

# Cranial Suture Complexity in White-Tailed Deer (*Odocoileus virginianus*)

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**ABSTRACT** Neurocranial expansion and mastication are commonly implicated as the two major biomechanical factors affecting suture morphology. In deer the antlers provide an additional source of biomechanical stress acting on the skull. Equivalent stresses are not found in females, who lack antlers. We analyzed the complexity and interdigitation of the interfrontal and coronal sutures that surround the antler-bearing frontal bones of ( $n = 67$ ) white-tailed deer (*Odocoileus virginianus*) to 1) evaluate changes in suture morphology throughout ontogeny, and 2) test the hypothesis that male deer have more complex sutures than females. Two methods were used to quantify suture morphology: fractal analysis and length-ratios (actual suture length divided by direct straightline length). Both techniques produced similar results, although the two methods cannot be considered equivalent. Suture complexity increases markedly throughout ontogeny, but appears to level off after animals have reached adulthood. Cranial size in males, but not females, continues to increase in adults. No significant increase in suture complexity with age in the adult cohort was detected. While deer are highly dimorphic in size and the presence of antlers, no significant differences existed between males and females for any measure of suture complexity. No consistent patterns emerged between suture complexity and skull size or antler characteristics. The presence of antlers appears to have a minimal effect on suture complexity in white-tailed deer. Factors that may contribute to the lack of dimorphism in suture complexity are discussed. *J. Morphol.* 267:841–849, 2006.

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The family Cervidae (Mammalia, Artiodactyla) is unique among mammals in the possession of antlers, bony appendages that develop from pedicels located on the frontal bones of the skull. Due to the presence and use of antlers, the frontal bones and surrounding sutures of male cervids are likely subject to biomechanical stresses that are not commonly experienced by most other mammals. In contrast, female cervids do not possess antlers (except caribou/reindeer, *Rangifer tarandus*). Therefore, females are subject to a cranial loading regime more typical of mammals, in which mastication and brain expansion are the two predominant biomechanical factors affecting suture growth and morphology (Sun et al., 2004).

Cranial sutures are critical for postnatal intramembranous growth of the skull. However, sutures appear to lack any intrinsic growth potential (Opperman, 2000); they produce new bone in response to external stimuli such as the static tensile forces caused by the expanding brain and dura (Ogle et al., 2004; Henderson et al., 2004), the angiogenic environment of the sutures (Henderson et al., 2004), and the dynamic forces generated during mastication (Herring and Teng, 2000; Sun et al., 2004). In addition to facilitating cranial growth, sutures also help absorb the stresses placed on the skull during impact and mastication (Jaslow, 1990; Jaslow and Biewener, 1995; Herring et al., 2001). Increasing complexity (interdigitation) of a suture increases its ability to absorb energy by increasing the total surface area for collagen fiber attachment across the joint and by providing for obliquely attached fibers that are able to accommodate stress from different directions (Jaslow, 1990; Rafferty and Herring, 1999; Byron et al., 2004).

Because sutures are important both in skull growth and in the absorption of mechanical stress, we examined changes in complexity of these sutures throughout ontogeny and investigated whether the presence of antlers is associated with morphological variation in the ectocranial aspect of two sutures surrounding the antler-bearing frontal bones of white-tailed deer (*Odocoileus virginianus*). As with most cervids, the antlers of white-tailed deer are present only in males, and are grown and shed annually. Males of *O. virginianus* begin to develop antlers in the spring, typically in April to May in North America (Jacobson and Griffin, 1982; Smith, 1991). The antler develops enclosed within a sheath of skin (velvet) that supplies the growing bony inner core of the antler with blood. By August to September, the antler has reached its full size, and the

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velvet is removed by forcefully rubbing the antlers against trees and other vegetation. Mating season (the rut) occurs from October to January, a period when males compete aggressively for dominance and reproductive access to females. During this period, males engage in battles that involve butting, sparring, fencing, and wrestling with the antlers. While the primary purpose of antlers is for intraspecific combat (Clutton-Brock, 1982), males also use the antlers in territorial marking of trees and other foliage (Marchinton and Hirth, 1984). In addition to their physical role, antlers may function as structures for display and sexual advertisement. Antlers are shed in January to March, and the antler cycle continues.

