be published supporting or refuting this possibility.

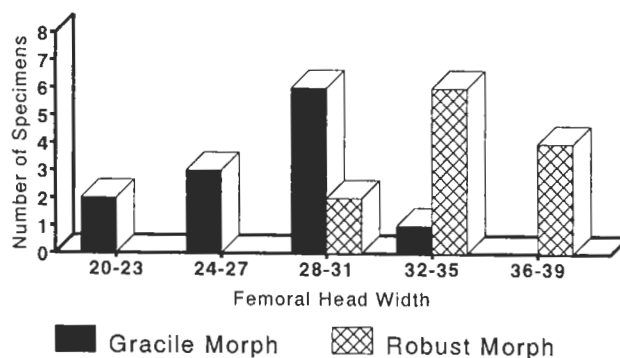
Raath (1990), studying femora for the Early Jurassic theropod *Syntarsus rhodesiensis*, also noted such a dimorphism. This finding is best illustrated in Figure 6-1 where the transverse width of the lesser trochanter (x-axis) is plotted against the maximum width of the femoral head (y-axis). The plot shows three clusters of points, two with relatively small values for the trochanter width and the third with a very robust width. Raath (1990) interprets the first two clusters as the juveniles and adult males, and the third as the robust females. He also asserts that sexual maturity can be inferred to have occurred at a femoral head width around 28 mm, where the robust females are asserted to have become robust. Figure 6-2 presents a histogram of femoral head widths, showing the distribution of the two morphs. An alternative explanation is that two different taxa are present but Raath favors sexual dimorphism because the differences are expressed in the reproductively critical area of the upper hind limb and because the more common robust morph is found in the same area as juveniles, to be expected for females. This example is far from conclusive, as yet, but certainly is encouraging.

Robust and Gracile Morphotypes in *Syntarsus rhodesiensis*



1

Possible Sexual Dimorphism in *Syntarsus rhodesiensis*



2

FIGURE 6—Sexual dimorphism in *Syntarsus rhodesiensis* redrawn from Raath (1990). Figure 6-1 is a bivariate plot of the transverse width of the lesser trochanter of the femur (mm.; x-axis) versus the maximum width of the femoral head (mm.; y-axis). Three clusters include juveniles with non-robust lesser trochanters (solid boxes), non-robust presumed males (open circles), and robust specimens, presumed to be the females (closed triangles). Possible age of sexual maturity indicated by dashed line. Figure 6-2 is a histogram of femoral head width showing the distribution of the two morphs. Values are in mm.

Robust and gracile forms have also been inferred for the most popular dinosaur, *Tyrannosaurus rex*. Carpenter (1990A), noted this difference in robustness in equivalent skeletal elements from the neck and hip. He asserted that the more robust morph is the female because the ischia in that form are more divergent (see Figure 7-1) and would allow the passage of large eggs more readily. As such, Carpenter identified a possible sex-specific character for testing the robust-gracile dimorphism as new specimens are found. Larson (1994) building on this observation, accepted the gracile-robust model (see Figure 7-2) and developed another sex-specific character based on research done by Eberhard Frey on crocodiles. Frey noted that the first caudal chevron in crocodiles was present only in males and served as an anchor for the muscles that controlled the intromittent organ (penis; Figure 8-1). Larson suggested that this also is to be ex-

