Shape of the canine diaphragm

MAURIZIO ANGELILLO,1 ALADIN M. BORIEK,2 JOSEPH R. RODARTE,2 AND THEODORE A. WILSON3
1Department of Civil Engineering, University of Salerno, Salerno 84084, Italy; 2Baylor College of Medicine, Houston, Texas 77030; and 3Department of Aerospace Engineering and Mechanics, University of Minnesota, Minneapolis, Minnesota 55455

Received 15 October 1999; accepted in final form 7 February 2000

Angelillo, Maurizio, Aladin M. Boriek, Joseph R. Rodarte, and Theodore A. Wilson. Shape of the canine diaphragm. J Appl Physiol 89: 15–20, 2000.—In an earlier study (Angelillo M, Boriek AM, Rodarte JR, and Wilson TA. J Appl Physiol 83: 1486–1491, 1997), we proposed a mathematical theory for the structure and shape of the diaphragm. Muscle bundles were assumed to lie on lines that are simultaneously geodesics and lines of principal curvature of the diaphragm surface, and the class of surfaces that are formed by line elements that are both geodesics and lines of principal curvature was described. Here we present data on the shape of the canine diaphragm that were obtained by the radiopaque marker technique, and we describe a surface that fits the data and satisfies the requirements of the theory. The construction of surfaces with this property is particularly important in applications to diaphragm mechanics; modeling; chest wall.

IN MOST SKELETAL MUSCLES, muscle bundles lie along straight lines, and the functional force exerted by the muscle is the direct force that acts along the axis of the muscle bundle. In the diaphragm, the muscle bundles lie on a curved surface, and their functional force, the force that balances transdiaphragmatic pressure (Pdi), is exerted in a direction orthogonal to the surface. A curved muscle bundle exerts a force in the direction of muscle curvature, and the magnitude of this force is proportional to curvature. If the direction of muscle curvature is orthogonal to the surface, the line of the muscle bundle is a geodesic of the surface, and the entire transverse force contributes to Pdi. If the muscle bundles lie along the line of maximum curvature, the orthogonal force, for a given axial force, is maximal. In an earlier study (1), we argued that certain shapes would allow all muscle bundles to have these optimal properties, and we described the class of surfaces for which the geodesics and lines of principal curvature coincide. The construction of surfaces with this property can be summarized as follows. The line elements that are simultaneously geodesics and lines of principal curvature must lie in planes, and all line elements must have the same shape. If the line elements are not circular, their orientation is restricted. If the line elements are circles, their orientation is immaterial, and the surface shape is determined by the radius of the circles and an arbitrary line. The arbitrary line can be taken as the line of centers of the circles, with the circles lying in planes perpendicular to the line of centers. Surfaces formed by circles that lie in planes normal to a line of centers are known as cyclides. They are like the surface of a Slinky with an arbitrary line for the axis of the Slinky.

The theory of diaphragm shape was supported by observations on the shape of the canine diaphragm in a limited region, the midcostal region. In this region, the shape is approximately that of a right circular cylinder, with the muscle bundles lying in planes normal to the axis of the cylinder (2, 5, 7). A circular cylinder is a particularly simple example of a cyclide. For a cylinder, the line of centers is a straight line, and the surface is formed by circular arcs that lie in planes normal to the line of centers.

In the earlier study (1), a complete surface that is qualitatively similar to the shape of the canine diaphragm was constructed by combining two simple cyclides, a torus and a sphere. A torus is a cyclide with a line of centers that is a circle, and a sphere is a cyclide with a point as the line of centers. The diaphragm-like surface was formed by joining spherical caps to a segment of a torus. The outer part of the torus and cap was taken to represent the costal diaphragm, and the inner part to represent the crural diaphragm. Although this model shape is similar to that of the diaphragm, differences between it and the true diaphragm shape are apparent. In particular, this model does not describe the gap between the costal and crural muscles that is occupied by the central tendon, and the ratio of the dorsal-ventral to lateral dimensions of the model is smaller than that of the diaphragm.

In this study, we report more extensive data on the shape of the canine diaphragm, and we describe a theoretical surface that was fit to the data. The data on diaphragm shape were obtained by measuring the lo-
citations of radiopaque markers that had been attached along muscle bundles of the diaphragm of a dog. Separate cyclides were fit to the data for the costal and crural diaphragms, and these two cyclides were joined at their laterodorsal ends. The data are well fit by the cyclides, and the observed structure of the dorsal region of the diaphragm, where the costal and crural diaphragms join, matches constraints imposed by the theory. Thus it appears that the structure and shape of the entire canine diaphragm are consistent with the theory.