While the actual strains experienced during use of the antlers in *Odocoileus virginianus* have not been measured, it seems probable that they are quite high, especially when the mass of the animals (90–135 kg in prime males in North America; Smith, 1991) and the length and breadth (resultant moment arm) of the antlers are taken into account. A cadaveric study measured the strains on the coronal suture of goats (*Capra hircus*, animals that are about half the mass of male deer) during butting as approaching 10,000  $\mu\epsilon$  (Jaslow and Biewener, 1995). However, it is difficult to assess how well this can be extrapolated to deer because they use their antlers in different ways compared to the fairly stereotyped and very high-impact head-butting behavior of horned goats. Deer wrestle and push with their antlers interlocked during intermale aggression (Marchinton and Hirth, 1984). In fact, the characteristic branching pattern of antlers probably serves to facilitate this sort of interlocking, wrestling combat, while protecting the animal (Clutton-Brock, 1982). During the rut, males will lock antlers repeatedly, sometimes wrestling for up to an hour, and even rarely incurring fatalities of both animals when their antlers become inextricably entangled during combat (Spomer, 1996). The intensity of intermale aggression generally increases as the rut progresses, with battles of the greatest intensity and duration occurring among similarly sized dominant males (Marchinton and Hirth, 1984). Antlers are also rubbed against vegetation to remove velvet, and are used to forcefully scrape and mark trees, creating bark-stripped signposts known as “buck rubs” that help establish dominance, territory, and convey intersexual signals (Marchinton and Hirth, 1984; Smith, 1991). Consequently, the strains that are placed on sutures by the use of antlers are likely to be high, complex, and irregular, involving tension and compression from multiple directions, depending on the activity for which they are used. The loading patterns and biomechanical environment in deer are quite different from the sudden high-impact loading that occurs during butting in sheep and goats. In light of our current knowledge of cranial sutures, it is of interest to assess how the presence of

antlers and the unusual biomechanical forces incurred by their use affects suture morphology.

Two different approaches have been used to quantify gross suture morphology: computing a ratio of the total length of the suture relative to the straight-line distance between its starting and ending points (Jaslow 1989; Anton et al., 1992; Rafferty and Herring, 1999), and using fractal analysis to quantify the complexity of the suture (Long, 1985; Hartwig, 1991; Long and Long, 1992; Monteiro and Lessa, 2000; Lynnerup and Jacobsen, 2003; Byron et al., 2004). Byron et al. (2004) employed both techniques and found that the two produced similar analytical results; however, their sample was fairly small and they did not attempt to examine extensively the relative merits of the two techniques.

The major goals of this research project included quantifying the changes in suture morphology that occur throughout ontogeny, assessing whether suture complexity continues to increase in adults, examining potential anatomical correlates of cranial suture morphology, and assessing sexual dimorphism in suture complexity to evaluate the hypothesis that the presence of antlers in male white-tailed deer is associated with an increase in complexity of the cranial sutures. Two different techniques for quantifying suture complexity were employed and their relative utility was compared.

## MATERIALS AND METHODS

Dry skulls ( $n = 67$ ) of individuals of white-tailed deer (*Odocoileus virginianus*) were measured and digitally photographed at collections maintained at the North Carolina Museum of Natural History (Raleigh, NC), the University of Tennessee (Knoxville, TN), Appalachian State University (Boone, NC), and the University of North Carolina at Asheville (Asheville, NC). The specimens were predominantly collected in the southern Appalachian Mountains. Each individual was assigned an age estimate based on tooth eruption and wear patterns, a well-established approach that has been widely used to provide a reasonably reliable estimate of age in deer (Sauer, 1984; Ramsey et al., 1993; Dimmick and Pelton, 1994; Hamlin et al., 2000). Males and females reach sexual maturity around 1.5 years of age (Smith, 1991), so the sample was subdivided into an adult cohort (dental age score  $\geq 1.5$  years), consisting of 29 males and 20 females, and a juvenile cohort consisting of 13 males and 5 females. The mean dental age score of adult females ( $2.8 \pm 1.2$  years, standard deviation [SD]) was not significantly different than the mean dental ages of adult males ( $2.5 \pm 0.9$ ).

Eight linear measurements were taken on each skull to quantify its overall size and shape: 1) bizygomatic breadth, 2) breadth between the supraorbital foramina, 3) postorbital constriction, 4) length of the interfrontal suture, 5) length of the maxillary tooththrow, 6) external breadth of the maxillary tooththrow at the second molar, 7) nuchal breadth, and 8) maximum skull length. To capture the overall size of the skull, a composite size variable was calculated for each individual as the geometric mean of the first seven different measurements (on some specimens the premaxillae [*os incisivum*] were broken, making it impossible to measure total skull length). For males, the number of antler points, the minimum distance between the base of the antlers, the length of the beam, and the diameter of the antler beam at its point of attachment to the skull were also recorded.

Skulls were digitally photographed from a superior perspective to visualize the interfrontal and coronal (frontoparietal) sutures,

the sutures surrounding the frontal bones from which the antlers develop. Using Adobe PhotoShop 7.0 (San Jose, CA), transparent layers were imposed over the original digital photograph, and the suture was traced from the original photograph at 300 $\times$  magnification using a 3 px brush tool. The interfrontal and coronal sutures were traced on separate layers and analyzed separately. The interfrontal suture was traced for its entire length from its junction with the nasal bones anteriorly (nasion) to its junction with the coronal suture posteriorly (bregma). The coronal suture was traced laterally until it intersected with an imaginary line extending from the medial margin of the eye orbits. Suture tracings were then scaled to uniform dimensions (700  $\times$  100 pixels for the interfrontal suture; 200  $\times$  400 pixels for the coronal suture, with the larger dimension corresponding to the long axis of the suture) and saved as bitmap files, which could be read by the fractal analysis software. Scaling was performed to facilitate visual comparison of the sutures; both techniques used for quantifying suture complexity are scale-invariant and therefore scaling the images does not affect the results.