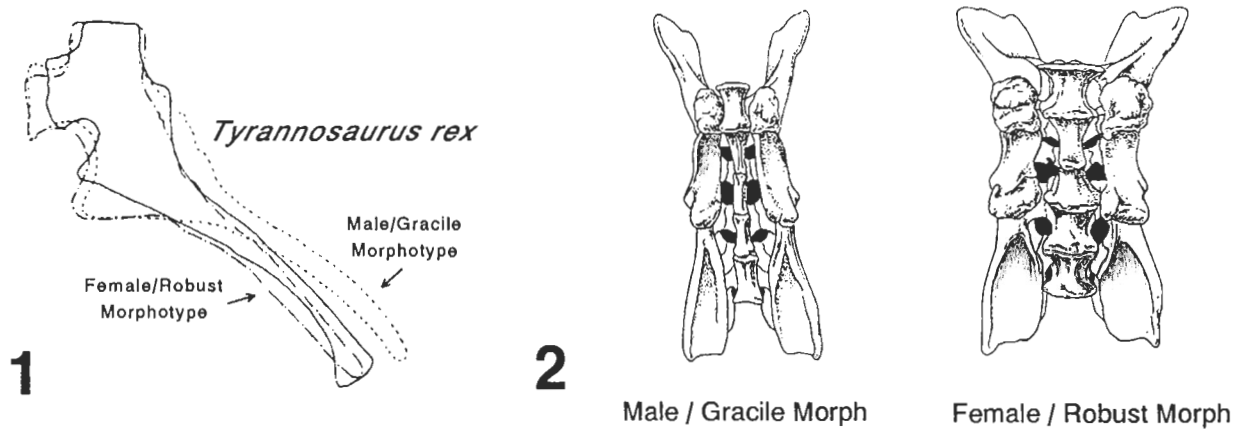


FIGURE 7—Robust and gracile morphotypes in *Tyrannosaurus rex*. Figure 7-1, redrawn from Carpenter (1990A) shows ischia for three specimens with the gracile morphotype more horizontally oriented. The less horizontal robust morphotype position would allow a greater angle and easier passage of eggs. Consequently it is considered the probable female morphotype. Figure 7-2, redrawn from illustrations done by Dorothy Sigler Norton for Larson (1994), shows pelvises from gracile and robust morphs.

pected in *Tyrannosaurus rex* (Figure 8-2) but has only tested this with a single gracile specimen (Museum of the Rockies, 555), which had the chevron, as predicted by the reversed dimorphism model. Obviously, this must be tested further with other specimens.

The reversed sexual dimorphism model is considered reasonable because it follows the patterns seen in birds of prey, where dimorphism tends to be reversed and the differences larger as the prey gets larger and more active (see Amadon, 1975). The prey for *T. rex* presumably would be very large and active and, consequently, the large difference in size (in this case robustness) between the two morphs would be reasonable.

Surprisingly, theropods are probably an excellent group for the study and documentation of sexual dimorphism despite the problems outlined above. The presence of possible sex-specific characters and apparently distinct morphotypes should make it possible to develop rigorous studies to test these assertions, especially for taxa where any reasonable sample size can be found.

Thyreophora.—This group of dinosaurs, including the anky-

losaurs and stegosaurs, should be great source for sexual dimorphism because of all the horns and plates and rugosities that are common in these taxa. However, very low sample sizes have reduced the ability of paleontologists to do more than just make observations of potential features. We hope sex-specific characters will be found to help lessen the difficulties.

For *ankylosaurs*, Carpenter (1990B) has suggested that differences present in the armor of different specimens of *Edmontonia rugosidens* and in the snout length in *Panoplosaurus* may indicate different sexes, but Coombs (1995) has rejected sexual dimorphism as a viable option for variability seen in ankylosaurian tail clubs. The literature is greater for *stegosaurs* and Carpenter (personal communication, 1996) has suggested that possibilities for determining sexes in stegosaurs are starting to become clearer. Spassov (1982) following Davitashvili (1961) has suggested that stegosaur plates served, at least in part, as display organs during sexual combat and, consequently, might be expected to show dimorphic trends. Galton (1982) mentions sexual dimorphism as an explanation for the different number of sacral

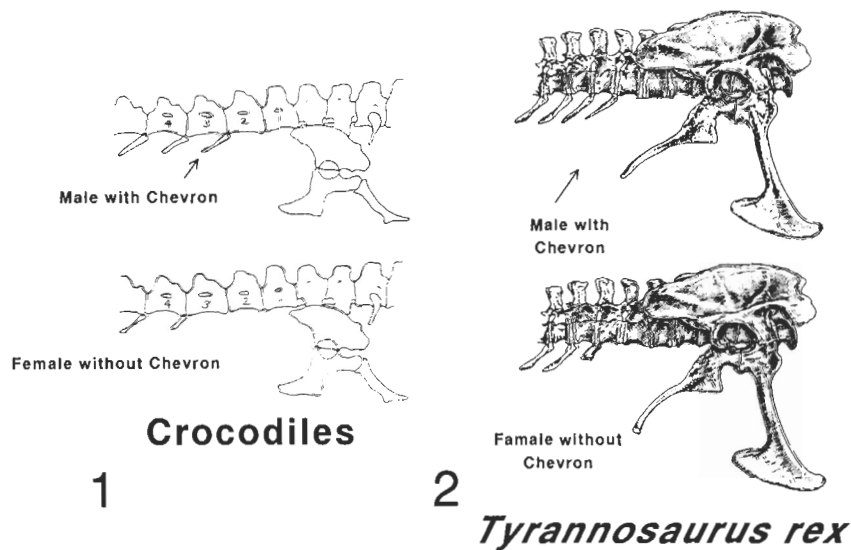


FIGURE 8—Caudal chevron in crocodiles and *Tyrannosaurus rex*. Redrawn from ones done by Dorothy Sigler Norton for Larson (1994). Figure 8-1, dimorphs with and without the chevron in crocodiles. Figure 8-2, the same for *T. rex*.

