Vascular Supply of the Femoral Head in Sheep—Implications for the Ovine Femoroacetabular Impingement Model

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ABSTRACT: Sheep hips have a natural non-spherical head similar to a cam-type deformity in human beings. By performing an intertrochanteric varus osteotomy, cam-type femoroacetabular impingement can be induced experimentally. In sheep, the aspherical portion is located superiorly—exactly matching the region where the superior retinacular vessels enter the femoral head–neck junction in human beings. In order to fully exploit the potential of this experimental FAI model, a safe osteochondroplasty of the superior asphericity would need to be done without the risk of avascular necrosis. The aim of this study was to describe the vascular anatomy of the femoral head in sheep from the aorta to the retinacular vessels in order to perform safe femoral osteochondroplasty of the superior femoral asphericity in sheep. Sixty-two ovine hips were analyzed using CT angiography (30 hips), post mortem intravascular latex injection (6 hips), vascular corrosion casting (6 hips), and analysis of the distribution of vascular foramina around the femoral head–neck junction in macerated ovine femora (20 hips). The ovine femoral head receives its blood supply from anterior retinacular arteries from the lateral femoral circumflex artery, and from posterior retinacular arteries from the medial femoral circumflex artery. The superior aspherical portion is free of vessels. Detailed knowledge about vascular anatomy of sheep hips is of clinical significance since it allows to perform osteochondroplasty of the superior aspherical portion in the experimental ovine FAI model safely without the risk of osteonecrosis. © 2018 Orthopaedic Research Society. Published by Wiley Periodicals, Inc. J Orthop Res

Keywords: FAI and morphology hip; animal model; vascularity

Cam-type femoroacetabular impingement (FAI) has been clearly associated as one of the major contributors for so-called primary hip osteoarthritis.[1–3] Despite the reproducible success of surgical treatment for this condition in a short- to mid-term follow-up,[4–6] several clinically relevant questions remain unanswered[7]: What is the natural course of untreated FAI? When is it too late for joint preserving surgery? What is the effect of prophylactic surgery? Which biochemical magnetic resonance imaging methods corresponds best with the histological grade of osteoarthritis? What is the effect of cartilage therapies on the histological cartilage regeneration?

Answering these questions in human beings is difficult, time-consuming, and often not possible due to ethical considerations such as performing surgery in asymptomatic patients or second look arthroscopies to harvest samples for histological examinations. In addition, investigating the clinical outcome of cartilage therapies typically requires observational intervals of several years or even decades. An appropriate animal model could be helpful to answer these issues since animals age considerably faster than human beings. The degenerative process of osteoarthritis in animals thereby typically takes place within several months.[8]

The sheep has been introduced as an experimental animal model for FAI to address the above-mentioned questions.[7–9] Due to their natural asphericity of the femoral head–neck junction, a cam-type FAI pathomechanism can be induced by a closed wedge intertrochanteric varus osteotomy. It could be shown that this leads to similar, time-dependent early chondrolabral lesions as in the human hip, which can be monitored by magnetic resonance imaging.[9]

The location of asphericity differ between sheep and human: In the sheep hip it is located superolaterally and in the human the asphericity is located anterosuperior. In the human hip, the superolaterally area contains the retinacular vessels to the femoral head—the most important and only relevant blood supply for the femoral epiphysis.[10,11] An osteochondroplasty in the human femur should therefore spare this area to avoid avascular necrosis of the femoral head.[12] To perform a safe osteochondroplasty in the proposed FAI sheep model, exact knowledge of the topographical anatomy of the blood supply to the ovine femoral head is required to prevent iatrogenic avascular necrosis. The aim of the study was to describe the detailed vascular anatomy of the femoral head in sheep and to compare its topographical course to human beings.

METHODS

Permission was obtained from the local veterinary board to perform this anatomical study (Kantonales Veterinäramt Zürich, Switzerland). This study was performed in accordance with the Swiss National Laws of animal welfare and protection and according to the guidelines of good laboratory practice (GLP) of the World Health Organization.[13]

The study was designed to describe the vascular tree from its origin of the abdominal aorta to their entrance into the femoral head including the topographical anatomy. Similar to the description of the vascular anatomy of the femoral head in

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human beings and other species,[10,14–16] four methods were used in a total of 62 ovine hips: Three-dimensional (3D) computed tomography (CT) angiography, colored silicone injections, vascular corrosion casting, and gross analysis of the distribution of vascular foramina at the femoral head–neck junction.