Two approaches were used to quantify the ectocranial aspect of the sutures: fractal analysis and suture length ratios. Fractal analysis was performed using Benoit 1.3 software (TruSoft International, St. Petersburg, FL), and the Fractal Dimension (FD) was extracted for each image using the Ruler Dimension Method. Fractal analysis has been used to quantify suture complexity in mice (Byron et al., 2004), caiman (Monteiro and Lessa, 2000), and humans (Lynnerup and Jacobsen, 2003). Essentially, the FD is an index of the space-filling properties of an object (Cross, 1997). A straight line has a fractal dimension of 1, while a solid plane has a fractal dimension of 2. As a line becomes more convoluted, it fills more space and its fractal dimension increases towards 2. The Ruler Method (also known as the perimeter-stepping or coastline method; Cross, 1997) computes the FD by counting the number of steps,  $N(d)$  (which is equivalent to overall line length) taken by walking a divider (ruler) of decreasing length  $d$  along the image, and plotting the logarithm of  $N(d)$  versus the logarithm of  $d$ . The FD is the slope of this plot. In more complex lines, using shorter rulers ( $d$ ) will produce longer overall length,  $N(d)$ , resulting in a steeper slope of the plot and a higher value for the FD.

Another method used to quantify suture complexity involves generating a length ratio (LR), which is calculated as the total length of the suture divided by the straightline distance between its starting and ending points. This approach has been successfully used to document sexual dimorphism in cranial sutures of wild sheep, *Ovis orientalis* (Jaslow, 1989), and to quantify changes in suture morphology of culturally modified human skulls (Anton et al., 1992). A similar approach has been used to quantify the interdigitation of sutures in cross-section (Rafferty and Herring, 1999). From the above suture tracings, the total length of the suture was measured using the wand feature of Scion Image (Scion, Frederick, MD), which highlights and computes a perimeter around an object of interest (suture). Because the suture tracings were only about 2 pixels in width after standardizing image size, suture length (in pixel units) was calculated by dividing the perimeter in half. The direct straightline distance between the starting and ending points of the suture was measured using the linear ruler tool. Like the FD, the LR method provides a measure of spatial packing. Unlike the FD, which generally ranges from 1–2 for complex lines, the LR is a measure of how much longer the line is than minimally necessary, and so begins at 1, but theoretically has no upper maximum. Final statistical analyses were conducted using Minitab 13.32 (State College, PA).

## RESULTS

Figure 1 illustrates the images obtained after tracing the sutures and highlights some of the variation in the morphology of sutures and their associated FD and LR values. Results from both the FD and LR methods of quantifying suture complexity

showed no significant deviations from normality when assessed using Anderson–Darling and Kolmogorov–Smirnov tests. The adult, mixed-sex coefficient of variation (CV) was 5.6% for the FD of the interfrontal suture and 6.1% for FD of the coronal suture, both of which were within the range of CVs for linear morphometric measurements (4.7–8.1%). The CVs for the LR measure of complexity were much higher, 26.8% for the interfrontal suture and 28.6% for the coronal suture. Both the FD and LR methods for quantifying suture complexity indicated that the complexity of the interfrontal suture was strongly correlated with the complexity of the coronal suture (FD:  $r = 0.74$ , LR:  $r = 0.76$ , Table 1). The FD and LR methods of quantifying suture complexity were also highly correlated with each other, but did not produce identical results (Table 1).

For the total sample, all measures of suture complexity were positively correlated with age ( $r$ -values from 0.66–0.71 after log-log transformation,  $P \leq 0.001$ ), to a degree that was slightly lower than the correlation of physical size (composite size variable) with age ( $r = 0.79$  after log-log transformation) (Table 1; Fig. 2). Qualitatively, both sutures begin as essentially straight lines in neonates and early juveniles. Throughout ontogeny and into adulthood, the anterior (nasal) half of the interfrontal suture remains quite straight, while the posterior (neurocranial) half of the suture becomes increasingly interdigitated, having its most complex portion near the junction with the coronal suture (Fig. 3). In adults, the interdigitated posterior portion of the interfrontal suture is always limited to the braincase, occasionally extending as far anteriorly as the supraorbital foramina (middle of the orbit), while the anterior portion of the interfrontal suture extends onto the nasal area (snout) of the skull and remains essentially straight throughout its course. In comparison, the coronal suture develops fairly uniform complexity throughout its course, and is more complex overall than the interfrontal suture (interfrontal FD =  $1.19 \pm 0.10$ , coronal FD =  $1.49 \pm 0.18$ , paired  $t$ -test,  $t = 18.6$ ,  $P < 0.001$ ; interfrontal LR =  $2.30 \pm 0.82$ , coronal LR =  $4.40 \pm 1.80$ , paired  $t$ -test,  $t = 13.1$ ,  $P < 0.001$ ). Sutural bones (ossicles developing in the suture, apparently the result of an oxbow-like process, where the meandering suture curves back and connects with itself) were occasionally observed, especially in the coronal suture, but complete synostosis (fusion and obliteration of the external aspect of the suture) was not observed in any of the deer in our sample.

