

A GEOMETRIC MORPHOMETRIC ANALYSIS OF THE NAVICULAR BONE IN
HUMANS, CHIMPANZEES, BABOONS, AND *HOMO HABILIS* (OH 8)

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ABSTRACT

A GEOMETRIC MORPHOMETRIC ANALYSIS OF THE NAVICULAR BONE IN HUMANS, CHIMPANZEES, BABOONS, AND *HOMO HABILIS* (OH 8)

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This is the first thesis based on geometric morphometric comparison of the navicular bone across different primate species. The navicular bone is involved in three important functions in the modern human foot related to human obligate bipedalism. Obligate bipedalism is a distinguishing feature of humans and by comparing how the overall size and shape of the navicular bone differ among modern humans, chimpanzees, baboons, and fossil Olduvai Hominid 8 (*Homo habilis*), paleoanthropologists will be able to better describe the evolution of bipedalism in our lineage. I found that the OH 8 navicular is more similar in shape to that of modern humans and more similar in size to chimpanzees. Bones of the foot, such as the navicular, can therefore be used to assess the mode of locomotion in a fossil species and can aid in the placement of new fossils within the hominin lineage.

CHAPTER I

INTRODUCTION

Most experts agree that the development of obligate bipedal locomotion was one of the most significant adaptations to occur within the hominin lineage, and today, of all extant primates, only humans are obligate bipeds (Le Gros Clark 1947; Leakey and Hay 1979; Susman and Stern 1982; Senut and Tardieu 1985; Susman et al. 1985; White and Suwa 1987; Latimer and Lovejoy 1989; Gebo 1992; Spoor et al. 1994; Clarke and Tobias 1995; Presuschoft 2004). When possible hominin fossils are found, certain skeletal elements are assessed in conjunction with each other to determine if a specimen was an obligate biped and therefore belongs within the hominin lineage. These skeletal elements range from the position of the foramen magnum, hip orientation and shape, curvature of the vertebral column, presence or absence of the valgus knee, and the presence or absence of a longitudinal arch in the foot. The bipedal foot is particularly specialized in both its anatomy and its function, which makes perfect sense because it is the only physical structure that is in direct contact with the ground during bipedalism, and subsequently, is under strong selective pressure to deal with both balance and propulsion in a highly efficient way (Susman and Stern 1982). Therefore, increased knowledge about the relationship between structure and function in the foot bones of our hominin ancestors and relatives, as well as extant primates, is central to our understanding of the origins and evolution of bipedalism. Most of the research done on the hominin foot has focused on the calcaneus because it is the first part of the foot to touch the ground during walking

and absorbs most of the shock of heel strike (Elftman 1969; Lewis 1980) and on the size and position of the first metatarsal and hallux because walking with longer toes and a divergent hallux would be energetically costly and impede efficient bipedalism (Lewis 1980; Susman and Stern 1982; Wood 1992). Also, the calcaneus is frequently preserved in the fossil record. Less research has focused on other bones of the foot, such as the navicular bone. Therefore in this thesis, I compare the shape and size of the navicular bone in modern humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*) and baboons (*Papio sp.*) with the fossil navicular Olduvai Hominid 8 (OH 8, at 1.8 Ma) of *Homo habilis*.

The navicular is only one of 26 skeletal elements that make up the human foot (D'Aout 2008), thus making the foot the most dynamic structure in the human body (Elftman 1969). The navicular is a “boat-shaped” bone that is located medially in the midfoot between the talus posteriorly and the three cuneiform bones anteriorly. It is involved in three important functions in the modern human foot related to our obligate bipedalism. The navicular bone forms the uppermost portion of the medial longitudinal arch and acts as a keystone of it (Klenerman and Wood 2006). Where the talus and navicular bones articulate on the inside of the mid-foot, the talonavicular joint is formed, which is the lowest of the three separate ankle joints (Langdon et al. 1991; Cartmill and Smith 2009). This joint neighbors two additional structures, the calcaneocuboid and the subtalar joints (Aiello and Dean 2002). Together, they provide stability across the midfoot and allow the foot and ankle to flex during walking and other physical activities (Aiello and Dean 2002). Along with the talus, calcaneus and cuboid, the navicular bone is also involved in the formation of the transverse tarsal joint, which acts as a fulcrum in the

midfoot during locomotion (Meldrum 2004). The arrangement of the sub-tarsal and transverse tarsal joint axes along with supination and pronation permits the conversion mechanism that is needed for bipedal movement (Langdon et al. 1991). A series of small articulations like these in the ankle and foot make it one of the most complex and unique areas of the skeleton (Sarmiento et al. 2000; Meldrum 2004; White et al. 2005; Klenerman and Wood 2006; D'Aout et al. 2008).

In comparison to modern humans, the talonavicular and calcaneocuboid joints of haplorhines (including chimpanzees and baboons) are positioned parallel and adjacent to each other, but they are widely separated. Additionally, haplorhines have an elongated calcaneus (Ankel-Simons 2000). The navicular elongates concomitantly and becomes more or less quadrangular. Ape naviculars are characterized by a convex facet on the medial cuneiform, over the superolateral two-thirds, and a concavity of the inter-medial one-third of the medial cuneiform (Clarke and Tobias 1995). These differences and others seem to be related to the fact that all primates, except modern humans, have varied locomotor and postural repertoires (Schmitt 2003; D'Aout et al. 2004). For example, chimpanzees move quadrupedally on the ground and in an arboreal setting. During quadrupedal locomotion, chimpanzees use knuckle-walking, in which the dorsal side of the middle phalanges of the hand supports the upper body weight, while the soles of the feet are on the ground and function as propulsive organs (Klein 1999; Zihlman 2000; Freeman and Herron 2004; Meldrum 2004). During quadrupedal locomotion, a chimpanzee's plantigrade foot exhibits an anterior pillar lacking firmness through the longitudinal arch, but also exhibits a greater mobility of the mid-tarsal joint (Elftman 1969). Chimpanzees also travel efficiently in arboreal settings by climbing, swinging and

clinging to branches. They use their long, powerful arms to brachiate, and their opposable big toes enable a prehensile grip on branches (Klein 1999). Prehension in the foot causes the anterior portion to rotate at the calcaneocuboid joint and the navicular to ride up on the talar head, which pushes the calcaneus against the navicular at the calcaneonavicular articulation (Aiello and Dean 2002). This closely packs the joints together, stabilizing the foot and allowing it to grasp a rounded branch. Chimpanzees are also capable of facultative bipedal locomotion; however, unlike humans, they usually only use this mode of locomotion if they need to travel while carrying objects in their hands (Sinclair 1986; Klein 1999; Videan and McGrew 2002). In comparison with chimpanzees, baboons are primarily terrestrial quadrupeds, placing their hands and feet in a digitigrade position (Klein 1999), and although they often stand bipedally, especially when “lookouts” stare across savannas, baboons spend less time walking bipedally (Ankel-Simons 2000:108; Stanford 2002:90). There have been no detailed studies done on the navicular bone of baboons.

Homo habilis (2.3–1.4 mya) was a small-bodied hominin that exhibited a mosaic of primitive and derived post-cranial skeletal elements, but had the ability to produce rudimentary tools (McHenry 1991 & 1992; Lewis 1980; McHenry and Berger 1998; Kidd 1999; Wood and Collard 1999). Most paleoanthropologists conclude that this species was a terrestrial biped that retained arboreal potential. The foot of specimen OH 8 is similar to modern humans but research has suggested that during bipedal locomotion the foot was utilized in a way that is unique to *H. habilis* (Sarmiento 2000).

Questions and Hypotheses

Q1: Is the shape of the OH 8 (*H. habilis*) navicular more similar to modern humans, to chimpanzees, or to baboons?

H₀: The shape of the OH 8 navicular will be similar to all of the extant study species.

H₁: The shape of the OH 8 navicular is most similar to modern humans.

H₂: The shape of the OH 8 navicular is most similar to chimpanzees.

H₃: The shape of the OH 8 navicular is most similar to baboons.

Q2: Is the size of the OH 8 (*H. habilis*) navicular more similar to modern humans, to chimpanzees, or to baboons?

H₀: The size of the OH 8 navicular will be similar to all of the extant study species.

H₁: The size of the OH 8 navicular is most similar to modern humans.

H₂: The size of the OH 8 navicular is most similar to chimpanzees.

H₃: The size of the OH 8 navicular is most similar to baboons.

CHAPTER II

MATERIALS AND METHODS

Study Sample

The sample size for this study totaled 106 adult navicular bones from the three extant species: *Papio sp.* (N = 20: 10 female, 10 male), *Pan troglodytes* (N = 26: 15 female, 11 male), modern *Homo sapiens* (N = 60: 25 females, 35 males), which were compared to the fossil Olduvai Hominid 8 (OH 8) navicular from *Homo habilis*. No approval was needed from the Institutional Review Board (IRB) or the Institutional Animal Care and Use Committee (IACUC) because my research did not use live animals or live humans. Complete navicular bones from the left side were obtained and measured for each of the study subjects. The baboon samples were from the Bramblett Baboon Collection housed at the University of Texas at Austin. The *Papio sp.* sample came from several wild baboon populations near the Darajani Primate Research Station, Kenya, and had known body weights within the normal ranges for adult male and female baboons (Bramblett 1969). The chimpanzee and modern human samples came from the Hamann-Todd Osteological Collection housed at the Cleveland Museum of Natural History. The wild chimpanzees selected for this study were all from known locations, adult status and sex (Cleveland Museum Osteological Records). The modern human sample fit within average heights and weights for males and females. The fossil OH 8 (*H. habilis*) is comprised of all of the left tarsal and metatarsal bones, but no phalanges (Day and Napier

1964). All the tarsals, except for the posterior part of the calcaneus, are completely preserved.

Measurements

The overall length and width (mm) of the naviculars was assessed using a STORM electronic digital sliding caliper (3C301). When the distal view of the navicular was facing the observer and the tubercle was pointing down (toward the ground), the superior and inferior apex points were used to the overall length of the navicular. The overall width of the navicular was taken from the widest superior and inferior apex points when the navicular was held in anatomical position. Each navicular was placed on a clay stand and held in place with an adhesive putty/clay mixture to avoid damaging the bone (Figure 1). The clay stand consisted of oil-free clay, and the putty/clay mixture was composed of poster tack and artist's kneaded eraser. The Cleveland Museum of Natural History provided me with a cast of the disarticulated foot bones of OH 8.