Three-dimensional CT angiography was performed in vivo in 15 female Swiss alpine sheep (The age of the sheep was between 1.4 and 3.4 years which corresponds to a young adult human being). All sheep underwent standard general anesthesia after sedation with intramuscular Xylazine (0.1 mg/kg body weight [BW]) and preemptive analgesia with intramuscular Buprenorphine (0.01 mg/kg BW). Anesthesia was induced with intravenously applied Ketaminhydrochloride (3–5 mg/kg BW) in combination with intravenous Diazepam or Midazolam (0.1 mg/kg BW) and Propofol (0.4–0.6 mg/kg BW), and maintained via inhalation with maximum 5 Vol% Isoflurane in oxygen and a constant rate infusion with Propofol. All sheep were then positioned supine in a standard CT scanner (Siemens Somatom Sensation Open Scanner, Erlangen, Germany) with the hind leg fixed in extended position to minimize artifacts. A CT scan with 1.0 mm slice thickness, 0.5 mm interslice distance, 120 kVp voltage, and 240 mAs exposure was performed after intravenously administered contrast agent (Ultravist-370, Bayer, Switzerland). Commercially available software (OsiriX version 5.7.1, Geneva, Switzerland) was used for segmentation of the virtual 3D models.

Colored silicone injections were performed in three sheep (six hips), which were sacrificed as part of other research projects not involving the pelvis and the hind leg. Before euthanasia, all sheep received a bolus of 5,000 IE of heparin intravenously to prevent the formation of blood clots. After sacrifice, a cannula was fixed in the abdominal aorta and vascular washing was performed with standard Ringer's solution. We then injected 260–290 ml of colored silicone (S3/S6/S10, Biodur, Heidelberg Germany) under manual pressure. All specimens were then stowed at 4°C for 24 h for the polymerization of the silicone before dissection.

Vascular corrosion casting was performed in three sheep (six hips). The sacrifice, the preterminal administration of heparin, and the vascular washing did not differ from the colored silicone injections. Analogously, 260–290 ml of a two-component epoxy resin (Biodur E20, Heidelberg, Germany) were injected under manual pressure until reflux of the venous vessels became evident. A standard large external fixator (DePuy Synthes, West Chester, PA) was fixed to the ilium and the femur to bridge the joint. The specimens were then polymerized in a hanging position for 24–48 h. Finally, they were macerated in a potassium hydroxide bath for several days and then washed in distilled water until the specimen was cleared of residual tissue, fat, and cartilage.

The distribution of the vascular foramina was analyzed using macerated femurs from 20 ovine femora that have been available from the anatomical collection of our university. We used the same method as presented for human beings.[14] The femoral head was subdivided into 12 sectors with a clock system. Six o'clock was set to be toward the femoral shaft, 12 o'clock was defined at the most superior portion, 3 o'clock was consistently defined anteriorly in both left and right hips per convention. The amount and distribution of vascular foramina at the head neck junction was counted by one of the authors (NW) and documented photographically. Only foramina with a diameter of more than 0.4 mm were included which was ensured by using a 21-gauge syringe needle.

RESULTS

Aorta

The abdominal aorta bifurcates at the level of the sixth lumbar vertebra into the left and right internal and external iliac arteries (Fig. 1). The external iliac artery proceeds anteriorly to the psoas major and minor muscles and the ilium on the iliac fascia. It gives off the deep iliac circumflex artery, which supplies blood to the muscles and skin of the lower abdominal wall (Fig. 2). Toward its way to the lacuna vasorum, the external iliac artery gives off the deep femoral artery within the pelvis, prior to traversing beneath the inguinal ligament (Figs. 2 and S1). It finally becomes the femoral artery after passing beneath the inguinal ligament and through both heads of the sartorius muscle. The femoral head is then provided with blood supply by two different vessels, one arising from the femoral artery and the other from deep femoral artery (Fig. S2).

Femoral Artery

The femoral artery gives off the lateral femoral circumflex artery (LFCA) approximately three centimeters (2.8–3.7 cm) after penetrating the two heads of the sartorius muscle, a specific feature of this muscle in sheep. In the proximal part of the hind leg, the femoral artery lays medially on the vastus medialis muscle in the femoral canal along the femoral shaft. More distally, it passes through the adductor canal where it becomes the popliteal artery. The femoral artery gives off the saphenous artery, the descending genicular artery, and three branches (proximal/medial/distal) of the caudal femoral arteries (Fig. S3).