Examination of Figure 2 and subdivision of the sample into adults and juveniles indicate that the relationship between age and suture complexity is mostly attributable to an increase in suture complexity throughout ontogeny and juvenile development. When the adult cohort (individuals with dental age scores  $\geq 1.5$  years) was analyzed separately, no significant correlation was detected between den-

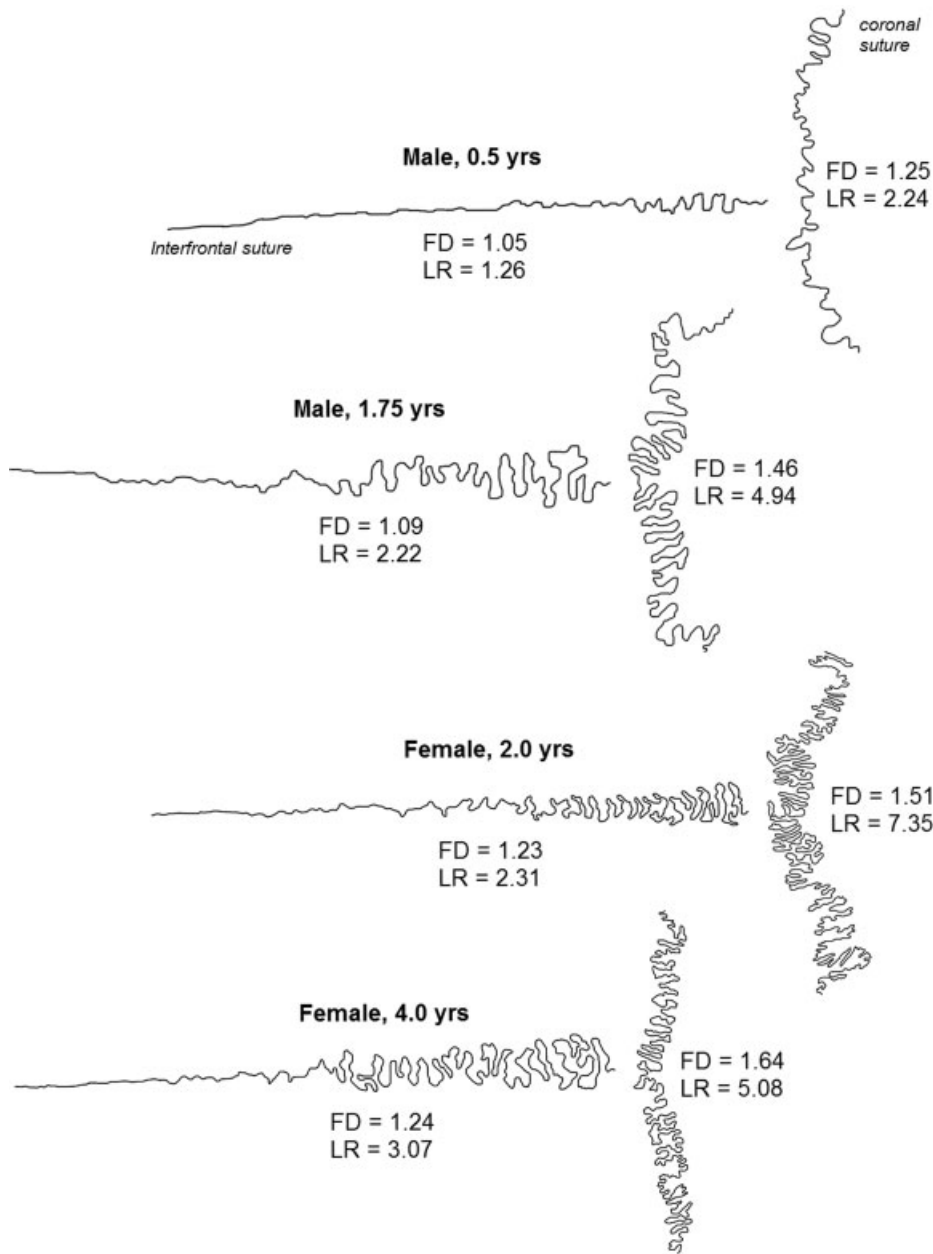


Fig. 1. Illustrations of suture tracings in *Odocoileus virginianus*, showing Fractal Dimension (FD) and Length Ratio (LR) values that were calculated for the interfrontal suture (left) and the coronal suture (right) for four individuals. Note that images were scaled to the same size. The specimens depicted here were selected to demonstrate some of the variation in suture complexity values, not necessarily to demonstrate any particular trend in suture morphology.