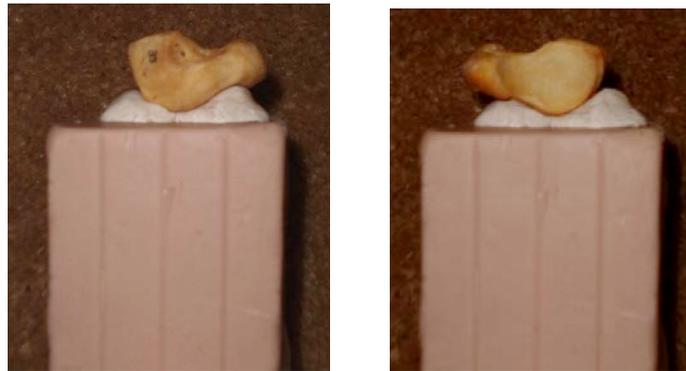


Figure 1. Distal and proximal views of a chimpanzee navicular on a clay stand.

Each navicular was orientated with the dorsal side down and the cuneiform facets facing the observer. The navicular rested on the dorsal side of the mesocuneiform facet on one attachment rod, while the other attachment rod was placed between the ectocuneiform facet with the tubercle angled slightly towards the ceiling. Once the

navicular was secured on the clay stand, the MicroScribe G2 (version 5.0.0.2) digitizer was homed. The navicular landmarks were digitized as XYZ landmark coordinates, and these coordinates were uploaded into a Microsoft Excel file. After each landmark point on a navicular bone was digitized into XYZ coordinates, the MicroScribe G2 digitizer was rehomed. The following articular facets and their landmarks were digitized into XYZ coordinates: talar facet (talocrural joint), cuboid facet, ectocuneiform facet, mesocuneiform facet, and the entocuneiform facet (Sarmiento et al. 2000; White et al. 2005) (see Appendix 1 for facet definitions). The human navicular differs from apes because it does not always articulate with the cuboid, the cuboid facet is not always present, and humans exhibit a proportionally smaller tibialis posterior appearance (Aiello et al. 2007). Seventeen individuals from the modern human sample lacked the cuboid facet.

Navicular landmarks (Table I, Figures 2 and 3) were recorded using an Immersion MicroScribe G2 (version 5.0.0.2) 3-D digitizer. These landmarks were defined based on the dorsoplantar axes.

Table 1. List of Navicular Landmarks

Landmark	Location
A	ectocuneiform facet medial apex of mediolateral diameter
B	ectocuneiform facet later apex of mediolateral diameter
C*	mesocuneiform facet lateral apex of dorsoplantar diameter
D*	endocuneiform medial apex of mediolateral diameter
E	endocuneiform facet lateral apex of mediolateral diameter: the most lateral point on the most inferior apex of articular surface
F	endocuneiform facet inferior apex
G	mesocuneiform facet inferior apex
H	ectocuneiform facet inferior apex
I	medial apex of talar facet when the cuboid facet is in the superior position
J	lateral apex of talar facet when the cuboid facet is in the superior position
K	inferior lateral apex of cuboid facet
L	superior lateral apex of cuboid facet
M	inferior medial apex of cuboid facet of mediolateral diameter
N	superior medial apex of cuboid facet of mediolateral diameter
R	widest point between I and J on dorsal side of the talar facet
S	widest point between I and J on plantar side of the talar facet
Z**	if C and D are not separate landmarks, then the widest most projecting point inferior and superior on the mesocuneiform facet (instrumentally assessed) plus G

*C and D: if not visible, then C and D should be marked on their respective sides of the ridge that separates the mesocuneiform and entocuneiform facets

**Z was created to insure homologous landmarks across species

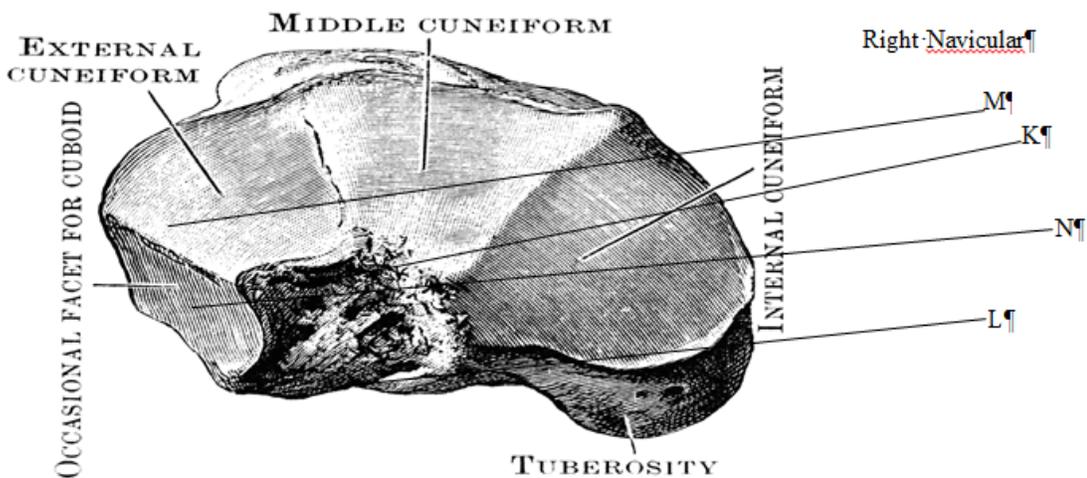


Figure 2. Distal view landmarks K-M of cuboid facet on right navicular.

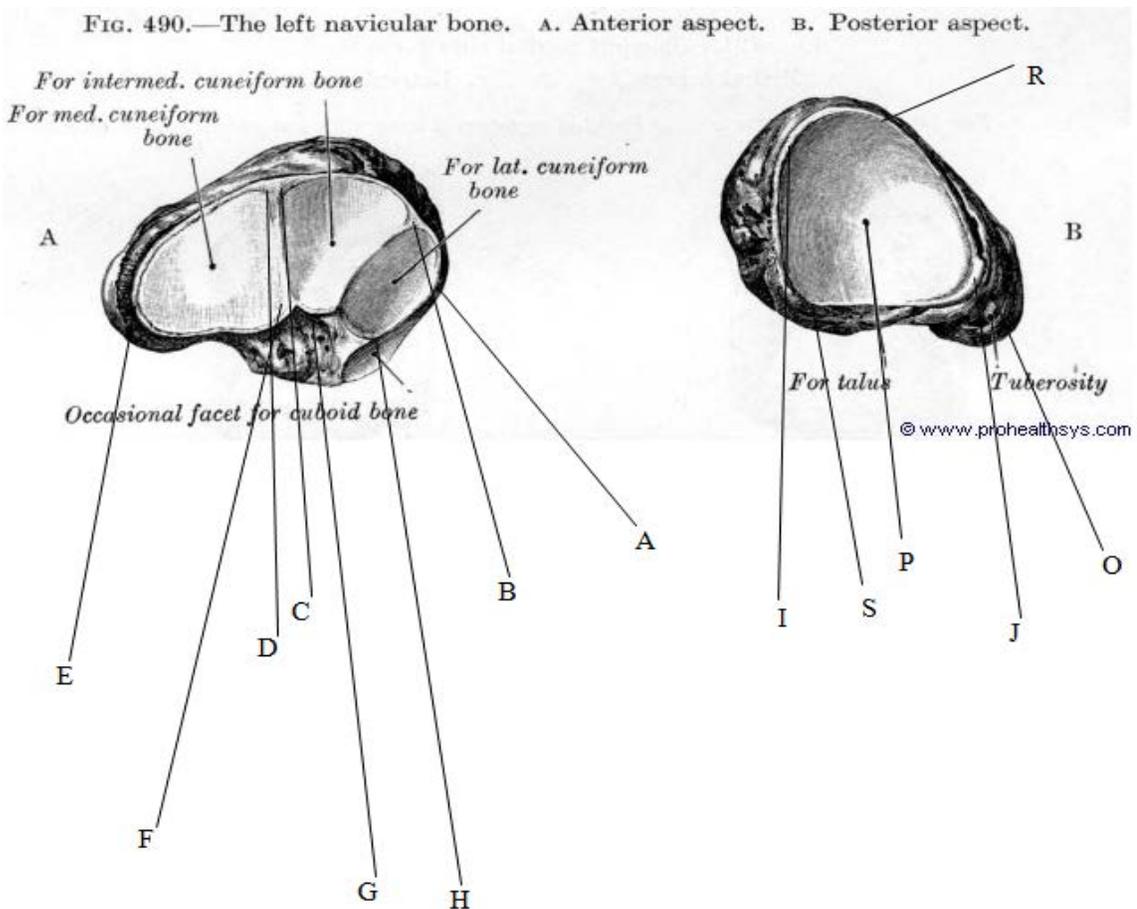


Figure 3. Left navicular: distal view of landmarks A-H of cuneiform facets and proximal view of landmarks I, J, R and S.

The following statistical analyses were utilized to assess shape: a general procrustes analysis, canonical variate analysis, principal components analysis and a Mahalanobis distances analysis. A general procrustes analysis compares the shape of objects by generating a weighting factor that compensates for differences in the scale of objects (Klingenberg 2011). The canonical variate analysis captures the relationship between a set of predictor variables and a set of criterion variables by the canonical correlations and by the sets of canonical weights. This analysis assumes normal distribution. The principal components analysis converts a set of possible correlated observations into a set of linearly uncorrelated values called principal components. The principal components are independent only if the set of data is mutually normally distributed. The principal components analysis defines new orthogonal coordinate systems that describe variances in a single dataset. A Mahalanobis distance analysis is a descriptive statistic that provides a relative measure of a data point's distance from a common point (encyclopediaofmath.org). It also identifies and gauges the similarity of an unknown sample set to that of a known sample.

To assess the size differences between the study species, the centroid sizes were calculated and were used to compute two ANOVA tests. An ANOVA is a parametric test that assumes normal distribution and is applied to two or more samples (Cozby 2009). It assesses and compares the means and variance simultaneously and answers the question: do all the samples come from the same population?