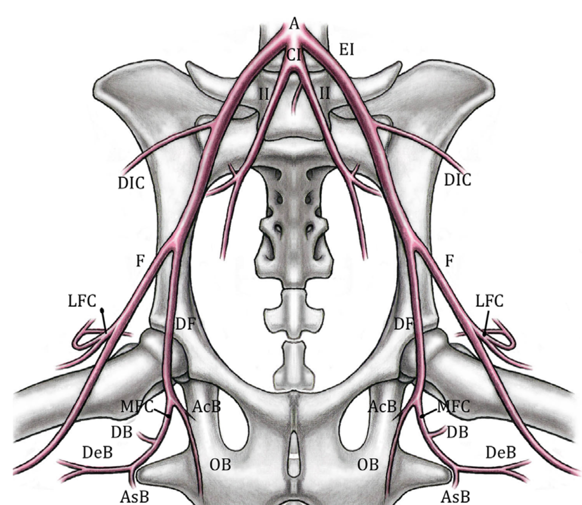

Figure 1. Illustration of the ovine pelvic blood supply starting at the distal aorta through the main contributing branches of the proximal femur (MFC and LFC). Common iliac artery (CI), internal iliac artery (II), external iliac artery (EI), deep iliac circumflex artery (DIC), femoral artery (F), lateral femoral circumflex artery (LFC), deep femoral artery (DF), acetabular branch (AcB), obturator branch (OB), medial femoral circumflex artery (MFC), deep branch (DB), ascending branch (AsB), descending branch (DeB).

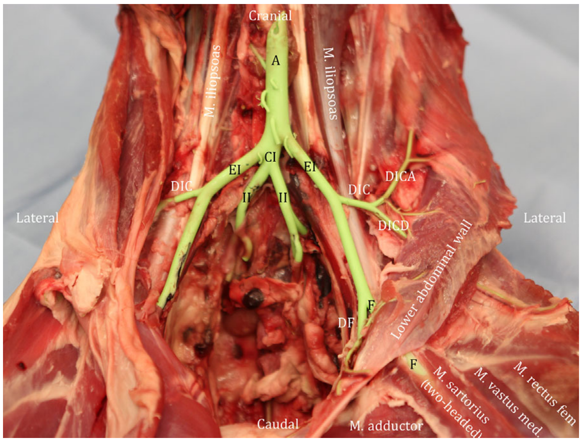

Figure 2. Anatomic ovine pelvic specimen prepared with colored silicone injection demonstrating topographic pelvic vascular anatomy. Notably, the external iliac artery (EI) bifurcates into the femoral artery (F) and deep femoral artery (DF) prior to passing under the inguinal ligament. Common iliac artery (CI), internal iliac artery (II), external iliac artery (EI), deep iliac circumflex artery (DIC), deep iliac circumflex ascending branch (DICA), deep iliac circumflex descending branch (DICD), femoral artery (F), deep femoral artery (DF).

Lateral Femoral Circumflex Artery (LFCA)

The lateral femoral circumflex artery arises from the femoral artery within the femoral canal between the two heads of the sartorius muscle, a specific feature of this muscle in sheep. In one hip, the LFCA originated exceptionally from the deep femoral artery. It then runs between the vastus medialis and the rectus femoris muscles toward the anterior aspect of the hip joint (Fig. S4). Two branches then arise: The descending branch, and a common trunk which subsequently subdivides into an ascending and transverse branch.

The ascending branch moves cranially supplying parts of the iliopsoas and gluteus muscles. Near the superior acetabulum, there were constant anastomoses with the superior gluteal arteries. In addition, it gives off a branch toward the anterior hip joint capsule penetrating it at the level of the head–neck junction. This branch finally subdivides into 1–4 terminal branches lying in a synovial fold (the anterior retinaculum) between 2 and 5 o'clock and supplying the femoral epiphysis (Figs. 3 and S5). There were no macroscopic vessels at the superior asphericity (Fig. S6).

The transverse branch supplies the vastus intermedius and lateralis muscles. The terminal transverse branches anastomoses with branches from the medial femoral circumflex artery.

The descending branch supplies the quadriceps muscles.

Deep Femoral Artery

The deep femoral artery arises from the external iliac artery. Before it crosses under the inguinal ligament through the lacuna vasorum, it gives off the pudendoepigastric trunk with two branches: The caudal epigastric and the cremasteric artery. Distal to the inguinal ligament, it runs between the iliopsoas and pectineus