**MODELING AND ANALYSIS**

In the earlier study (1), we obtained the description of surfaces that are formed by lines that are simultaneously geodesics and lines of principal curvature of the surface. Cyclides are members of this class. Here we extend the modeling to describe two elements that are needed in the fitting of cyclides to the data on diaphragm shape. These new elements are a cusp in the line of centers of a cyclide and a joint between cyclides with different radii.

A cyclide is a surface formed by circles that lie in planes that are perpendicular to an arbitrary line with their centers on the arbitrary line. Because the line of centers is arbitrary, the cyclide is a flexible surface with a variety of shapes. If the line of centers is a straight line, the surface is a right circular cylinder. If the line of centers is a circle, the surface is a torus with curvature both along the direction of the circular line elements and in the direction perpendicular to the circular line elements. A transition from a right cylinder to a torus is illustrated in Fig. 1. In Fig. 1A, the line of centers, or axis, of a cyclide is represented by the line \( x(s) \), where \( x \) is the vector position of the points on the axis and \( s \) is a scalar coordinate measured along the axis. The radius of the circular arcs of this cyclide is \( r \).

To the left of point \( A \) in Fig. 1A, the line \( x(s) \) is straight, and to the right of point \( A \), it is a circle with radius \( R \). At the arc that intersects point \( C \), the surface of the cyclide changes from a right circular cylinder to a torus. The curvature of the surface in the direction of the line elements remains equal to \( 1/r \), but the curvature in the direction perpendicular to the line elements changes from 0 to \( 1/(r + R) \). With this construction of the axis, the curvature of the surface in the direction perpendicular to the line elements is limited. At most, the axis beyond point \( A \) degenerates into a point, and the surface becomes a sphere with radius \( r \) and curvature \( 1/r \).

It is clear from Fig. 1A that, if the tangent to the axis changes direction continuously, the surface is continuous. A discontinuous change in the direction of the tangent is not allowed. If the tangent to the axis changed direction discontinuously, the orientation of the plane of the line element, which is perpendicular to the axis, would be discontinuous, and a gap would occur in the surface. However, a discontinuous change of 180° is an exception to the rule. That is, if the direction of the tangent changes by 180°, forming a cusp in the line of centers, the orientation of the plane perpendicular to the tangent does not change, and the surface is continuous. This possibility is illustrated in Fig. 1B. Here, the axis doubles back on itself through a cusp at point \( A \). In this example, the axis is a straight line up to point \( A \), and the axis is continued beyond point \( A \) by a circle with radius \( R \) that is tangent to the axis at point \( A \). At point \( C \), the curvature of the surface in the direction perpendicular to the line elements changes from 0 to \( 1/(r - R) \). Thus a continuous surface with a sharper change in surface curvature can be represented by a cyclide with a cusp on the line of centers.

---

**Fig. 1.** Cyclide with an axis \( x(s) \), where \( s \) is the distance along the axis. The surface of the cyclide is formed by circular arcs with radius \( r \). The circular arcs lie in planes that are perpendicular to \( x(s) \) with the centers of the arcs on \( x(s) \). The axis changes at point \( A \) from a straight line to a circle with radius \( R \), and the surface changes at point \( C \) from a right cylinder to a torus. A: the axis continues forward at point \( A \), and the radius of curvature of the surface in the direction transverse to the circular arcs is \( r + R \). B: the axis reverses through a cusp at point \( A \), and the radius of curvature of the surface is \( r - R \).
Next, the construction of a joint between cyclides with different radii will be described. Joints between two cyclides with centers $x_1(s_1)$ and $x_2(s_2)$ and radii $r_1$ and $r_2$ are shown in Fig. 2. The two cyclides are pictured as having separate edges to the left of point $C$ in Fig. 2 and meeting along a joint line $j(s_1)$ to the right of point $C$. We require the surface to be continuous and, in addition, to be smooth, i.e., that the slope of the surface be continuous across $j(s_1)$. These conditions on the surface can be translated into conditions on the geometry of the axes of the two cyclides. The line of intersection of the planes of the circular line elements that intersect at $C$ is denoted $CBA$ in Fig. 2A. In order for the slopes of the surfaces of the two cyclides to match at $A$, the perpendicularly to the surfaces at this point must coincide. That is, the line $CBA$ must be normal to both surfaces, and, hence, points on the axes of both cyclides must lie on $CBA$. In the example shown in Fig. 2A, $r_1 > r_2$. $AC$ has length $r_1$, and $BC$ has length $r_2$. Thus $AB = r_1 - r_2$. These conditions on the axes must be satisfied at every point along the joint $j(s_1)$.