CHAPTER III

RESULTS

Seventeen individuals from the modern human sample lacked the cuboid facet. However, results from all analyses were essentially the same whether these 17 individuals were included in the analyses or not. Therefore, I used the total sample of 106 adult navicular bones from *Papio sp.* (N = 20: 10 female, 10 male), *P. troglodytes* (N = 26: 15 female, 11 male), modern *Homo sapiens* (N = 60: 25 females, 35 males), and the fossil Olduvai Hominid 8 (OH 8) navicular from *H. habilis* to assess shape and sex-specific size differences in the navicular among the study species.

Navicular Shape

Classification criterion for the canonical variate analysis, which was computed along with a principal components analysis, was by study species. The variation among study species was scaled by the inverse of the within-group variation. The canonical variate analysis indicates that CV1 explains 63.56% of the variation in the shape of the navicular among the study species, while CV2 explains 34.32%, and CV3 explains 2.12% (Figures 4, 5). A clear separation exists between the modern *Homo sapiens* sample and the *Papio sp.* and *Pan troglodytes* samples. In Figure 4, the OH 8 fossil (*Homo habilis*) fits well within the *H. sapiens* sample and within the CV1 and CV2 axes. In Figure 5, the OH 8 fossil is an outlier but still falls closer to the *H. sapiens* sample on the CV1 and CV2 axes.

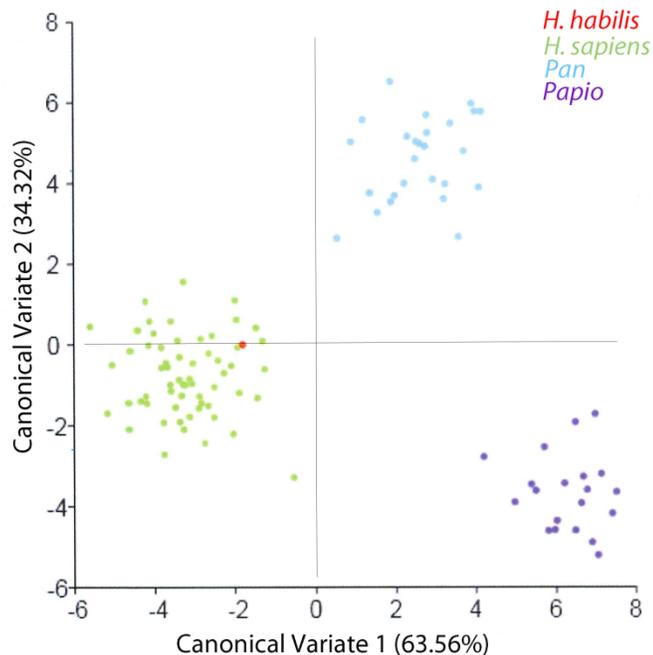


Figure 4. Canonical variate 1 vs. canonical variate 2. CV1 separates the graph into left and right which shows *H. habilis* falls within the *H. sapiens* samples. CV2 separates the graph into top and bottom sections. Also, there are clear separations between the *H. sapiens*, *Pan*, and *Papio* samples.

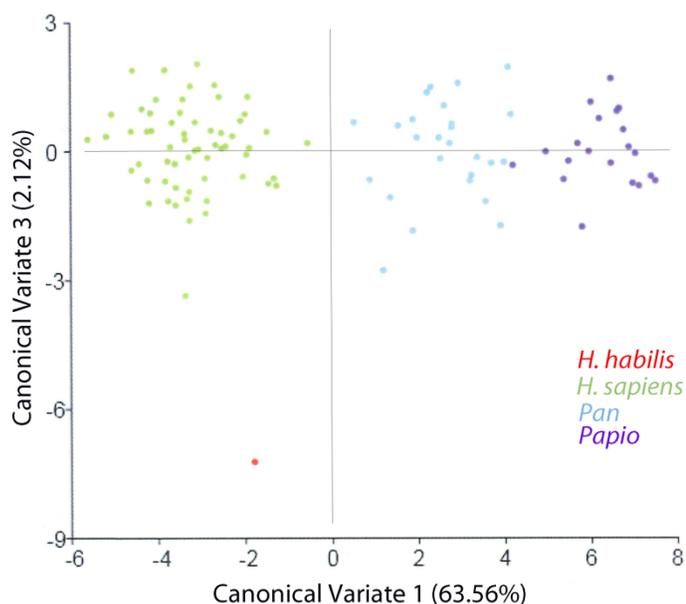


Figure 5. Canonical variate 1 vs. canonical variate 3. CV1 separates the graph into left and right sections and shows OH 8 is most similar to *H. sapiens* even though it is an outlier. CV3 separates the graph into top and bottom.

The Mahalanobis distances analyses assessed the smallest distance value is between modern *H. sapiens* sample and the OH 8 fossil (*Homo habilis*), while the largest distance value is between *Papio sp.* and OH 8 fossil (Table 2). All the *p* values from permutation tests between the study species are statistically significant. Although these results indicate there are observable navicular shape differences between all the study species, the greatest similarity is between the modern *H. sapiens* sample and the OH 8 fossil. Although modern *H. sapiens* and OH 8 are most similar in shape, at a 0.01 confidence level they are significantly different, thus making *H. habilis* unique.

Table 2. Distance values (below the diagonal) and *p* values (above the diagonal) for Mahalanobis distances among taxa (10000 permutation rounds)

	<i>H. habilis</i>	<i>H. sapiens</i>	<i>P. troglodytes</i>	<i>Papio sp.</i>
<i>H. habilis</i>	----	0.01	<0.0001	0.05
<i>H. sapiens</i>	7.50	----	<0.0001	<0.0001
<i>P. troglodytes</i>	9.67	7.92	----	<0.0001
<i>Papio sp.</i>	11.46	9.92	9.92	----

Navicular Size

Because it is not known whether the OH 8 foot is that of a male or female *H. habilis* (Day and Napier, 1964; Susman and Stern 1982), I compared OH 8 navicular separately with males and females from the other study species.

The mean average size for female naviculars differs between the modern *H. sapiens*, *P. troglodytes* and *Papio sp.* samples, with *Papio sp.* females having the smallest naviculars and modern *H. sapiens* females having the largest naviculars (Table 3). The mean average size for male naviculars is greatest for the modern *H. sapiens* sample,

while the mean average size for the *P. troglodytes* and *Papio sp.* samples is only one standard deviation apart (Table 3).

Table 3. Descriptive data for mean centroid size for female and male *Homo sapiens*, *Pan troglodytes* and *Papio sp.*

Females	<i>Homo sapiens</i>	<i>Pan troglodytes</i>	<i>Papio sp.</i>
Number	25	15	10
Mean	47.12	36.41	23.35
Standard Deviation	2.23	3.08	1.37
Minimum	42.62	32.46	21.29
Maximum	51.93	43.87	25.38
Males	<i>Homo sapiens</i>	<i>Pan troglodytes</i>	<i>Papio sp.</i>
Number	35	11	10
Mean	52.83	40.32	28.40
Standard Deviation	3.27	2.06	1.19
Minimum	46.89	38.00	26.04
Maximum	58.30	44.80	30.17

Results of an ANOVA comparing all female study subjects with *Homo habilis* (OH 8) indicates significant size differences between the study species in mean navicular size (ANOVA: df=3, corrected sum of squares=4473.61, mean square=1401.51, F value=244.79, $p<0.0001$). *Homo habilis* (OH 8) is most similar to female *Pan troglodytes* in terms of mean size (Table 4, Figure 6).

Table 4. Comparisons of differences between means of centroid size for the female study taxa

	Differences Between Means	95% Confidence Limits	
<i>H. habilis</i> - <i>P. troglodytes</i>	0.59	-5.99	7.18
<i>H. habilis</i> - <i>H. sapiens</i> †	10.12	3.62	16.62
<i>H. sapiens</i> - <i>P. troglodytes</i> †	10.72	8.64	12.81
<i>P. troglodytes</i> - <i>Papio sp.</i> †	13.06	10.46	15.66
<i>H. habilis</i> - <i>Papio sp.</i> †	13.65	6.97	20.34
<i>H. sapiens</i> - <i>Papio sp.</i> †	23.81	21.39	26.16

† indicates significance at the 0.05 level

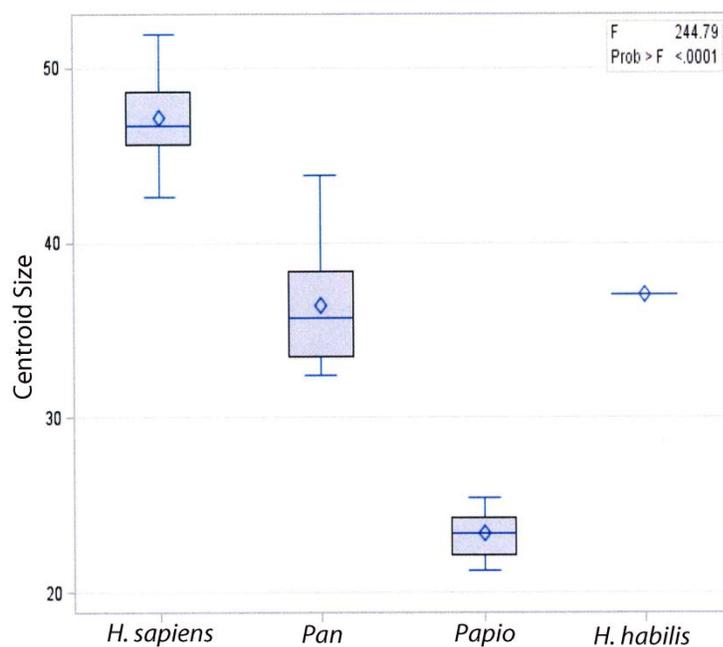


Figure 6. Comparison of mean centroid size for all female study subjects with *Homo habilis* (OH 8).

Results of an ANOVA comparing all male study subjects with *Homo habilis* (OH 8) indicates significant differences between the study species in mean navicular size

(ANOVA: $df=3$, corrected sum of squares=5586.05, mean square=1722.09, F value=217.423, $p<0.0001$). *Homo habilis* (OH 8) is most similar to male *Pan troglodytes* in terms of mean size (Table 5, Figure 7).