TABLE 1. Correlation matrix for different measures of suture complexity (FD = fractal dimension; LR = length ratio) in *Odocoileus virginianus*

	FD interfrontal	FD coronal	LR interfrontal	LR coronal
FD interfrontal	1.00	—	—	—
FD coronal	0.76	1.00	—	—
LR interfrontal	0.68	0.69	1.00	—
LR coronal	0.78	0.70	0.81	1.00
Dental age*	0.70	0.66	0.71	0.68

Correlations are based on entire sample ( $n = 67$ ). Cells contain  $r$ -values; all are significant at  $P < 0.001$ .

\*Values for dental age are based on log-log transformed of data.

tal age and any measure of suture complexity. When analyzed separately, males showed a significant increase in skull size with age ( $r = 0.51$ ), but no similar relationship existed for females. No patterned relationship existed between suture complexity and any of the individual linear measurements or antler characteristics. Likewise, no significant associations between composite size and any measure of suture complexity were detected in the adult cohort (Fig. 4).

For the adult cohort, male deer were significantly ( $P < 0.05$ ) larger than females in almost all linear morphometric measurements, including the composite size variable. No significant sexual dimor-

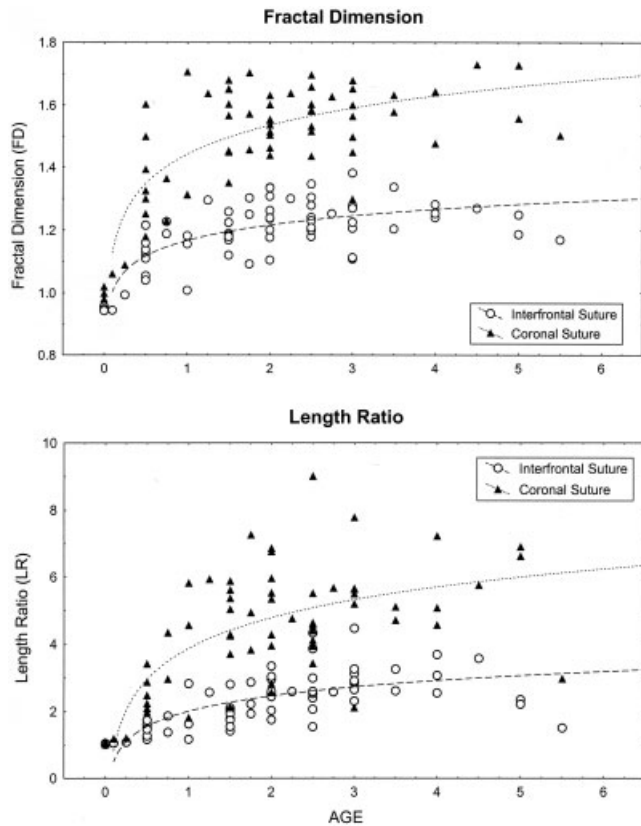


Fig. 2. Scatterplots of Fractal Dimension (top graph) and Length Ratios (bottom graph) against age score based on dental wear and eruption in *Odocoileus virginianus*. Solid symbols indicate the interfrontal suture, hollow symbols indicate the coronal suture. A logarithmic fit line is included for each suture. Log-log-transformed correlation values are presented in Table 1.

phism was detected in any measure of suture complexity for either suture (Table 2).

## DISCUSSION

The results demonstrate that while the two different measures of suture complexity are correlated, they are not identical measures of the same morphological phenomenon. From these results and others (Byron et al., 2004), it appears that both techniques produce similar results. Fractal dimensions are ultimately measures of self-similarity, and fractal analysis is ultimately a test of scale invariance (Mandelbrot, 1989). Sutures belong in a category of natural fractals, which show degrees of self-similarity, yet are not completely self-similar (Mandelbrot, 1989). This fractal degree of scale invariance may be of interest and utility in certain developmental or histological settings to describe the growth and patterning of sutures; however, the biomechanical parameter that may be of more interest to morphologists is the overall interdigitation of the sutures at the gross morphological level and how this property is related to the loading environment

of the joint. For this purpose, we suggest that LRs are better indicators of the cumulative surface area that is packed along the length of the suture as it becomes more interdigitated. LRs are probably more intuitive and easier to interpret functionally, and may also be more directly comparable among different taxa.

Few comparative data are available to place the suture complexity of deer within a broader mammalian context. However, suture complexity in *Odocoileus virginianus* is relatively high compared to the other species for which comparable data have been published. The LRs of the coronal suture of both male and female white-tailed deer (see Table 2) are comparable to the mean values calculated for male wild sheep ( $5.41 \pm 0.49$  SD), but much greater than reported for female sheep ( $1.66 \pm 0.15$ ) (Jaslow, 1989). White-tailed deer also appear to equal or exceed the interdigitation of female goats (*Capra hircus*), who were reported to have an LR of 2.0–6.5 for the same suture (Jaslow, 1990). The LR for the coronal suture in white-tailed deer greatly exceeds that of humans ( $2.32 \pm 0.10$  SE; calculated from data in Anton et al., 1992). The sutures of both male and female deer are highly interdigitated, and appear to be built to withstand a great amount of stress when considered in the context of the limited comparative data currently available.