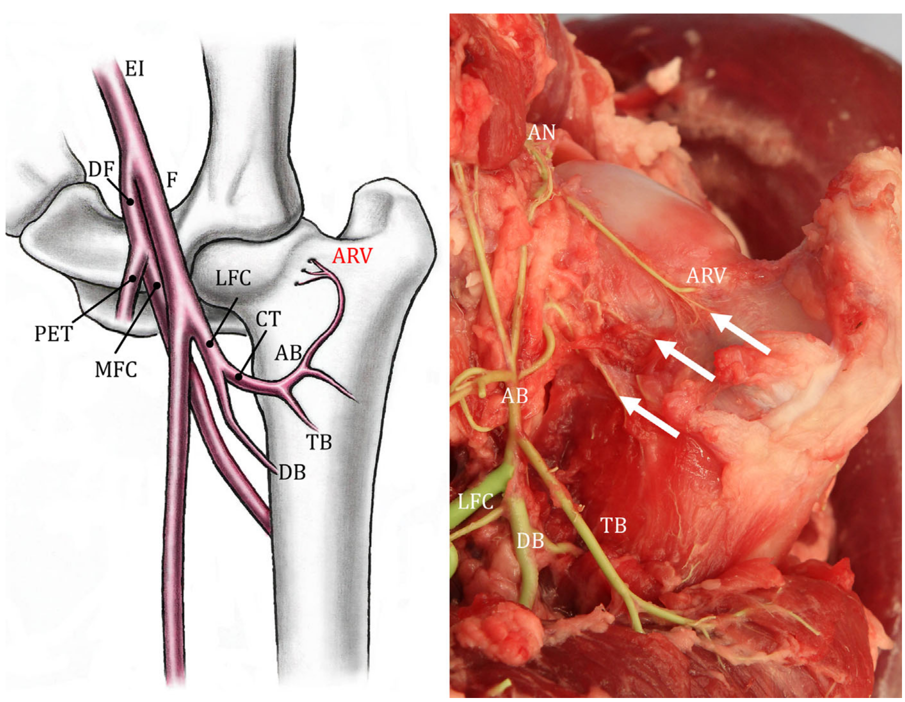

Figure 3. Illustration and ovine anatomic dissection prepared with colored silicone injection demonstrating the anterior retinacular vessels entering the anterior femoral head–neck junction. The anterior retinacular vessels (ARV) originate from the ascending branch (AB) of the lateral femoral circumflex artery (LFC). External iliac artery (EI), deep femoral artery (DF), pudendoepigastric trunk (PET), femoral artery (F), lateral femoral circumflex artery (LFC), common trunk (CT), descending branch (DB), transverse branch (TB), ascending branch (AB), anterior retinacular vessels (ARV).

muscles (Fig. S7). Progressing distally toward the adductor muscles, it gives rise to the dominant medial femoral circumflex artery, which is larger than its continuing branch that descends toward the adductor muscles.

Medial Femoral Circumflex Artery (MFCA)

The medial femoral circumflex artery constantly derives from the deep femoral circumflex artery, divides into five distinct branches, and eventually terminates within the adductor muscles. In sheep, it is the functional continuation of the deep femoral circumflex artery and has the following five branches along its course: The acetabular, obturator, deep, ascending, and descending branches (Fig. 4).

The deep branch of the MFCA runs distal to the obturator externus muscle and winds around the posterior aspect of the femur (Fig. S7). It gives rise to a consistent trochanteric branch, which runs between the quadratus femoris and the fused conjoint tendon of the external rotators. This tendon is mainly formed by the two gemelli muscles, the obturator externus muscle and the small piriformis muscle; there is no obturator internus muscle in sheep. The main division of the deep branch crosses under the conjoint tendon of the external rotator muscles and penetrates the capsule just proximal to their insertion in the piriformis fossa (Fig. 5). The terminal two to four branches course within the posterior synovial fold (the posterior retinaculum) and perforate the femoral head approximately 2–5 mm lateral to the cartilage-bone junction. The aspherical portion was macroscopically free from vessels (Fig. S8).

We found a mean of 9 ± 10 (range, 4–15) vascular foramina per sheep. One hundred and one foramina (55%) were in the posterior, and 83 (45%) in the anterior hemisphere. There were three main peaks. The most frequent location was between 2 and 3 o'clock (19%), followed by 10–11 o'clock (15%) and 7–8 o'clock (12%). Only 14% of all foramina were located at the level of the asphericity between 11 and 1 o'clock (Fig. 6).

DISCUSSION

The ovine FAI model is an established model for induction of inclusion-type FAI.[8] Experimentally inducing a cam lesion in sheep has demonstrated significant damage and degenerative changes of the cartilage and labrum at the corresponding location within the acetabulum in vivo. The relationship between cam location and the location of chondrolabral damage was also reported in humans, and is thought to be causal in the development of osteoarthritis.[17–22] This reproducible model therefore provides an experimental platform, which has the potential to answer clinically relevant questions in the context of FAI. To fully exploit its potential and validate its use as a model for treatment of FAI, a safe osteochondroplasty that does not compromise femoral head blood supply or induce osteonecrosis is required. The prerequisite to a safe offset correction is the knowledge of the exact