They are met by allowing the continuation of one of the axes, say $x_1(s_1)$, to be arbitrary and requiring the second, $x_2(s_2)$, to lie on a curve with axis $x_1(s_1)$ and radius $r_1 - r_2$. This construction is shown in Fig. 2A. Here, $x_1(s_1)$ continues past point $A$ as a straight line, and $x_2(s_2)$ continues past point $B$ on a curved line that lies at a constant distance from $x_1(s_1)$. The joint $j(s_1)$ starts at $C$. At every point along $j(s_1)$, the perpendicular to the surface passes through the axes of both cyclides.

In the example shown in Fig. 2A, $x_1(s_1)$ continues in a straight line, and $x_2(s_2)$ curves around $x_1(s_1)$ at constant distance $r_1 - r_2$. In this example, $j(s_1)$ lies to the left of the directions of the tangents to both $x_1(s_1)$ and $x_2(s_2)$, and the surface of cyclide 1 extends only a short distance past point $C$. In order for the joint to continue within the angle formed by the tangents to $x_1(s_1)$ and $x_2(s_2)$, the axis of one of the cyclides must turn back through a cusp. This is illustrated in Fig. 2B. Here, $x_1(s_1)$ passes through a cusp at point $A$, and $x_2(s_2)$ must curve more sharply to remain at a constant distance from $x_1(s_1)$. With this construction, the direction of the tangent to $j(s_1)$ lies between the directions of the tangents to $x_1(s_1)$ and $x_2(s_2)$, and the surfaces of both cyclides continue further past point $C$.

METHODS

Experimental methods. The locations of points on the canine diaphragm were determined by using the radiopaque marker technique. The method and other features of the data obtained in this study have been reported previously (7). In a preparatory surgical procedure, 36 silicon-coated lead spheres and cylinders were stitched to the peritoneal surface of one hemidiaphragm of each of four bred-for-research beagles. To obtain data on the arcs of the muscle bundles, three or four markers were fixed along each of six muscle bundles of the costal diaphragm and two muscle bundles of the crural diaphragm, as shown in Fig. 3. Additional markers were placed at three points on the central tendon, at two points on the costal diaphragm on the sagittal midplane, and at two points on the costal-crural joint at the dorsal end of the costal diaphragm. The dog was allowed to recover from surgery for at least 3 wk. On the day of the study, the dog was anesthetized with pentobarbital sodium (30 mg/kg), intubated with a cuffed endotracheal tube, and placed in the test field of an orthogonal biplane fluoroscopic system. Biplane fluoroscopic images were taken during various respiratory maneuvers. The coordinates of the markers in the two orthogonal images were determined, and the three-dimensional coordinates of the markers were calculated from their coordinates in the two orthogonal images.

Data were obtained during quiet breathing and during inspiratory efforts with the airway occluded at different lung volumes in both the prone and supine postures. The data on the shape, length, and displacement of the three muscle bundles in the midcostal diaphragm and on the lengths of all muscle bundles in all dogs were reported earlier (5, 6, 9). Here, we use the data for the locations of all markers in one dog in one state; namely, end inspiration during quiet breathing in the prone posture. The individual dog was chosen because the spacing and alignment of the markers were best in this dog. End inspiration was chosen because it

Fig. 2. Joints between cyclides with axes $x_1(s_1)$ and $x_2(s_2)$ and radii $r_1$ and $r_2$. Line $AC$ is the intersection of the planes that are orthogonal to the axes. $A$ and $B$: the lines of centers intersect $AC$ at $A$ and $B$, and $AC$ is orthogonal to the surfaces of both cyclides. A joint between the cyclides, $j(s_1)$, starting at $C$ is shown by the dashed line. $A$: axis $x_1(s_1)$ continues past point $A$, and $x_2(s_2)$ curves around $x_1(s_1)$ at a constant distance $r_1 - r_2$. In that case, the direction of the tangent to $j(s_1)$ lies outside the range of directions between the tangents to $x_1(s_1)$ and $x_2(s_2)$. $B$: axis $x_1(s_1)$ reverses through a cusp at $A$, $x_2(s_2)$ curves more sharply, and the tangent to $j(s_1)$ lies between the tangents to $x_1(s_1)$ and $x_2(s_2)$.
is a physiological state in which the diaphragm is active. At end inspiration, the zone of apposition is smaller and diaphragm shape is less susceptible to distortion by nonuniform pressures than at end expiration.