Both techniques for quantifying suture morphology demonstrate that the complexity of both sutures increases dramatically throughout ontogeny. While we did not conduct a longitudinal study of suture growth, in our sample suture complexity reaches its maximum at sexual maturity (1.5 years) and does not significantly increase with dental age score after that. Around the time of sexual maturity, maximum brain size has probably been attained, and certainly the trajectory for brain growth declines markedly. The demands of mastication likely do not change significantly at this time, although there is seasonal, geographic, and individual variation in selection of food resources that may differ in mechanical properties (Biere, 1987; Weckerly and Nelson, 1990). When the adult cohort was analyzed separately, male deer showed a significant increase in skull size with age ( $r = 0.51$ ), but females did not. Longitudinal growth studies (Harmel et al., 1989) and cross-sectional studies (e.g., Osborne, 1993) have also demonstrated that male deer continue to increase in body mass and antler characteristics (points, size, and span) between 1.5 and 3.5 years. Our results suggest that cranial size of male deer (only) continues to increase with age in adults; females do not show a similar trend. A significant shift in behavior occurs between 2- and 3-year-old males. Younger and smaller males (2 years or less) commonly spar with larger opponents, while older, larger males (3 years and greater) spar more frequently with smaller rivals (Hirth, 1977). The stiffness of antlers in white-tailed deer also decreases significantly be-

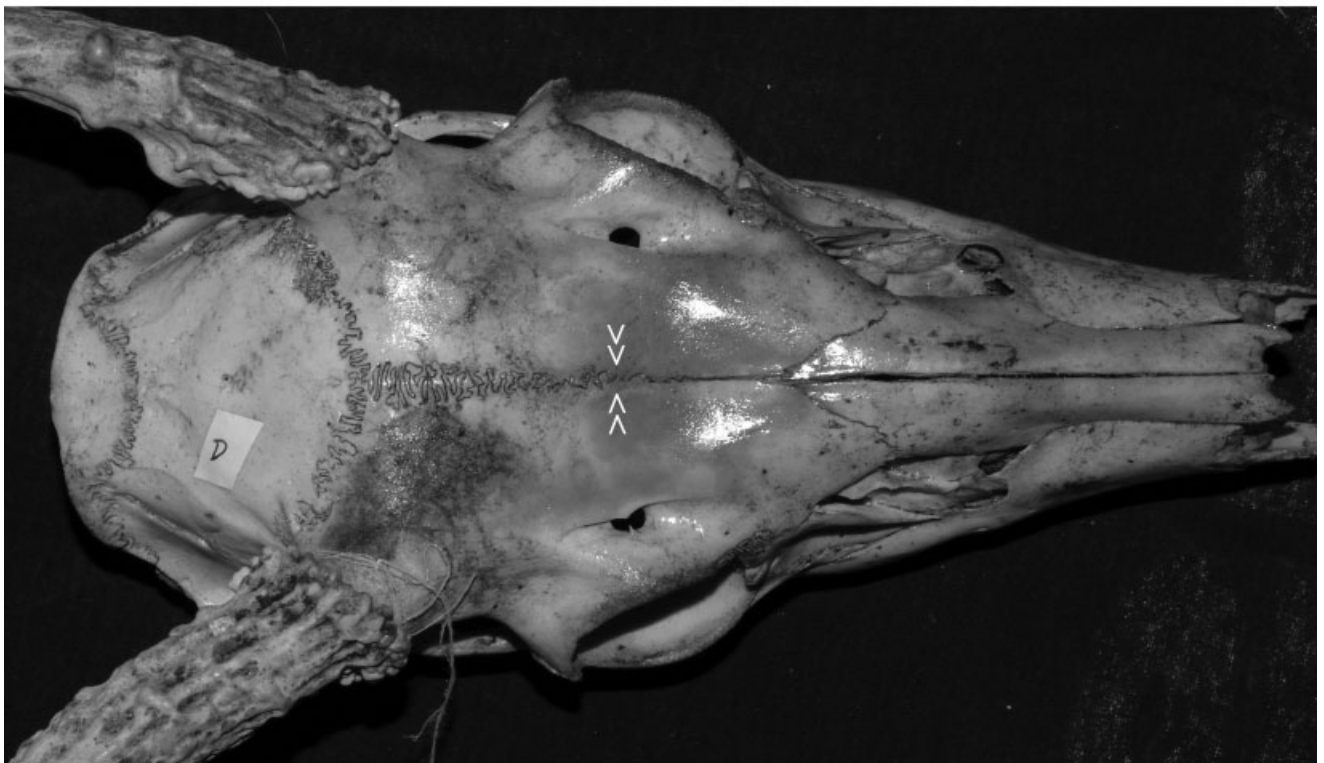


Fig. 3. Arrows indicate that the interfrontal suture of *Odocoileus virginianus* can be divided into a complex and highly interdigitated posterior portion and a relatively straight anterior portion. On the top graph, it can be observed that the bone containing the posterior aspect of the suture is thickened and raised into a torus running along its length. Specimen is a 2.5-year-old male.

tween 2 and 3 years of age (Blob and LaBarbera, 2001). However, there was no significant association between any measure of suture complexity and our dental age estimates, either when the sexes were considered separately or when the entire sample is analyzed together. Young adult males ( $\leq 2$  years) were not significantly different in suture complexity than older males ( $\geq 3$  years) (see Fig. 2). This does not refute the idea that sutures and surrounding bone remodel in adults (even to the extent that remodeling may affect the overall morphology of the suture); however, it indicates that the overall complexity of the ectocranial aspect of these sutures does not increase after sexual maturity, even though overall size in males continues to increase.