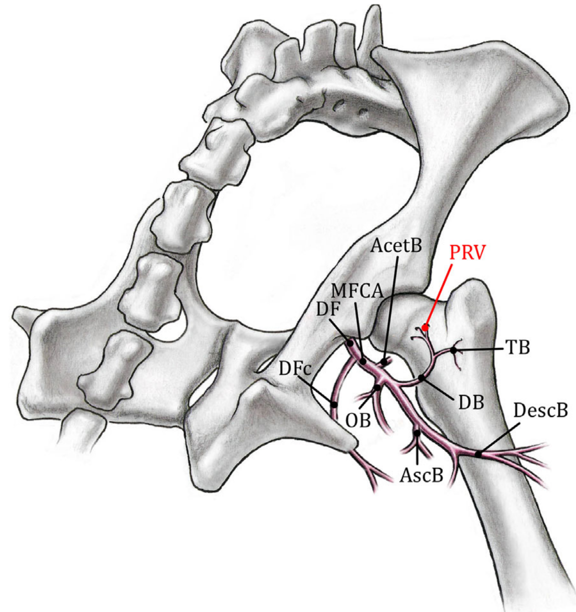

Figure 4. Illustration demonstrating the course and branches of the medial femoral circumflex artery (MFCA) in sheep. Several branches originate from the MFCA, but the most important for femoral head blood supply is the deep branch (DB), which gives of the trochanteric branch (TB) and posterior retinacular vessels (PRV), which enter the femoral head at the posterior femoral head–neck junction. Deep femoral artery (DF), medial femoral circumflex artery (MFCA), continuation of deep femoral artery (DFc), acetabular branch (AcetB), obturator branch (OB), deep branch (DB), trochanteric branch (TB), posterior retinacular vessels (PRV), ascending branch (AscB), descending branch (DescB).

topographical course of the ovine vascular supply to the femoral head.

The ovine vascular anatomy shares some similarities to humans, but distinct differences are noted (Table 1). Similar to human femoral head blood supply, ovine femoral head blood supply originates

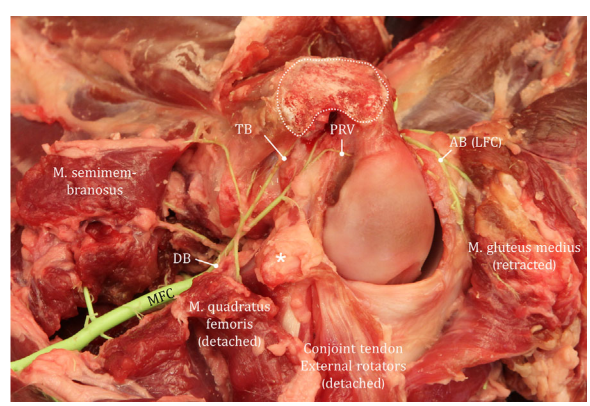

Figure 5. Ovine anatomic specimen prepared with colored silicone injection demonstrating the posterior retinacular vessels (PRV) supplying the posterior aspect of the femoral head–neck junction. The PRV are branches of deep branch (DB), which originates from the medial femoral circumflex artery (MFCA). The ascending branch (AB) of the lateral femoral circumflex artery (LFCA) can also be seen entering the anterior aspect of the femoral head–neck junction. The superior aspect of the proximal head–neck junction is devoid of vascular penetration, similar to the anterior and anterosuperior head–neck junction in humans. Trochanteric branch (TB).

within the pelvis after the aorta bifurcates in the lumbar region of the lower abdomen. While humans demonstrate two common iliac arteries which then become internal and external iliac arteries, the ovine blood supply distinctly separates into an external iliac and common internal iliac. Both human and ovine external iliac arteries give off smaller branches supplying the ilium and abdominal musculature, before becoming the femoral and deep femoral arteries. The pattern of bifurcation of the external iliac into the femoral arteries was noted to be different between humans and sheep, and has been supported in a prior study.[23] In humans, the external iliac artery traverses under the inguinal ligament, becoming the femoral artery, which gives two smaller superficial iliac and epigastric arteries before bifurcating into the deep femoral artery and femoral artery proper.[24–26] In sheep, the external iliac bifurcates becoming the femoral and deep femoral arteries within the pelvis, before traversing under the inguinal ligament. The LFCA and its division into a descending, ascending and transverse branch is comparable between humans

Table 1. Arterial Tree Describing the Femoral Head Blood Supply in Sheep and Human

Arterial Tree in Ovine Femoral Head Supply

- Aorta
  - Common internal iliac
    - Internal iliac
  - External iliac
    - Deep iliac circumflex
    - Femoral
      - Lateral femoral circumflex
        - Descending branch
        - Common trunk
          - Ascending branch
          - Anterior retinacular
        - Transverse branch
      - Saphena
      - Descending genicular
      - Caudal femoral arteries
        - proximal
        - medial
        - distal
      - Popliteal
    - Deep femoral
      - Pudendoepigastric trunk
        - Caudal epigastric
        - Cremasteric
      - Medial femoral circumflex
        - Acetabular branch
        - Obturator branch
        - Deep branch
          - Trochanteric branch
          - Posterior retinacular
        - Ascending branch
      - Descending branch