Numerical methods. The software Mathematica was used to compute the locations of points on the surface that represent the diaphragm. The surface was formed from two cyclides, representing the costal and crural diaphragms, with lines of centers, or axes, \( \mathbf{x}_1(s_1) \) and \( \mathbf{x}_2(s_2) \), respectively. The lines \( \mathbf{x}_1(s_1) \) and \( \mathbf{x}_2(s_2) \) were specified, and the circular arcs that represent the muscle bundles were generated. The parameters of the lines were adjusted to obtain a fit of the arcs of the cyclides to the data on the location of points on the muscle bundles. The lines \( \mathbf{x}_1(s_1) \) and \( \mathbf{x}_2(s_2) \) that represent the line of centers of the costal and crural diaphragms are shown in Fig. 4. In this figure, the \( x \)-axis lies in the lateral direction, and the plane \( x = 0 \) is the sagittal midplane of the dog. The \( y \)- and \( z \)-axes lie in the dorsoventral and caudocranial directions, respectively. The \( \mathbf{x}_1(s_1) \) was constructed as follows. First, a plane was fit to the data for the locations of the six markers at the chest wall on the six muscle bundles of the costal diaphragm. This plane lies 30° below the ventrodorsal direction and 20° below the lateral direction. The arc \( AB \) in Fig. 4 that forms the bulk of the line \( \mathbf{x}_1(s_1) \) is an arc of a circle with a radius of 9.5 cm that lies in the plane fit to the chest wall markers. A cusp at \( B \), a circular arc \( BC \), a cusp at \( C \), and a straight line \( CD \) were used to bring the ventral end of \( \mathbf{x}_1(s_1) \) to the midplane with a direction normal to the midplane. The dorsal end of \( \mathbf{x}_1(s_1) \) is a circular arc \( AE \) attached to \( AB \) through a cusp at point \( A \). This circular arc lies in a plane perpendicular to the plane of \( AB \), and its radius is 0.8 cm.

The \( \mathbf{x}_2(s_2) \) was constructed as follows. \( FG \) is an arc of a circle that lies in a plane that is normal to the midplane and inclined at 33° below the ventrodorsal direction. At point \( F \), the tangent to \( FG \) is orthogonal to the midplane, point \( G \) lies in the plane perpendicular to \( AB \) at \( A \), and the tangent to \( FG \) at \( G \) is orthogonal to the line \( AG \). The distance between \( A \) and \( G \) equals the difference in the radii of the two cyclides, \( r_1 - r_2 \). Thus point \( G \) in Fig. 4 corresponds to point \( B \) in Fig. 2B.

The continuation of \( x_2(s_2) \) beyond \( G \), segment \( GH \), lies in a plane that contains the tangent to \( FG \) at \( G \) and the line \( AB \). Segment \( GH \) was constructed by finding the intersection of this plane with the cyclide with \( AE \) as its center and radius \( r_1 - r_2 \).

The radii of the cyclides that represent the costal and crural diaphragms were chosen to be 3.7 and 2.3 cm, respectively.

RESULTS

The experimental and numerical results are reported graphically. Both are shown in Fig. 5. The locations of markers on muscle bundles are shown by solid circles connected by dashed lines, and the locations of markers on the central tendon and on the extension of the central tendon along the joint between the costal and crural diaphragms are shown by open circles. The arcs of the two cyclides of the numerical model are shown by lines. The joint between the cyclides is shown by the long dashed line.
The fit of the model to the data for the costal diaphragm was better than the fit for the crural diaphragm. The root-mean-square distance between the 29 markers on the muscle bundles and the model surface was 3 mm.

**DISCUSSION**

The muscle bundles of the diaphragm lie along curved lines, and, by virtue of the curvature, muscle tension is transformed into Pdi. For a given muscle tension, Pdi is maximum if the muscle bundles lie along lines that are both geodesics and lines of maximum curvature. The class of surface shapes for which the geodesics and lines of principal curvature coincide is restricted, and we have hypothesized that the shape of the diaphragm is a member of this class (1). Here, we have tested this hypothesis by matching a shape that is like those of the muscle bundles.

The data were fit by a surface formed by lines that are both geodesics and lines of principal curvature of the surface. The search for a fit was restricted to a simple subgroup of the class of theoretical surfaces. First, the shapes of the costal and crural diaphragms were modeled as cyclides, with independent radii of the two cyclides allowed. Second, simplifications were made in modeling the lines of centers of these cyclides. For most of their extent, these were assumed to be circular arcs that lie in a plane. In this way, the parameter space was reduced. The parameters of the model were those that describe the planes of the centers, the location and radii of the arcs of the lines of centers, and the radii of the cyclides. More complicated geometries were required at the joint between the costal and crural diaphragms, as described in METHODS.