One possible influence on the lack of increased suture complexity with age in males is that the antlers of male deer become less stiff with age (Blob and LaBarbera, 2001), while at the same time deer begin to spar more frequently with relatively smaller opponents (Hirth, 1977). Fighting larger opponents with stiffer antlers could place greater strain on the sutures in young males, resulting in increased suture complexity relative to that which may be predicted from physical growth trajectory. Females do not show a similar increase in size throughout adulthood, and therefore may lack any significant influences on suture morphology due to size.

The complex, interdigitated portion of the interfrontal suture is limited to the portion overlying the braincase, while the anterior portion of the suture, which extends toward the snout, remains essentially a straight line (Fig. 3). The coronal suture, which becomes highly interdigitated throughout its length, is also located entirely over the braincase. These facts, along with the apparent lack of change in

TABLE 2. *t*-Tests of differences in measures of suture complexity in adult males and females of *Odocoileus virginianus*

	Males (n = 29)	Females (n = 20)	<i>t</i> -Value
FD interfrontal	1.22 $\pm$ 0.014	1.24 $\pm$ 0.014	1.01 ( <i>P</i> = 0.32)
FD coronal	1.58 $\pm$ 0.018	1.54 $\pm$ 0.019	1.77 ( <i>P</i> = 0.08)
LR interfrontal	2.67 $\pm$ 0.139	2.51 $\pm$ 0.141	0.85 ( <i>P</i> = 0.40)
LR coronal	4.96 $\pm$ 0.272	5.40 $\pm$ 0.340	0.51 ( <i>P</i> = 0.32)
Composite size	73.7 $\pm$ 0.70	67.9 $\pm$ 0.65	6.05 ( <i>P</i> < 0.001)

Values are means  $\pm$  SE. Composite size was calculated as the geometric mean of seven linear measurements of the skull (see text).

suture morphology with increasing age (dental wear) in adults, suggest that factors such as the growth of the brain and dura may be especially important in determining the complexity of these sutures. However, the ability to age a skull accurately using dental wear declines with age (Hamlin et al., 2000; Van Deelen et al., 2000), and there were not enough older individuals (dental scores  $\geq 4$  years) in the sample to assess unequivocally the relationships between adult age, size, and suture complexity.

Surprisingly, *Odocoileus virginianus* exhibited no significant sexual dimorphism in suture morphology. Males are larger than females, but adult size is apparently unrelated to suture morphology. Together, these data indicate that suture morphology in *O. virginianus* is not demonstrably influenced by the presence of antlers. The mechanical environment created by antlers and their use and the endocrine signals that lead to antler development seem to have negligible effects on male ectocranial suture morphology compared to females. This lack of dimorphism could result from either the possibility that antlers do not contribute to increased suture complexity in males or that female deer have greater than expected suture complexity.

Several factors potentially contribute to the lack of dimorphism in suture morphology related to the presence and use of antlers in male *Odocoileus virginianus*. One possibility is that variation in unmeasured factors, such as bone thickness, collagen fiber arrangement, and internal suture form, may be sufficient to compensate for the biomechanical demands created by using antlers without requiring the macroscopic morphological modification of the ectocranial aspect of the suture. In white-tailed deer, the bone running along the sutures is raised and thickened compared to the rest of the vault bone. The morphological result is that a torus (ridge) of increased bone thickness can be seen and felt along each of the sutures in both male and female deer (see Fig. 3). We have not yet assessed whether this structure is dimorphic or not, or if its thickness relates to suture complexity. Quantification of these and other factors is necessary to accurately place ectocranial suture morphology within the overall

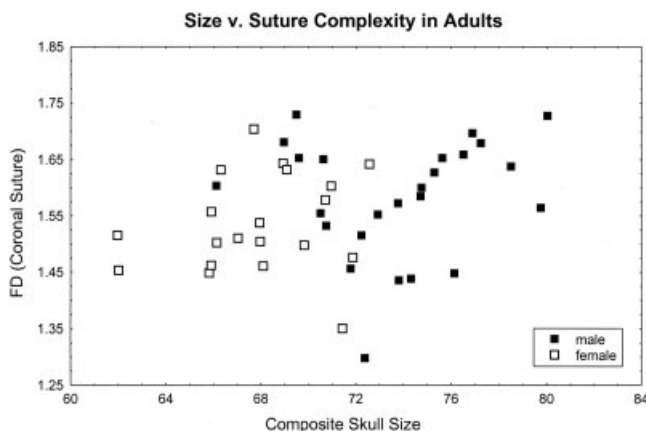


Fig. 4. Plot of Fractal Dimension (FD) for the coronal suture against composite skull size in adult *Odocoileus virginianus*. The two variables are not significantly correlated. Males were significantly larger in skull size, but no significant differences for FD existed between the sexes. The trend seen here holds for both measures of complexity (FD and LR) and is equivalent for the interfrontal suture.

context of the numerous parameters associated with cranial loading.