Table 5. Comparisons of differences between means of centroid size for the male study taxa

	Differences Between Means	95% Confidence Limits	
<i>H. habilis</i> - <i>P. troglodytes</i>	3.32	-4.48	11.11
<i>H. habilis</i> - <i>Papio sp.</i> †	8.60	0.77	16.43
<i>P. troglodytes</i> - <i>Papio sp.</i> †	11.92	8.66	15.18
<i>H. sapiens</i> - <i>P. troglodytes</i> †	12.51	9.93	15.09
<i>H. habilis</i> - <i>H. sapiens</i> †	15.83	8.26	23.40
<i>H. sapiens</i> - <i>Papio sp.</i> †	24.43	21.76	27.11

† indicates significance at the 0.05 level

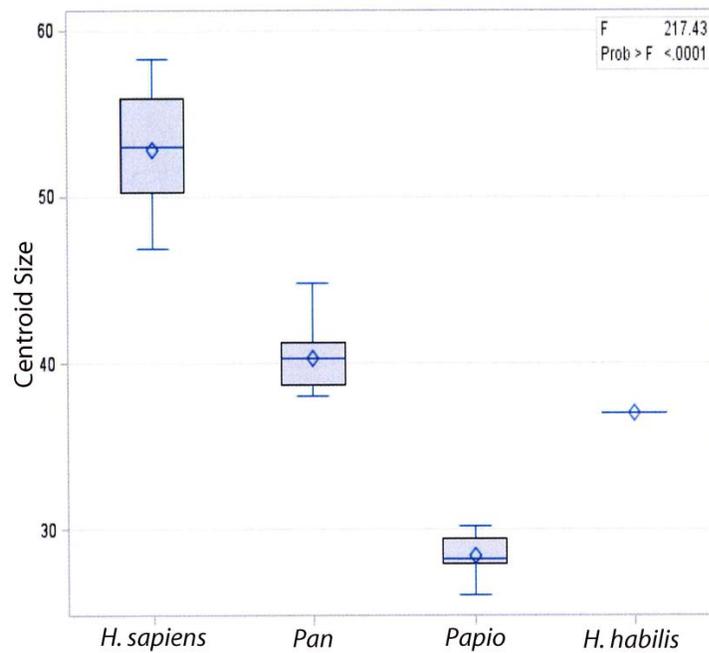


Figure 7. Comparison of mean centroid size for all male study subjects with *Homo habilis* (OH 8).

The fact that the navicular of OH 8 is most similar in size to chimpanzees corresponds to the estimated average height and weight of *H. habilis*, which fits within the known ranges of height and weight of chimpanzees. The estimated average heights for male and female *H. habilis* are 131 cm³ (4.3 ft) and 100 cm³ (3.3 ft), while the height ranges for male and female chimpanzees are 132-155 cm³ (4.3-5.1 ft) and 91-125 cm³ (3.0-4.1 ft) (McHenry 1991, 1992; Rowe 1996). Similarly, the estimated average body masses for male and female *H. habilis* are 37 kg (81.57 lbs) and 32 kg (70.55 lbs), while the body mass ranges for male and female chimpanzees are 36-42 kg (79.37-92.59 lbs) and 28-33 kg (61.72-72.75 lbs).

CHAPTER IV

DISCUSSION

Evidence for terrestrial bipedalism exists in the hominin fossil record 6-7 million years ago (Richmond and Jungers 2008). However, the evolution of bipedalism has not been a linear one with a neat series of steps from arboreal quadruped to obligate biped. Instead, there is growing evidence based on diversity of the body proportions of early hominins for significant variation in their modes of bipedalism and the extent to which they exhibited adaptations for arboreal locomotion (Johanson et al. 1987; Hartwig-Scherer and Martin 1991; Heinrich et al. 1993; Clarke and Tobias 1995; Berger and Tobias 1996; Leakey et al. 1998; McHenry and Berger 1998; Asfaw et al. 1999; Richmond et al. 2001; Ward et al. 2001; Harcourt-Smith and Aiello 2004; Haeusler and McHenry 2007).

Homo habilis is thought to have a mosaic of human-like and ape-like morphologies, especially in terms of its postcranial skeleton. Although clearly a terrestrial biped, limb reconstructions of *H. habilis* indicate humerofemoral proportions and relative limb strength similar to chimpanzees (Hartwig-Scherer and Martin 1991; Asfaw et al. 1999; Ruff 2009). The phalanges on the hand of *H. habilis* resemble those of apes insofar as they are robust, curved and built for powerful grasping, but they have broad tips similar to modern humans and a precision grip (Susman and Stern 1982; Marzke et al. 1992). Additionally, some bones of the wrist and attachment sites for flexor

tendons are more ape-like which may have been useful while climbing, as is a marked tubercle for a leg muscle useful for climbing (Hartwig-Scherer and Martin 1991; Wood 1992). But probably most pivotal to understanding the locomotion of *H. habilis* is its foot morphology. The Olduvai Hominid 8 (OH 8), *H. habilis* foot (at 1.8 Ma). It was originally suggested that it had a fully developed bipedal adaptation (Day and Napier 1964; Leakey et al. 1964), but others have since argued that it still retains evidence of an arboreal adaptation (McHenry and Berger 1998; Wood and Collard 1999). This thesis adds to the knowledge of the *H. habilis* foot with an analysis of the shape and size of the navicular.

Using geometric morphometric analyses, I found that the navicular of *H. habilis* (OH 8) was more similar to modern humans in shape compared to chimpanzees or baboons, while the size of the OH 8 navicular was most similar to chimpanzees. This mixture of primitive and derived traits is seen in other features of the OH 8 foot. The relative length of the OH 8 foot is similar to the relative length of the human foot and much shorter than the relative length of the ape foot (Susman and Stern 1982). Half the length of the human foot is made up of robust tarsals, while approximately one-third of the length of a chimpanzee foot is composed of the tarsal bones (Zihlman 2000). *H. habilis* has an adducted hallux but lacks a propulsive big toe (Wood 1992) and may have a certain degree of grasping function over and above what is present in modern humans (Lewis 1980). The plane of the first tarsometatarsal joint is similar to that of modern humans because the medial cuneiform faces distally. In apes and monkeys, the surface of the medial cuneiform is convex, while in modern humans and *H. habilis*, it is concave (Susman and Stern 1982). Similarly, the lateral cuneiform is rectangular in modern

humans and *H. habilis*, while in chimpanzees the dorsal view of the lateral cuneiform is square shaped. Yet the anterior medial cuneiform joint of the OH 8 metatarsal suggests that *H. habilis* retained a degree of grasping function, and the anterior part of the articulation between the intermediate cuneiform and lateral cuneiform and between the lateral cuneiform and cuboid are present as they are in apes but not in humans (Lewis 1980). Like modern humans, the inferior aspect of the *H. habilis* navicular is expanded at the attachment site for the subnavicular and plantar calcaneonavicular ligaments and the navicular tuberosity is reduced (Susman and Stern 1982). These features are important for the maintenance of the longitudinal arch. However, the morphology of the cuboid, which is bent dorsally in OH 8 as it is in apes, does not support the existence of a human longitudinal arch for *H. habilis* (Lewis 1981). In modern humans the cuboid has a plantar bend that is consistent with its position as the keystone of the lateral part of the human longitudinal arch. Further, the articular surface on the navicular for the cuboid is present in chimpanzees, normally absent in modern humans, but present in OH 8. The cuboid of OH 8 resembles modern humans in that it has a flange on the inferomedial side of the bone that articulates with an opposing concavity on the anterior face of the calcaneus, while this flange in chimpanzees is located in a more medial position (Lewis 1980).

While some researchers conclude that *H. habilis* exhibits a modern human-like calcaneocuboid joint (Susman 1983; Langdon et al. 1991; D'Aout et al. 2004), others argue that this joint differs from humans in that it does not allow the calcaneus to swing laterally, which tenses the plantar ligaments and provides additional support for a longitudinal arch (Lewis 1980). The presence of a longitudinal arch significantly improves the bipedal gait efficiency; however, most of the features of OH 8 suggest that

the longitudinal arch may have been absent and that the weight transfer through the OH 8 foot in both standing and walking was different than it is in the modern human foot (Lewis 1980; Susman 1983; Wood 1992; D'Aout et al. 2004). Finally, OH 8 has an ape-like talus (Lewis 1980) and a primitive talonavicular joint (D'Aout et al. 2004) in which the articular facet of the talus suggests extreme plantarflexion potential (Wood 1974). Hominins are disadvantaged for arboreal living due to the large base of support that is produced by the rigid hominin tarsal plate (Langdon et al. 1991).

What do all of these features of the OH 8 fossil mean for the bipedalism of *H. habilis*? In short, this mixture of ape-like and human-like traits in the *H. habilis* foot has led most researchers to conclude that from a functional stand point, OH 8 possesses a derived bipedal morphology in the legs and feet while retaining some climbing potential (Lewis 1980; Susman and Stern 1982; Langdon et al. 1991; Wood 1992; McHenry and Berger 1998; Wood and Collard 1999). Susman and Brain (1988) argue the morphology of the first metatarsal of OH 8 indicates that *H. habilis* was an earlier grade of bipedalism, which means it would have lacked the transfer of weight to the medial side of the foot and fully onto the great toe (i.e., the toe-off mechanism) during the final half of the stance phase of the walking cycle. Interestingly one model, which is based on a study of the calcaneus, talus, cuboid and navicular of OH 8, suggests that the medial and lateral columns of the *H. habilis* foot evolved at different times (Kidd 1999). Kidd argues that the talus and navicular of OH 8 are essentially ape-like, but that the calcaneocuboid articulation is markedly human-like. In Kidd's view, the medial column of OH 8 is essentially ape-like with no medial longitudinal arch and an opposable toe, but the lateral column had remodeled to a human-like degree. Kidd proposes that the lateral side of the

hominin foot evolved first to stabilize mid-tarsal flexibility as an adaptation to increased terrestriality, and the medial side followed. Since *H. habilis* was a small-bodied hominin (McHenry 1991 & 1992) lacking large, projecting canines and with only rudimentary tool-making skills, it is likely that a selective advantage would have derived from its ability to sleep, escape, and perhaps occasionally feed in trees (Lewis 1980; McHenry and Berger 1998; Kidd 1999; Wood and Collard 1999).