The data for the separate costal and crural muscles were well fit by cyclides. That is, the data are consistent with the constraint that the curvature of the muscle bundles be the same at all points along each muscle. The radius of the cyclide that represents the costal diaphragm is 3.7 cm. This is in the range of the values of 4.3 ± 1.3 cm reported by Boriek et al. (5) for the radius of curvature of the muscle bundles in the midcostal region of four dogs at end inspiration in the prone posture. The radius of the cyclide that represents the crural diaphragm is 2.3 cm. We know of no other data on curvature of the muscle bundles of the crural diaphragm.

Over most of the extent of the costal and crural diaphragms, the muscles are separated by a gap that is bridged by the central tendon. As a result, the shapes of these segments of the muscles are relatively independent. At the dorsal ends of these muscles, they join directly, and their shapes must accommodate the joint.
The theory of diaphragm structure and shape was extended to include rules for constructing a joint between cyclides. Cusps in the lines of centers of the cyclides were required to construct surfaces with a joint that curved sharply like that of the diaphragm. We want to emphasize that the lines of centers are mathematical constructs that are useful in describing and constructing cyclides but have no physiological reality. The surface of the model, which corresponds to the diaphragm, is smooth and continuous, despite the presence of cusps in the line of centers. With a cusp in the line of centers of the costal diaphragm, the model fit the observed properties of the dorsal region of the canine diaphragm well. That is, the pattern of changing orientations of the muscle bundles in this region matches the requirements for joining the two cyclides.

The radius of curvature of the muscle has mechanical significance. Pdi is balanced by an orthogonal force that is proportional to membrane tension and surface curvature. To be specific, Pdi equals the sum of the products of membrane tension and curvature in the two directions of principal curvature. In the costal diaphragm, curvature in the direction of the muscle bundles is smaller than in the crural diaphragm, but curvature in the second principal direction, the direction transverse to the muscle bundles, has the same sign as curvature in the direction of the bundles, and the product of tension and curvature in the second principal direction contributes to the orthogonal force that balances Pdi. In the part of the crural diaphragm that is near the sagittal midplane of the dog, curvature in the second principal direction has the opposite sign from that in the direction of the muscle bundles, and tension in the second principal direction reduces the orthogonal force. Therefore, either tension in the direction of the muscle bundles must be larger in the crural than in the costal diaphragm, or the curvature of the muscle bundles must be larger, or both. Thus the greater curvature of the muscle bundles of the crural diaphragm is consistent with the requirements of mechanics. In the dorsolateral region where the costal and crural regions meet, curvature of the costal diaphragm in the direction transverse to the muscle bundles is larger than in the more ventral part of the costal diaphragm, and, in this region, both principal curvatures of the crural diaphragm have the same sign. Therefore, a smaller membrane tension is required to balance Pdi in the region of the joint. Because membrane tension equals force per unit area times thickness, the diaphragm can be thinner at the dorsal end, and it has been observed that it is (3, 8).

We think that the theoretical surface matches the data remarkably well. Both the locations of the markers and the orientations of the muscle bundles are well matched by the model. We used a cyclide with a line of centers that lies in a plane to represent the majority of the costal diaphragm, section AB in Fig. 4. As a result, the arcs that represent muscle bundles lie in planes that are perpendicular to the plane of the line of centers. The orientations of the four muscle bundles that lie in this region are consistent with this feature of the model. The part of the crural diaphragm near the midplane, section FG in Fig. 4, was also represented by a cyclide with its line of centers lying in a plane. Only one muscle bundle was marked in this region, and the lines of muscle bundles in this region are distorted by openings for the large vessels. Thus the data are insufficient to confirm or refute the model for the crural diaphragm. Also, the data are not sufficient to fix the numerical values of the parameters that describe the joint between the costal and crural diaphragms. However, the structure of the diaphragm and the data in this region match the structure of the model. That is, the observed location of the joint and the angles between the muscle bundles at the joint are qualitatively consistent with the model shown in Fig. 2B. In addition, the theory imposes a constraint on the orientation of the planes of the muscle bundles that meet at a joint. To join two cyclides with different radii of curvature, the lines of centers must wrap around each other, and the planes of the line elements must rotate toward the transverse plane of the dog. The data for two muscle bundles of the costal diaphragm and one muscle bundle of the crural diaphragm are consistent with this constraint.

This work was supported by National Heart, Lung, and Blood Institute Grant HL-46230 and by a travel grant from the University of Minnesota.

REFERENCES