ribs in specimens of *Kentrosaurus* and later (Galton, 1990) has suggested that sexual dimorphism may explain the different sized shoulder plates in *Lexovisaurus*. He states that no detailed study of the plates and armor of stegosaurs yet exists to truly document the phenomenon in this group.

Clearly, no solid examples of sexual dimorphism occur as yet in the thyreophoran groups. Because of the small numbers of individuals that are known for almost all taxa, finding sex-specific characters will be of great importance here.

Ornithopoda.—The ornithopods are one group where sexual dimorphism is to be expected because of analogies with ungulates, where sexual dimorphism is common. Inferences have been made but, surprisingly, only the lambeosaurines have very well defined examples.

For **heterodontosaurs**, a number of investigators (Steel, 1969; Thulborn, 1974; Molnar, 1977; Weishampel and Witmer, 1990) have noted the large caniniform teeth present in *Heterodontosaurus* and have suggested these might serve for purposes of sex recognition, display and/or combat. However, there are not enough specimens available at this time to allow this to be studied quantitatively. For **hypsilophodonts** there is a similar, although stronger, suggestion by Galton (1974) of a dimorphism in the number of sacral ribs in *Hypsilophodon foxii*. The differences do not appear to be size-related and Galton favors an explanation of sexual dimorphism. If a strong functional argument can be made relating the variation to different sexes, then this might develop into a useful observation.

Iguanodonts would appear to be a perfect group for the development of strong cases for sexual dimorphism but this has yet to happen. Suggestions that the two different-sized species of *Iguanodon*; the much larger *I. bernissartensis* and the smaller *I. mantelli*, are possible sexual dimorphs goes back to discussions by Van Beneden (1881), Dollo (1882), and Nopcsa (1929) but Norman (1980, 1986) argues strongly that these two species are taxonomically distinct. Clearly, the large numbers of specimens available from multiple mass-death horizons strongly suggests that cranial and postcranial patterns in morphometric variation be studied in *Iguanodon* with an eye for sexual dimorphism. Gilmore (1925) has suggested a possible case of size-related sexual dimorphism among six species of *Camptosaurus* from the Jurassic of Utah. The bizarre morphology of "*Iguanodon*" *orientalis* (see Norman and Weishampel, 1990, page 513), manifested as a large, inflated nasal area, suggests that sexual dimorphism might be present in that taxon, if multiple specimens can be obtained.

Hadrosaurs represent one of the most studied groups of dinosaurs because they are abundant in the Late Cretaceous sediments and are often found articulated and in bone-beds. Not surprisingly, some of the best cases of sexual dimorphism have been described from this group. It is surprising, however, that little is known for the hadrosaurines despite their abundance. We would suggest that detailed studies be concentrated here. The lambeosaurines, on the other hand, have been the subject of many comments by Abel (1924), Nopcsa (1929), Wiman (1931), Russell (1946) and leading to the seminal papers by Hopson (1975) and Dodson (1975). The conventional wisdom for the lambeosaurines now assumes that the species known for the bizarre *Parasaurolophus* are probably dimorphs (Hopson, 1975) and that the lambeosaurines include a large number of over-split species that represent juveniles and sexual dimorphs of single species. Dodson (1975) studied this latter problem (see Figure 9 for a diagram illustrating the variable morphologies recognized for selected lambeosaurines) and was able to reduce twelve species from three genera to three dimorphic species within two genera of lambeosaurines. It is reasonable to expect well-devel-