CHAPTER V

CONCLUSION

The navicular bone has rarely been assessed when it comes to looking at the evolution of bipedalism and there has been no published literature regarding the baboon navicular. As suggested by previous literature, *Homo habilis* (Olduvai Hominid 8) exhibits a mosaic of ape and human skeletal traits (Lewis 1980; Susman and Stern 1982; Langdon et al. 1991; Wood 1992; Wood and Collard 1992; McHenry and Berger 1998). A geometric morphometric analysis of the navicular bone of *H. habilis* (OH 8) found it is most similar in shape to modern humans and most similar in size to chimpanzees. *Homo habilis* had the ability of terrestrial bipedal locomotion but also retained arboreal locomotion (Lewis 1980; Susman and Stern 1982; Hartwig-Scherer and Martin 1991; Langdon et al. 1991; Wood 1992; Wood and Collard 1992; McHenry and Berger 1998; Asfaw et al. 1999; Ruff 2009). The results of this research suggest the navicular bone can be used when assessing mode of locomotion. Thus, if a fossil is discovered and the navicular is present, it can be assessed in accordance with other skeletal traits to assess mode of locomotion and aid in the phylogenetic placement.

However, it is important to recognize that this argument and many of the arguments concerning the bipedalism of *H. habilis* are based solely on the analysis of a single fossil specimen, OH 8. Not only are there differing interpretations of the features of the OH 8 foot as mentioned above, but there is disagreement over whether it is from a subadult or adult *H. habilis* (Day and Napier 1964; Susman and Stern 1982) and whether

it belongs to the genus *Homo* or *Australopithecus* (Wood 1974 & 1992; Lewis 1980; Susman and Stern 1982). The OH 8 fossil was not directly associated with *H. habilis* cranial or dental material but was largely assigned to *Homo* based on initial analyses that placed it closer to modern humans than to earlier hominins (Day and Napier 1964). Critical to the question of taxonomic affinity of the OH 8 foot is the morphology of its talus and the existence of the contemporary KNM-ER 813 (1.64 mya) talus from Koobi Fora, Kenya (Leakey and Wood 1973; Gebo and Schwartz 2006). Multiple analyses indicate that the KNM-ER 813 talus is much more similar to modern human tali than is the talus of OH 8 (Leakey and Wood 1973; Wood 1974; Lewis 1980; Wood 1992; D'Aout et al. 2004). This implies that there were different hominin ankle morphologies existing at a similar point in time and has led Wood (1974 & 1992) and Wood and Collard (1999) to assign KNM-ER 813 to the genus *Homo* (*ergaster?*) and OH 8 to the genus *Australopithecus*.

In this research, only the left navicular bone was used, and it would be of interest to use the right navicular bone when the left is not present. Since the skeletal body is symmetrical, the right navicular should exhibit the same size and shape as the left navicular.

Many of the navicular bones belonging to known australopithecines are from the right side of the body. The navicular landmark data collected in this study from the left naviculars of modern humans, chimpanzees, baboons, and *H. habilis* (OH 8) could be mirror-imaged and compared to the australopithecine naviculars. Because extant chimpanzees primarily live in open-forest and woodland environments, as did *Australopithecus afarensis* (Hunt 1994), such a comparison may show that the A.

afarensis navicular is more similar in shape and size to chimpanzee naviculars than to modern human or baboon naviculars. Wood (1992:790) states, “only when morphological studies, embracing both function and life history are integrated with the contextual, and behavior, evidence will increase our knowledge and understanding of the emergence and early evolution of our own genus.”

APPENDICES

Appendix 1. Facet Definitions (from White et al., 2005)

The talar facet is where the talus anatomically articulates distally with the navicular bone and is also called the talocrural joint.

The talar facet is located on the proximal side of the navicular when the nonarticular surface is dorsal and the tubercle is medial.

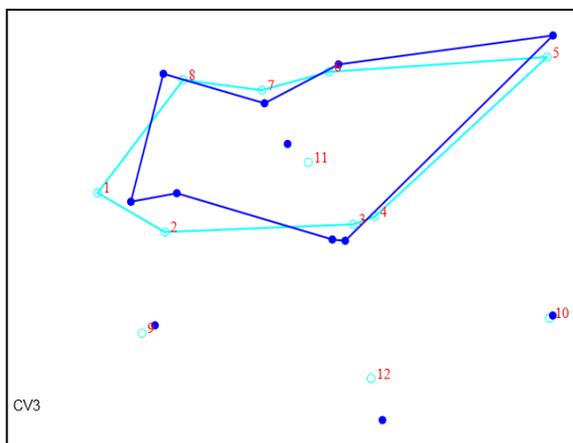
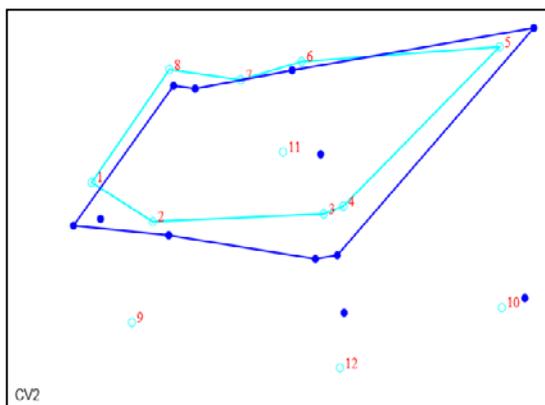
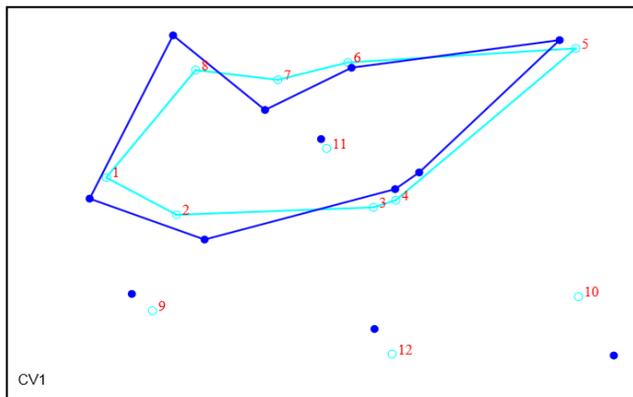
The cuboid facet is located where the navicular anatomically articulates with the cuboid but this does not occur in all individuals.

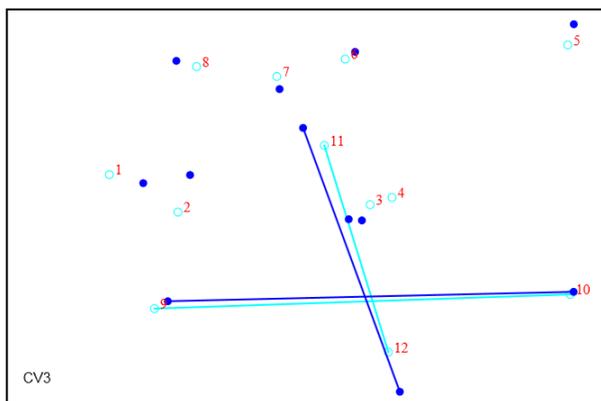
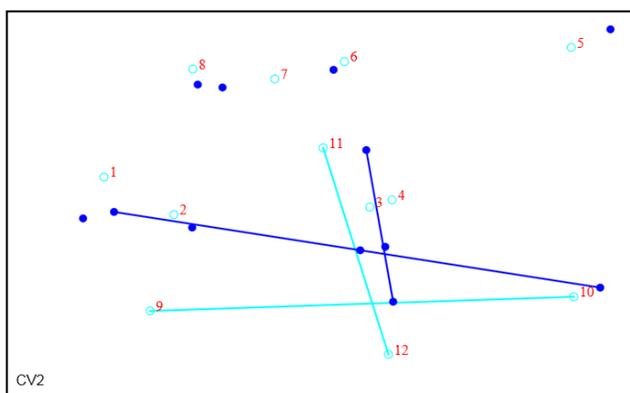
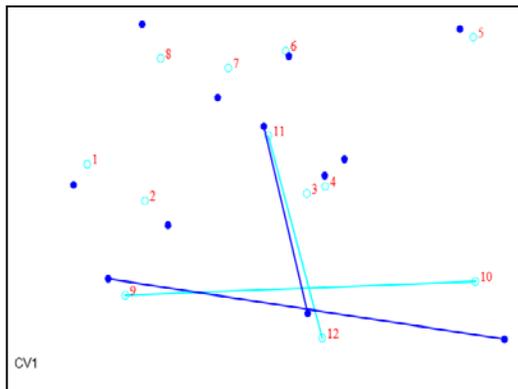
The entocuneiform facet is located where the medial (first) cuneiform anatomically articulates with the distal portion of the navicular bone.

The mesocuneiform facet is located where the intermediate (2nd) cuneiform anatomically articulates with the distal portion of the navicular bone.

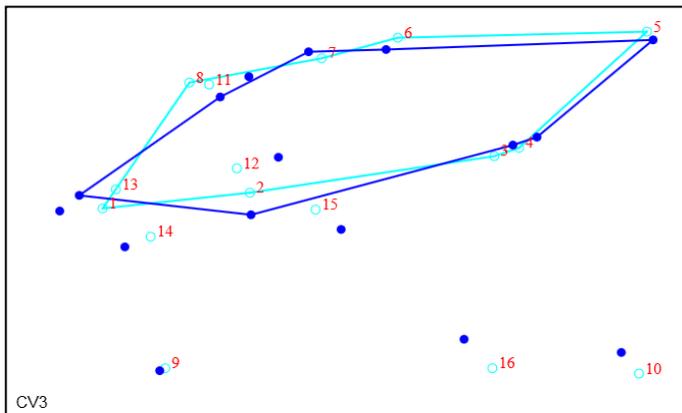
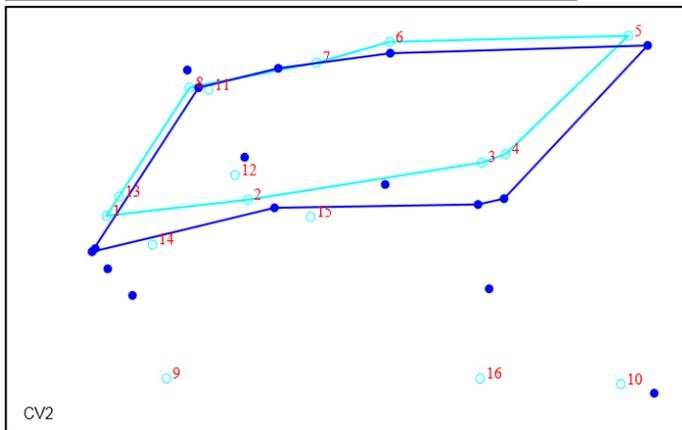
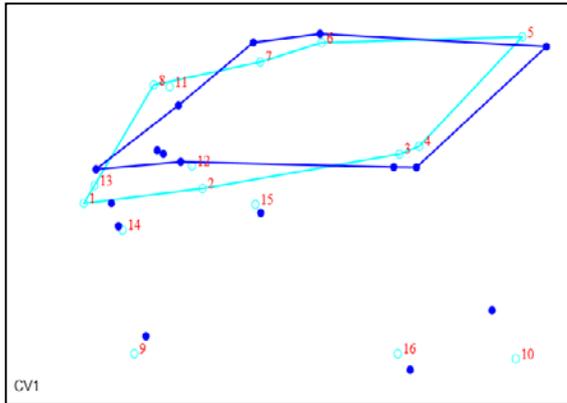
The ectocuneiform facet is located where the lateral (3rd) cuneiform anatomically articulates with the distal portion of the navicular bone.