Antler (in both *Odocoileus virginianus* and red deer, *Cervus elaphus*) is tougher and more damage resistant than typical postcranial long bone, and antler bone can dissipate almost 10 times more energy than ordinary bone can dissipate during impact loading tests (Zioupos et al., 1996; Blob and LaBarbera, 2001). Antler has a lower mineral content, lower density, lower Young's Modulus ( $E$ ), greater fracture resistance, and a greater tendency to create isolated microcracks that enable post-yield deformation (Zioupos et al., 1996; Currey, 1999). The energy-absorbing properties of antler may ultimately help dissipate the mechanical strain that reaches the sutures, minimizing any osteogenic response at the sutures.

Another possible contribution to the lack of dimorphism in deer sutures is that deer simply do not use their antlers frequently enough to influence the activity of osteoblasts to produce a quantifiable alteration of suture morphology. A male white-tailed deer will have antlers for roughly three-fourths of the year, and use them extensively in marking territory and fighting during only 5–6 months of the year (Kile and Marchinton, 1977). For about half of the year, and indeed for the vast majority of each day during the season when antlers are used, the dynamic loading regime on the skulls of male deer is ostensibly equivalent to that of female deer. Although antlers may generate extreme biomechanical stresses when used, the minimum frequency of stimulus (at a high magnitude) needed to produce an overall change in suture morphology is unknown, and it is possible that stresses from the use of antlers are not frequent enough to alter osteogenic patterns. The regular and cyclical loading and microstrain associated with factors such as mastication may produce a stronger signal influencing suture morphology, effectively drowning out the osteogenic signals from antler presence and use. However, this seems contradicted by at least two factors. First, even when antlers are not used directly as tools, their physical mass and weight (200–1,500 g; Harmel et al., 1989) may create static tension on the skull and its sutures (and possibly oscillatory strains during locomotion). Second, research has shown that sheep, which also have relatively infrequent but extreme loading on the sutures, are extremely sexually dimorphic in suture morphology (Jaslow, 1989).

An additional possibility for these results is that the loading experienced at the sutures from antler use may be too variable to create a biomechanical environment that has a gross effect on suture form. In general, orthopedic experiments have demonstrated that static tension promotes bone deposition, while static compression limits growth at the suture, and compression often contributes to increasing interdigitation of the sutures (Sun et al., 2004). How-

ever, experimental research has shown that microscale oscillating strains, either compressive or tensile, promote suture growth (Mao, 2002; Kopher and Mao, 2003), but the effect of large scale, irregular loading on suture morphology has not been demonstrated empirically. The activities during which antlers are used are numerous, and different activities may create highly variable patterns of tension and compression on the skull and its sutures. For example, when deer grapple with the antlers interlocked, pulling in one direction may generate tension, while pushing would cause compression. Perhaps the variable biomechanical signals from the use of antlers create an irregular and "confusing" osteogenic environment that does not promote a regular and patterned response from osteoblasts.

A final consideration that must be seriously evaluated is that perhaps female deer are exceptional in their high degree of suture complexity. While comparative samples are limited, female white-tailed deer have much more complex sutures than reported for female wild sheep, and are within the range or greater than female goats (Jaslow, 1989, 1990). Therefore, perhaps it is the female deer that develop unexpectedly high suture complexity. There are few compelling morphological or behavioral differences that immediately appear to account for increasing suture complexity in females. Females have a slightly higher molar surface area relative to body mass (Van Deelen et al., 2000), and some equivocal research has indicated that females are more selective feeders than males, who consume coarser forage (Beier, 1987; but see Weckerly and Nelson, 1990). However, these differences do not seem to be sufficient to explain a radical increase in suture complexity in females. Instead, the greater possibility is that a strong genetic or developmental signal, for example, from the expanding brain and dura, dictates the majority of suture complexity in deer, independent of the sex of the individual.

Further research is needed to understand how and why such strikingly dimorphic animals, which appear to have such extremely different biomechanical loading on the skull, lack any sexual dimorphism in cranial suture complexity. To obtain a complete picture of the role of suture complexity in deer, the stresses and strains placed on the skull during the use of antlers must be measured, and the mechanical energy that the antlers transmit to the sutures be assessed. Gathering behavioral data on the frequency and duration of the various activities for which antlers are used will be very informative. Potentially important dimorphism in other aspects of cranial form, such as bone thickness and internal, histological, and microvascular aspects of suture morphology, must also be examined. A longitudinal study of suture growth is needed to document how and if suture morphology undergoes change or remodeling once sexual maturity and adult size have been attained. Finally, an analysis of suture mor-



phology throughout artiodactyls is necessary to place these findings within a broader phylogenetic and comparative context.

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