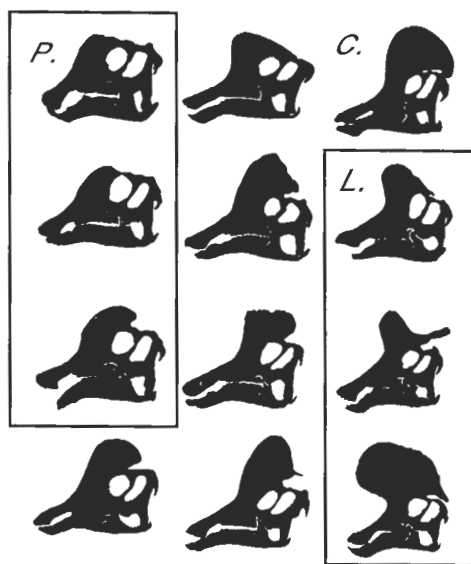


FIGURE 9—Cranial variation in three genera of lambeosaurine hadrosaurs. Redrawn from Dodson (1975). Different species for *Procheneosaurus* (P.), *Corythosaurus* (C.), and *Lambeosaurus* (L.). Boxes separate genera. Dodson's study showed only three valid but dimorphic species; *C. casuarius*, *L. lambei*, and *L. magnicristatus*. *Procheneosaurus* was considered to be a juvenile morphology.

oped dimorphism in any species of lambeosaurine with sufficient numbers of specimens.

Ornithopods show a great promise for the documentation of sexual dimorphism, although the only well-documented cases are among the lambeosaurine hadrosaurs. Detailed analyses for the many populations of *Iguanodon* and hadrosaurines should provide additional examples.

Marginocephalia.—The Marginocephalia, consisting of the Pachycephalosauria and Ceratopsia, contains the best studied dinosaurian examples of sexual dimorphism because both groups exhibit extreme cranial morphologies that allow dimorphism to be recognized relatively easily. Surprisingly, despite abundant postcranial material, relatively little work has been done correlating postcranial variation with the described dimorphic cranial variation. We see this as another area requiring more attention than it has received.

The **pachycephalosaurs** are characterized by their enlarged frontoparietal dome. Brown and Schlaikjer (1943) recognized that sexual dimorphism was probably a major explanation for the variation they were seeing in *Stegoceras* and noted one morphotype with a well-defined squamosal shelf. They assigned specimens with this shelf to the male morph, although they admitted they were doing this quite arbitrarily. Davitashvili (1961) and Galton (1970, 1971) independently decided that the dome was used as a weapon and display structure during intraspecific combat, which was supported later by Sues (1978) who demonstrated that this was possible with a functional analysis of the dome. Galton (1971) correctly noted that the specimens with the more highly developed domes had less well-developed squamosal shelves and assigned these as males, reversing Brown and Schlaikjer (1943), following models of sexual display and combat from within the Mammalia. Only one taxon, *Stegoceras validum*, is represented by enough material to study sexual dimorphism at all quantitatively. This was done by Chapman, et al. (1981; see discussion above) who documented a very strong case with large-domed males and flatter-domed females. There has been a great increase in the amount of new pachycephalo-

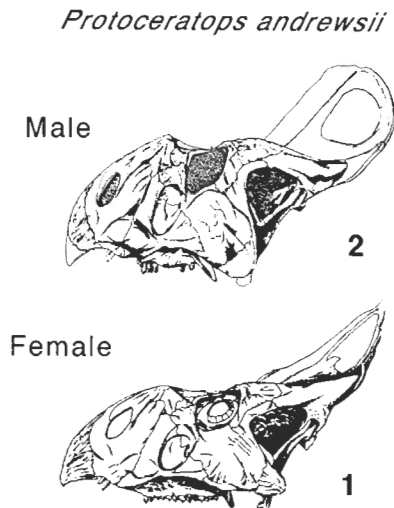


FIGURE 10—Sexual dimorphism in *Protoceratops andrewsii*. Examples of old male (Figure 10-2) and old female (Figure 10-1) specimens. Note greater development in the frill and nasal boss in the male. Redrawn from Dodson (1976).

saur material found in recent years and this, we hope, will allow sexual dimorphism to be studied in other pachycephalosaurs and in even more detail for *S. validum*.