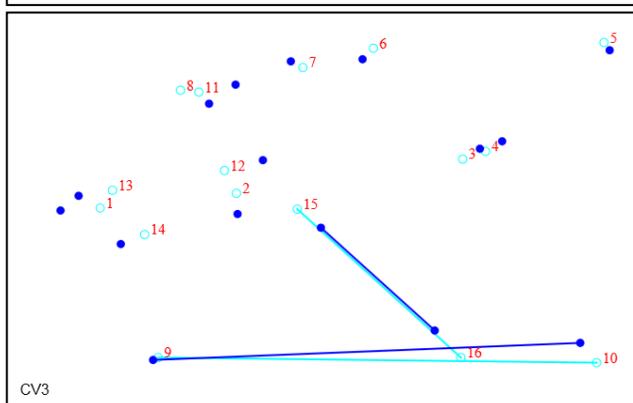
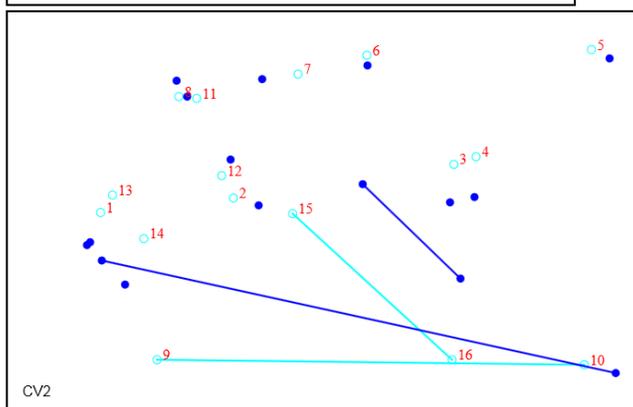
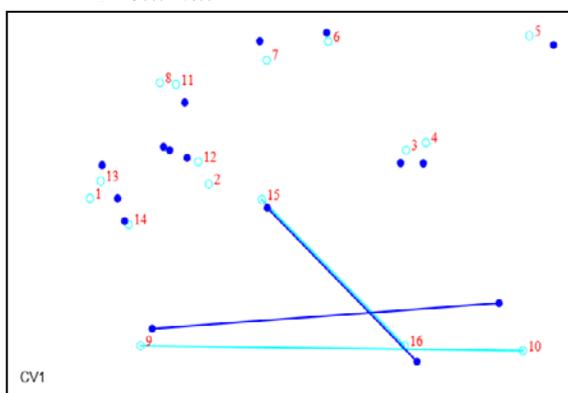
Appendix 2. Wireframes of distal and proximal view for CV 1, 2, and 3

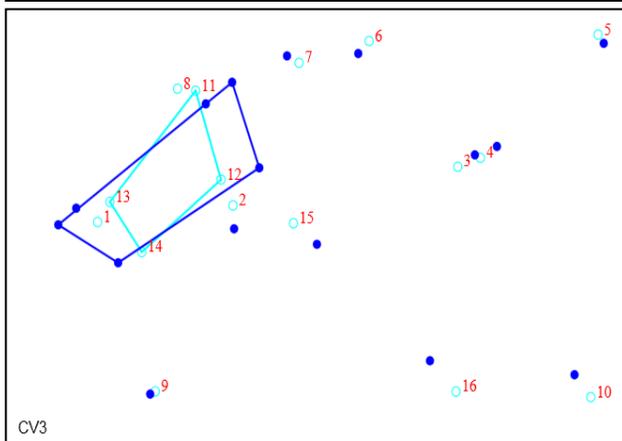
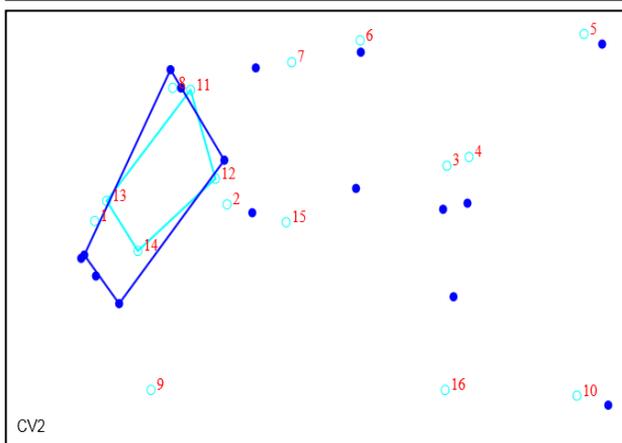
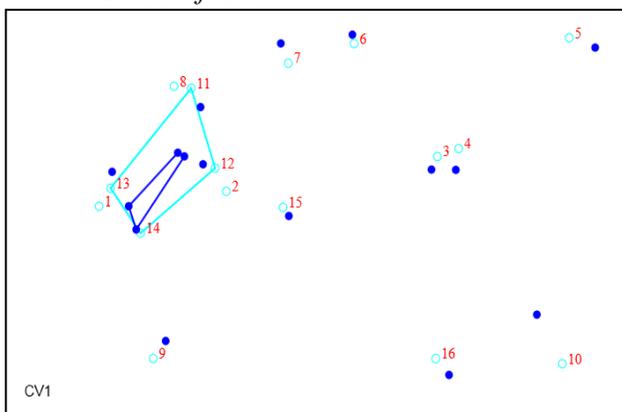
Distal

Proximal

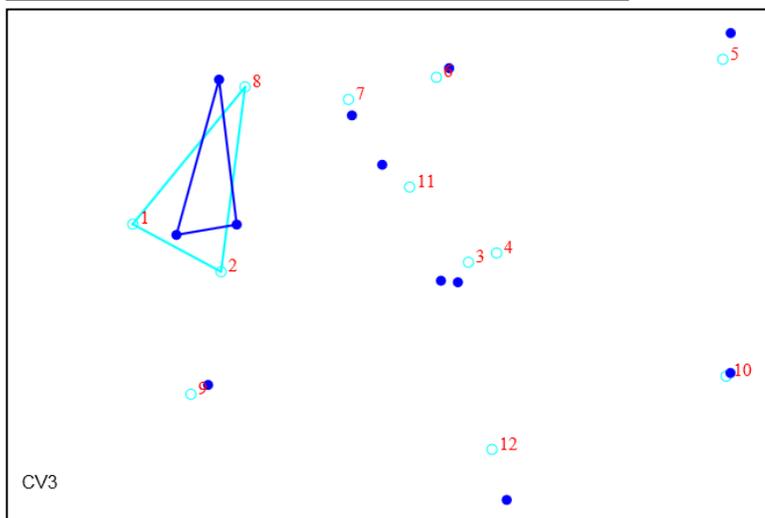
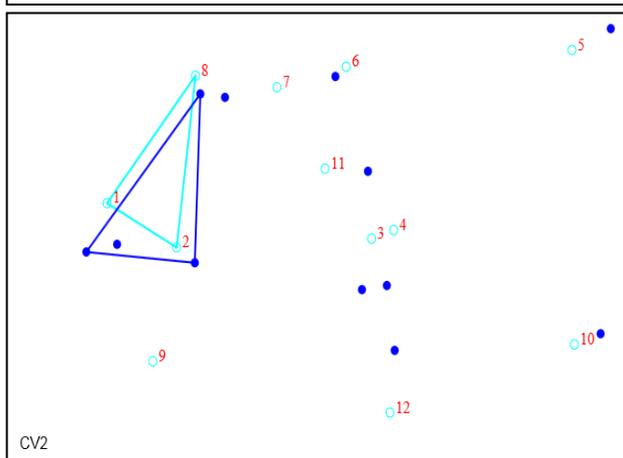
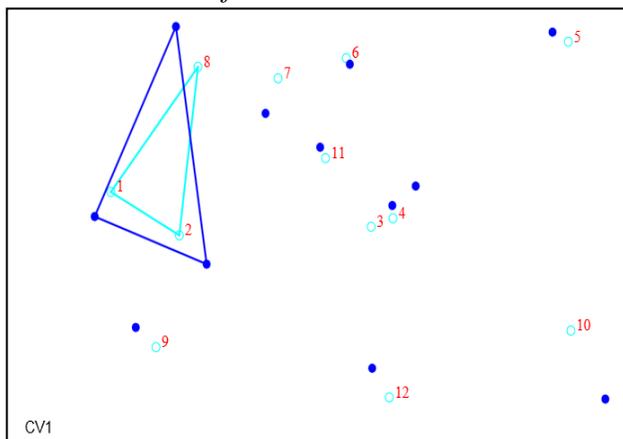
Appendix 3. Wireframe of distal view, proximal view, and cuboid facet for CV 1, 2 &3