Arterial Tree in Human Femoral Head Supply

- Aorta
  - Common iliac
    - Internal iliac
    - External iliac
      - Inferior epigastric
      - Deep circumflex iliac
      - Femoral
        - Superficial epigastric
        - Superficial circumflex iliac
        - Superficial external pudendal
        - Deep external pudendal
        - Descending genicular
        - Deep femoral
          - Medial circumflex femoral
            - Ascending branch
            - Descending branch
            - Superficial branch
            - Deep branch
              - Trochanteric branch
              - Inferior retinacular
              - Posterior retinacular
            - Acetabular branch
          - Lateral circumflex femoral
            - Descending branch
            - Common trunk
              - Ascending branch
              - Anterior retinacular
            - Transverse branch
          - Perforating
          - Cruciate anastomosis
        - Popliteal

The anterior retinacular branch from the lateral femoral circumflex artery in human beings is considered irrelevant for the blood supply to the femoral head.

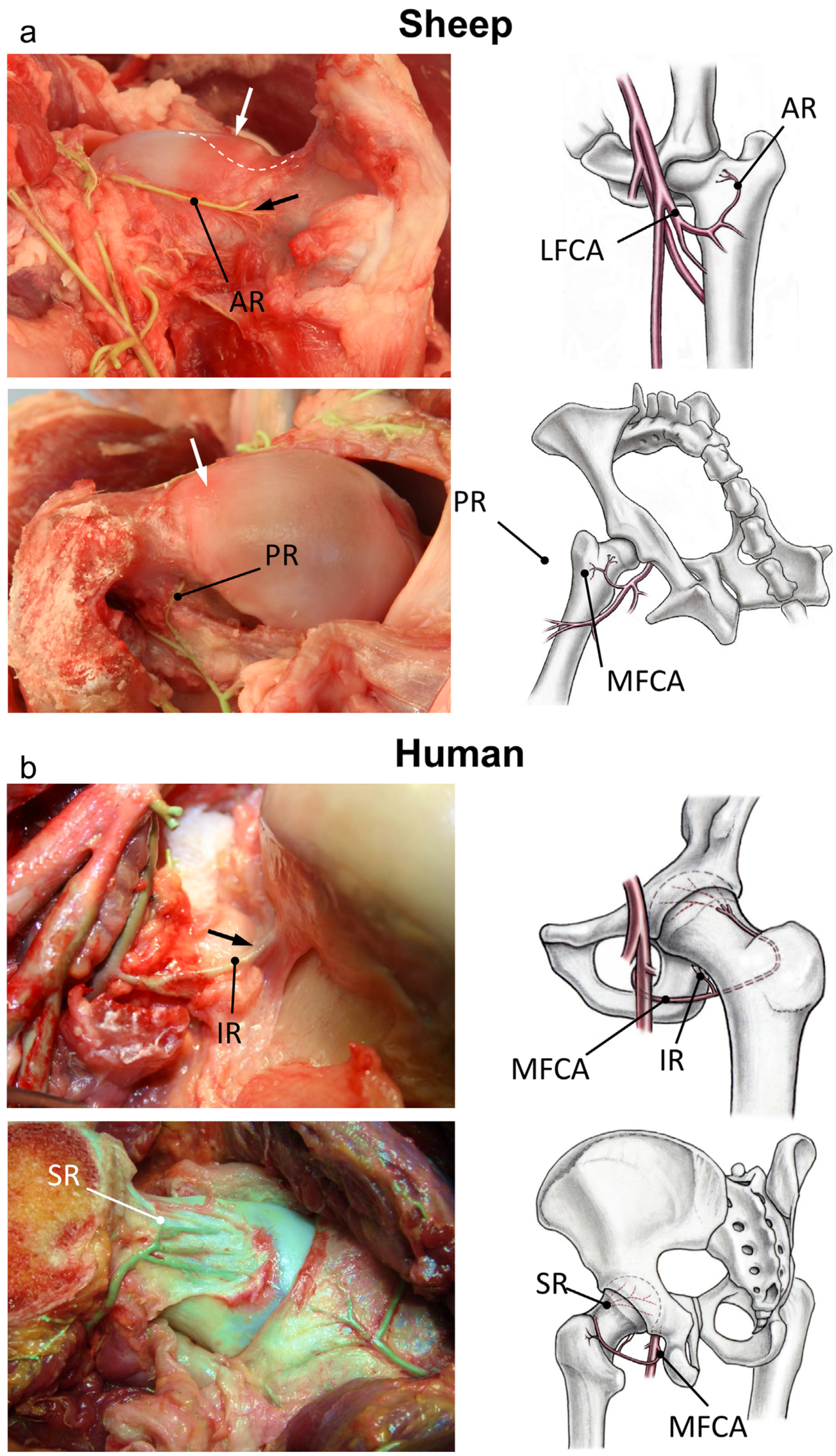

Figure 6. Illustrations and anatomic dissections with colored silicone injections of ovine (a) and human (b) proximal femoral blood supply. Ovine proximal femoral blood supply is provided via the anterior and posterior retinacular vessels, which originate from the lateral femoral circumflex artery (LFCA) and medial femoral circumflex artery (MFCA), respectively. Human proximal femoral blood supply is also provided by two groups of retinacular vessels via the superior and inferior retinacula, originating predominantly from the MFCA. Note the 90° difference in orientation when comparing the ovine and human specimens. The illustrations of human blood supply of the femoral are the courtesy of Morteza Kalhor, MD, Firoozgar Medical Center, Behafarin St, Tehran 48711, Iran (e-mail: kalhor.m@iums.ac.ir).

and sheep. The descending branch is an independent branch in both species. While the ascending branch is the superolateral continuation of the transverse branch in humans, it arises from a common trunk from the LCFA together with the transverse branch. The ascending branch anastomoses at the superior acetabular rim with the superior gluteal artery. While the MFCA derives mainly from the deep femoral artery (and less frequently from the femoral artery) in humans, it is the functional continuation of the deep femoral artery in sheep. The ovine MFCA subdivides into the obturator, acetabular, ascending, and deep branches, while the human MFCA subdivides into the superficial, ascending, acetabular, descending, and