The ceratopsians are the single group in the Dinosauria where sexual dimorphism has been accepted for a long time and for which there are a number of different examples available. That sexual dimorphism was probably present in this group was recognized very early on by workers studying ceratopsians. By the time of the study by Brown and Schlaikjer (1940A), it was commonly invoked to explain horn variation in that group. Unfortunately, it did little to slow the naming of new ceratopsian taxa. The most studied lineage, however, was the ontogenetic series of crania for *Protoceratops andrewsii*. Studies describing dimorphism in this taxon start with Brown and Schlaikjer (1940A, 1940B) and include discussions in Davitashvili (1961), Kurzanov (1972) and, especially, Dodson (1976). In that latter work, Dodson was able to describe in detail the morphologies of a supposed male and female morph in *P. andrewsii* using bivariate and multivariate approaches. These differences were then studied, and most confirmed by Chapman (1990) using shape analysis methods. Figure 10 shows reconstructions of older members of the two morphs of that species.

Other taxa of ceratopsians also have generated significant discussions of sexual dimorphism. Bakker (1986) suggests the "fin-tail" of *Montanoceratops* to be an organ of sexual display. Farlow and Dodson (1975) discuss in detail morphologies of the horns and frills of ceratopsians that might correspond to sexual display organs in recent mammals. This topic was again discussed in detail by Spassov (1979). Recent finds of ceratopsian fossils, and especially ceratopsian bone-beds, have led to suggestions of sexual dimorphism in *Pachyrhinosaurus* by Tanke (1988), in two species of *Chasmosaurus* by Godfrey and Holmes (1995), and in two new genera *Einiotaurus* and *Achelousaurus* by Sampson (1995). Other excellent examples are the result of synonymizing overly-split taxa using morphometric methods. One of the best examples of this is the study of the Chasmosaurinae, including the popular genus *Triceratops*, by Lehman (1990). In it, much of the variation in horn morphology within each genus of that group is explained as sexual dimorphism for a single species (see Figure 11), each with an erect-horned (male) and a forwardly-inclined horned (female) morph. Ostrom

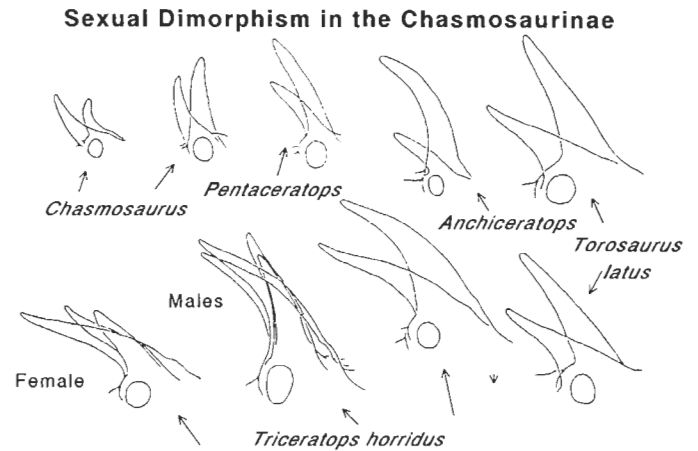


FIGURE 11—Sexual dimorphism in the chasmosaurine ceratopsians. Each genus, typically represented by a number of different species, is reinterpreted to be a single dimorphic species. Males have more erect horns, females more forwardly directed horns. Redrawn from Lehman (1990).

and Wellnhofer (1990) independently arrived at the same conclusion for *Triceratops*.

We conclude that the Marginocephalia will provide many more excellent examples of dimorphism. The abundance of specimens in the ceratopsians makes them perfect for such studies. The discovery of more and more new pachycephalosaurid material, always with the possibility of finding a bone-bed, will probably provide more specimens and taxa for expanding the work done by Chapman et al. (1981) on that group. One area of suggested research is in trying to find dimorphism in limb proportions. Following other dinosaurs, we would predict that it may be quite apparent in the hind limbs but not as apparent, or only manifested in size, in the fore limbs.

CONCLUSIONS

Dinosaurs are an excellent group for the study of sexual dimorphism. Many of the groups provide a challenge because of the lack of significant material for any one taxon. This problem sometimes can be overcome using sex-specific characters, if they can be found. Other groups (e.g., hadrosaurs and ceratopsians) provide significant material for detailed studies.

The patterns for sexual dimorphism described so far appear to fit the standard model, with the males larger and more extreme in their morphology. This fits their phylogenetic position between earlier archosaurs (crocodiles and pterosaurs) and birds, which all also tend to follow this conventional model. The exception is the possibility of reversed dimorphism in some theropods. Although far from well-established, studies on *Syntarsus* and *Tyrannosaurus rex* are well documented and strongly suggest significant effort be put into the study of sexual dimorphism in theropods.

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