Distal

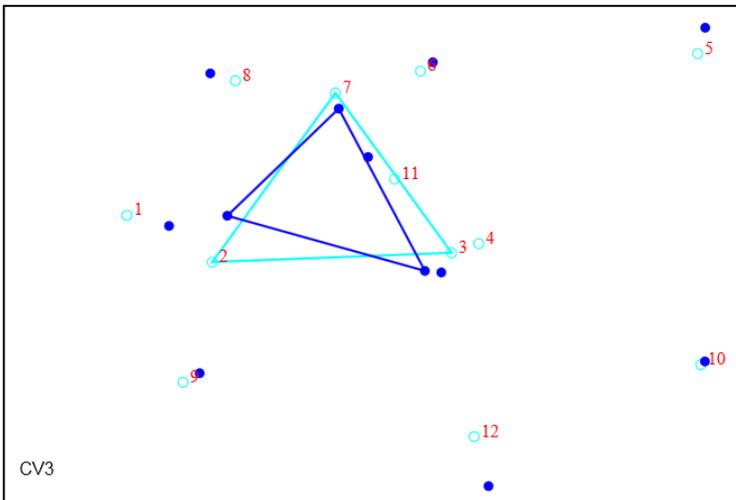
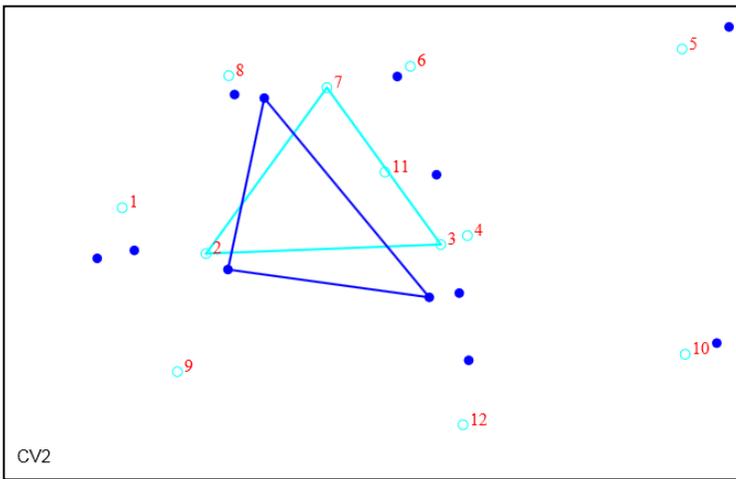
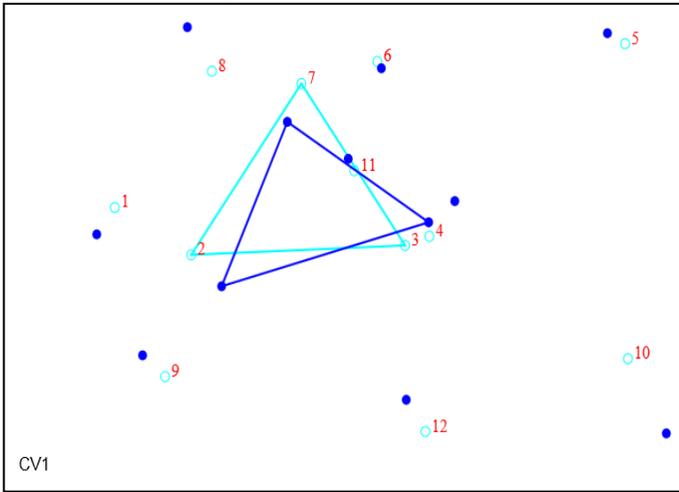
Proximal

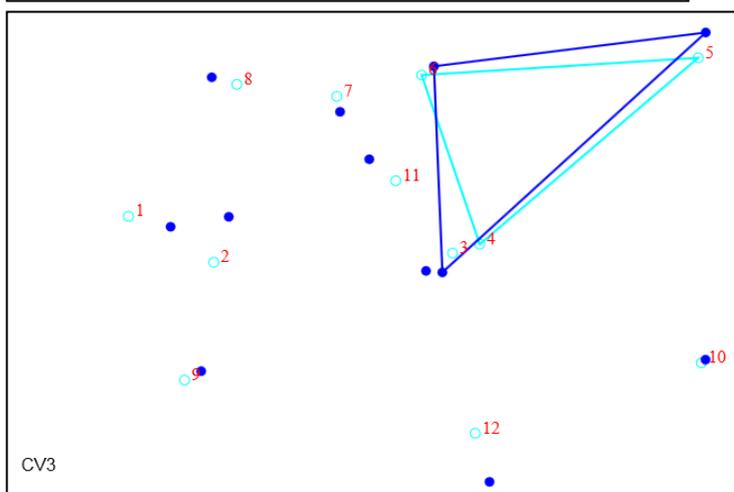
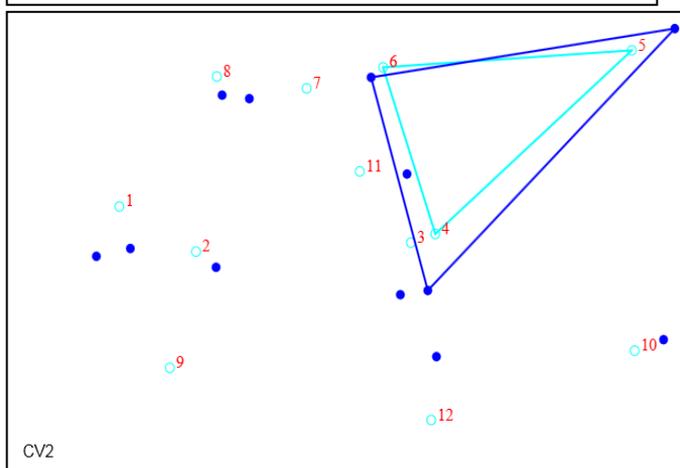
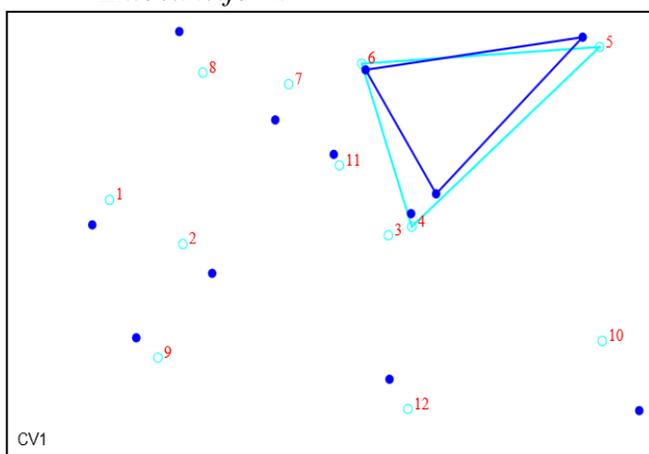
Cuboid facet

Appendix 4. Wireframe graphs of articular surfaces without cuboid (CV 1, 2 &3)

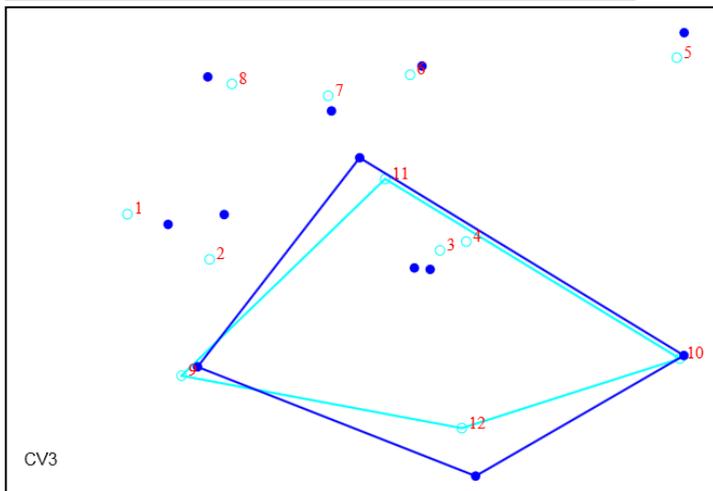
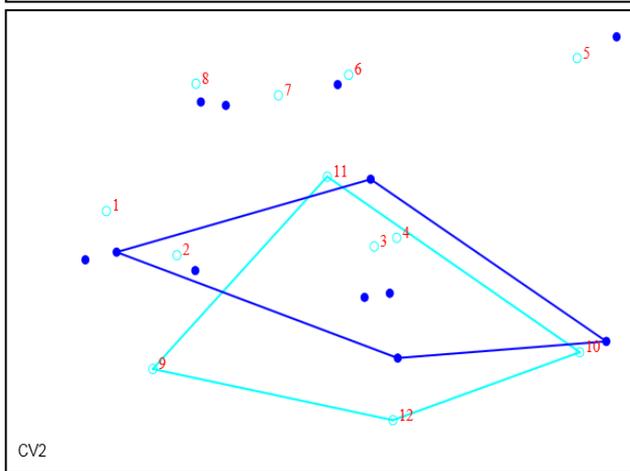
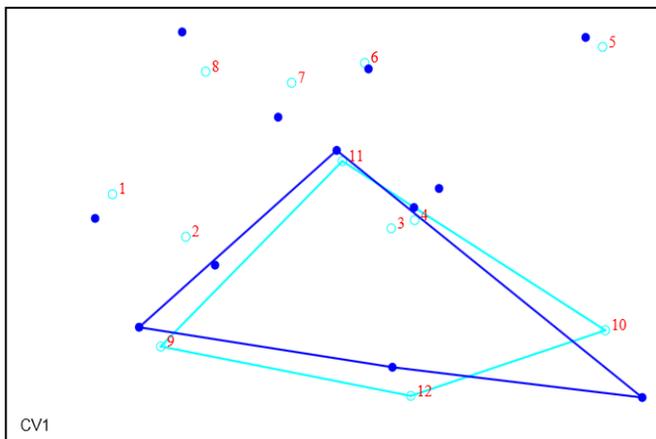
Ectocuneiform