deep branches. Importantly the femoral head blood supply for both humans and sheep is derived from the deep branch. The deep branch bifurcates into a trochanteric and retinacular branch in both species. In human beings, an additional inferior branch in the ligament of Weitbrecht is present. Analogous to humans, the trochanteric branch is given off between the quadratus femoris muscle and the short external rotators. Sheep have a conjoint tendon of the small piriformis, the gemelli and the obturator externus muscles. The obturator internus muscle is nonexistent. In contrast to humans, the deep branch of the MFCA crosses under this tendon. In humans, it winds around the obturator externus tendon and then crosses under the triceps coxae.

Although in human beings, the blood supply to the femoral head is mainly provided by the MFCA,[10,11,27–29] the ovine femoral head receives its blood supply consistently both from terminal branches of the MFCA and the LFCA. Distinctly, in humans both the MFCA and the LFCA typically arise as branches of the deep femoral artery, while in sheep, the LFCA branches off the femoral artery and the MFCA branches off the deep femoral artery. In both species, the femoral head receives its blood supply by very similar terminal branches via distinct synovial retinacular folds. In the human hip, both the superior and the inferior retinacular vessels arise from the MFCA. Minor, inconsistently found small branches from the LFCA (anterior retinacular vessels) are considered irrelevant in the literature. In sheep, the retinacular vessels derive from two distinct arteries: The anterior retinaculum from the LFCA and the posterior retinaculum from the MCFA (Fig. 6).

Despite several anatomic differences in the course of the vascular supply from the aorta to the MFCA and the LFCA, the important similarity to humans is that the ovine femoral head is mainly supplied by two arteries, which terminate in two distinct retinacular folds containing vessels that supply the femoral epiphysis. In both species the terminal branches within the retinacular folds are located approximately 180° to one another. However, because of the quadrupedal gait, the topographical entrance of the ovine retinacular vessels is rotated 90° compared to humans. Humans exhibit a superior and inferior retinaculum with an anterior or anterosuperior cam with a vessel-free posterior femoral head, while sheep demonstrate an anterior and posterior retinaculum, an induced superior cam, a relatively vessel-free inferior femoral head (Fig. 7). Similar to humans, the density of vessels decreases as distance from the retinacula increases, so the lowest density

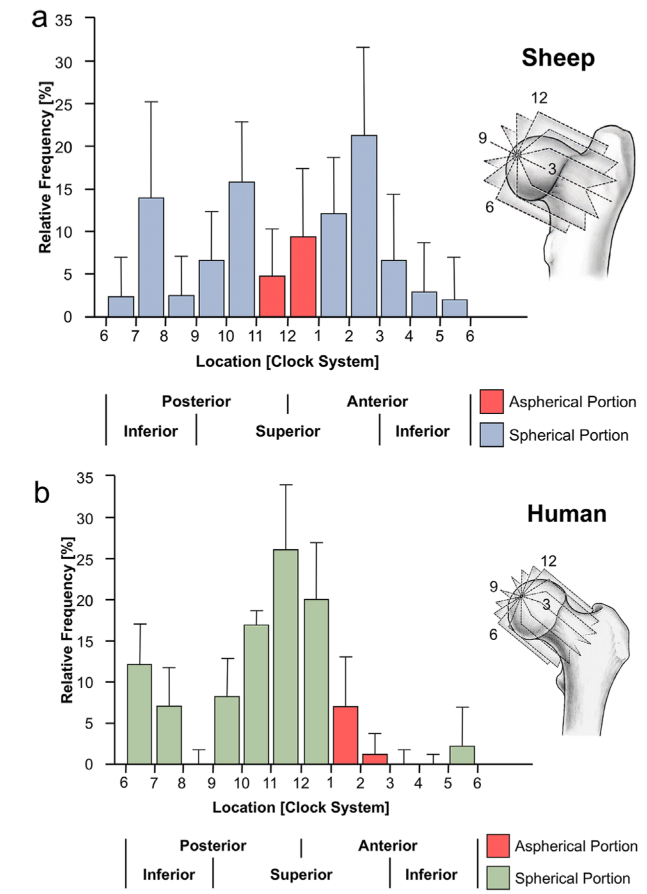

Figure 7. Graphs demonstrating the frequency of distribution and location of vascular foramina in sheep (a) and humans (b). In sheep, foramina were noted most frequently at the 2:00 to 3:00 position, in the anterior aspect of the femoral head–neck junction, with two other peaks noted at the 7:00 to 8:00 and 10:00 to 11:00 positions along the posterior aspect of the femoral head–neck junction. There were very few foramina at the 11:00 to 1:00 position, along the superior femoral head–neck junction, corresponding to the asphericity. Notably this is rotated 90° to the foramina distribution in humans, where the peak distributions are between 10:00 and 1:00 and 6:00 and 8:00 in the superior and inferior aspects of the femoral head–neck junction, respectively, while few foramina are seen from the 1:00 to 4:00 position, corresponding to the typical cam location in humans.[14]

of vessels is located 90° from the retinacula.[14] This vessel free area is typically noted from the 1:30 to 3:00 position (anterior and anterosuperior) in humans, which was similar in sheep, as the superior portion of the femoral head was macroscopically free from vessels. Safe and effective osteochondroplasty in this vessel free zone has been demonstrated in various human studies, as long as the resection avoids violating the attachment of the retinacular vessels, and by avoiding analogous retinacular vessels in the ovine model, safe and effective chondroplasty is possible as well (Fig. S9).[30–33]

Limitations of this study do exist. As this is an animal model, the differences in vascular anatomy, starting from the aorta and ending at the femoral head, may have more of an effect on proximal femoral blood supply than is currently understood. These variations may be a result of the quadrupedal nature of sheep, which cannot be properly related to the bipedal nature of human beings. While the intraosseous blood supply of the femoral head in human beings has been characterized in various studies, identifying which vessels are dominant and which areas of the femoral head each vessel supplies, the same has not been performed in ovine models. As a result, it is unclear if the anterior or posterior retinaculum is the dominant blood supply and what portion of the femoral head is supplied by each retinaculum. Despite this, knowledge of the location of each retinaculum still allows for a safe osteochondroplasty as long as the vessels at these locations are not violated.

The previously introduced ovine impingement model is highly representative of human cam-type FAI in its ability to demonstrate significant acetabular chondrolabral damage over time. This anatomic study further demonstrates the utility of this model, as the location of the vascular supply of the ovine femoral head is similar to that of the human. Additionally, the location of the induced ovine femoral head asphericity, representative of a cam deformity, is located in a zone relatively free of vessels, similar to the human cam deformity.[14,21] Therefore, we believe that this model will allow for a safe osteochondroplasty without the risk of osteonecrosis in an experimentally induced cam-type FAI model. This model will allow extensive investigation of cam-type FAI, including its natural history and progression, effects and timing of osteochondroplasty on the course of cam-type FAI, when preservation strategies are no longer of benefit, chondrolabral health from a histologic and imaging perspective after osteochondroplasty and more that otherwise would not be possible in humans due to time and ethical limitations. This model therefore provides excellent potential for future studies concerning cam-type FAI, its long-term effects and our ability to affect change through surgical intervention.

AUTHORS' CONTRIBUTIONS

MT: concept and design, analysis and interpretation of data, creation of figures, manuscript editing, to ensure integrity of work. NW: data collection, analysis and interpretation of data, creation of figures, initial draft. MKR: analysis and interpretation of data, initial draft, manuscript editing. KMN: data collection, initial draft, analysis and interpretation of data, manuscript editing. BVR: concept and design, analysis and interpretation of data, manuscript editing, critical review. SDS: data collection, analysis and interpretation of data, initial draft, creation of figures, ensure integrity of work. We hereby confirm that all authors have read and approved the final submitted manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.