Mesocuneiform

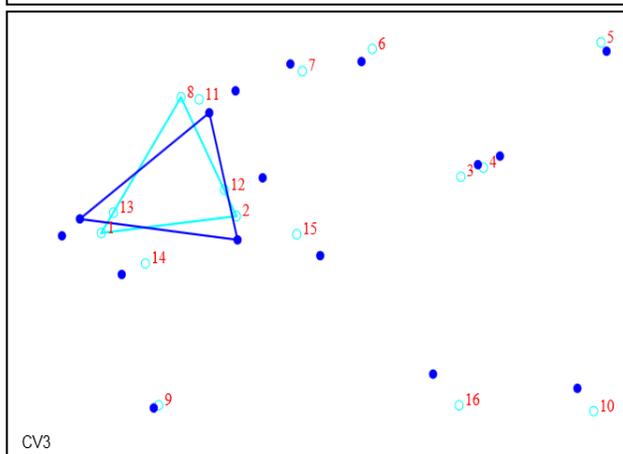
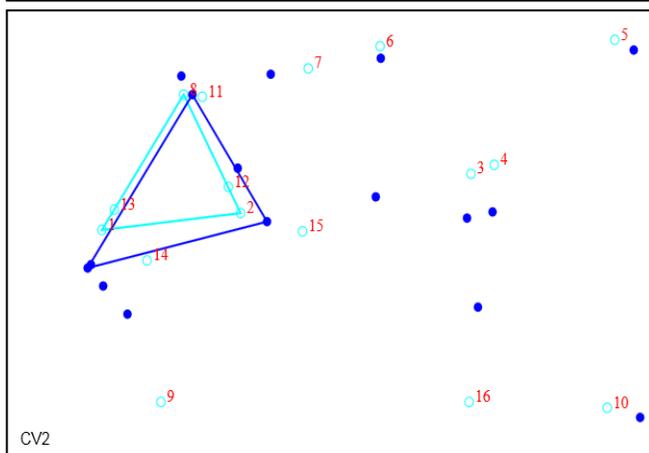
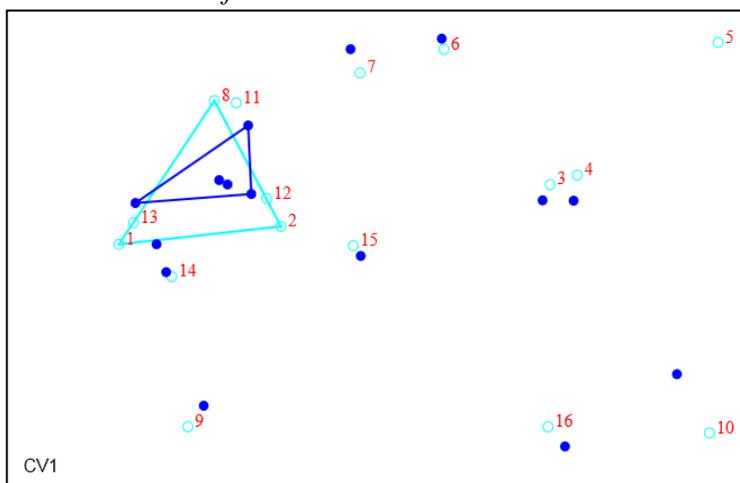


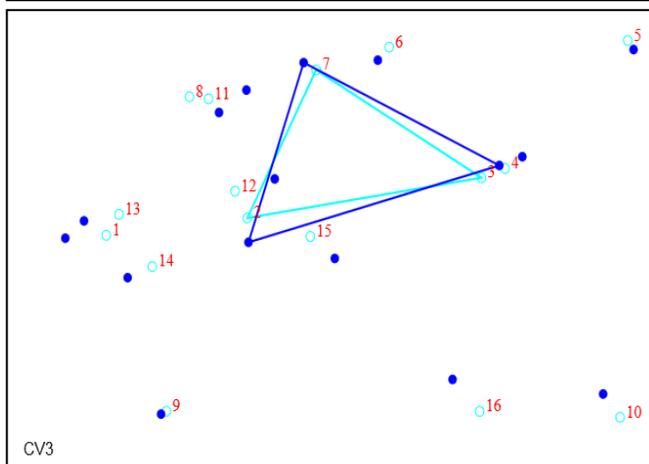
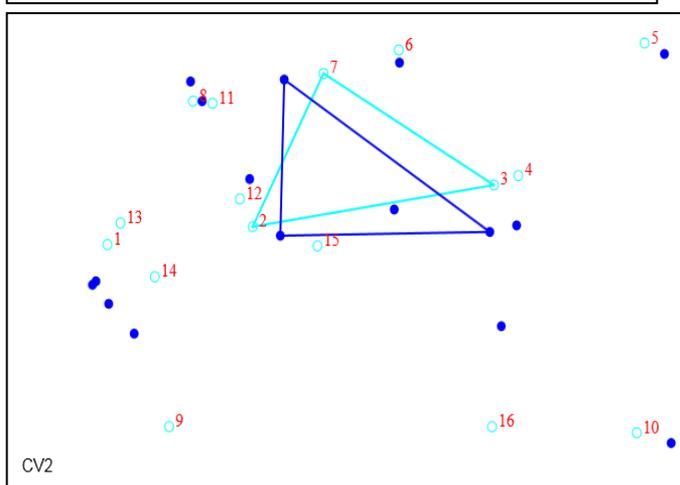
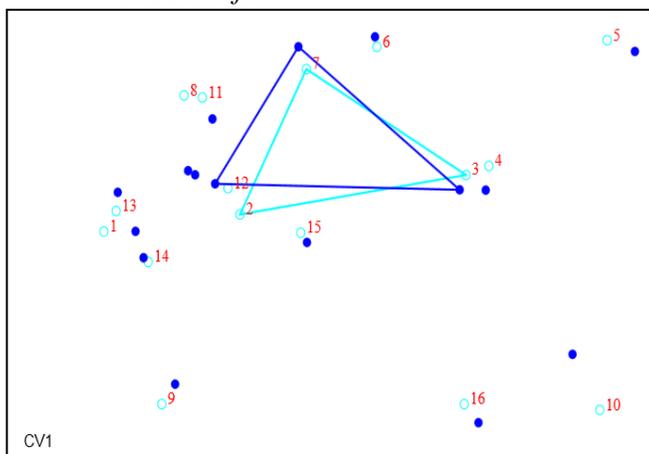
Entocuneiform

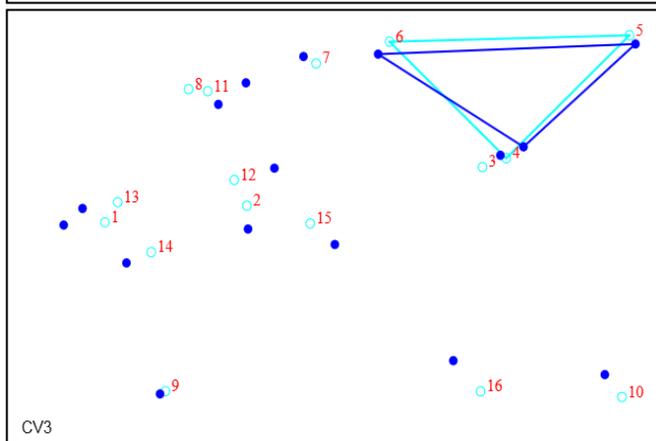
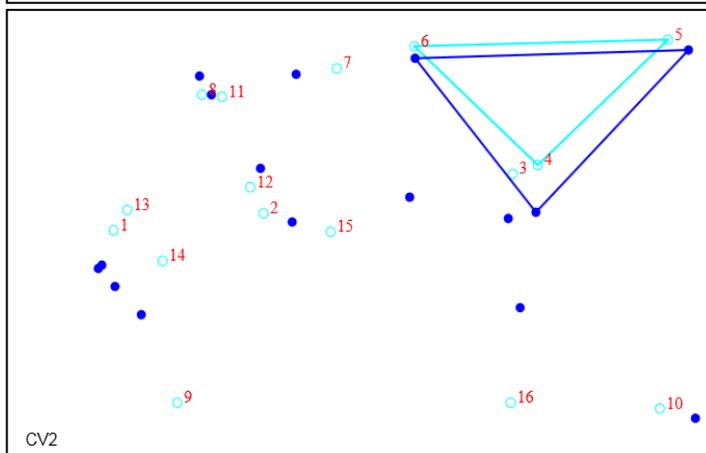
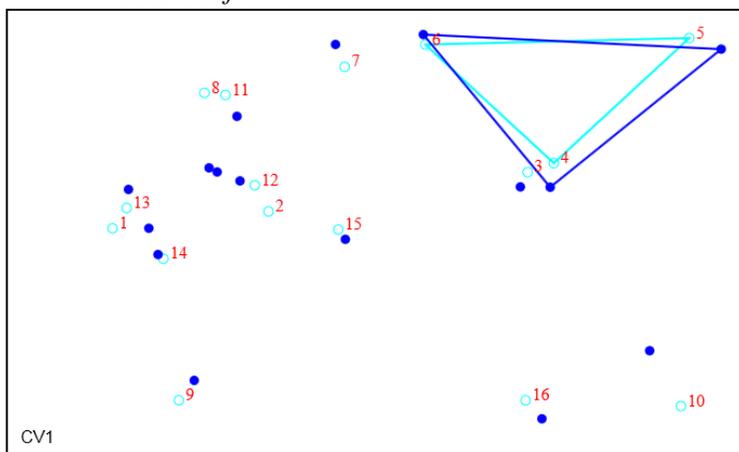
Talocrural Joint



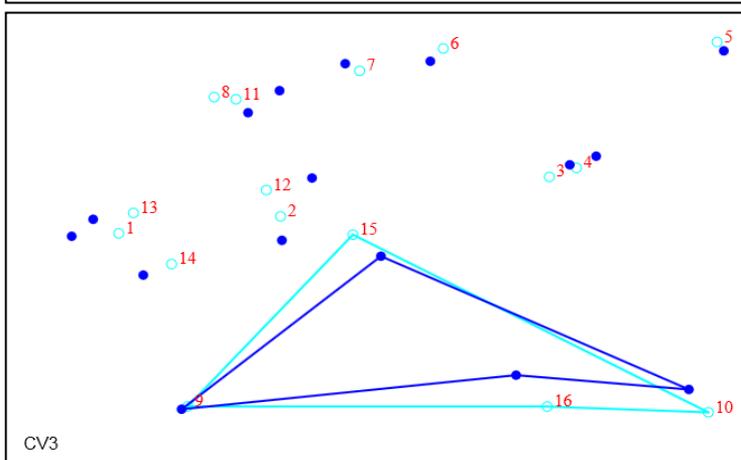
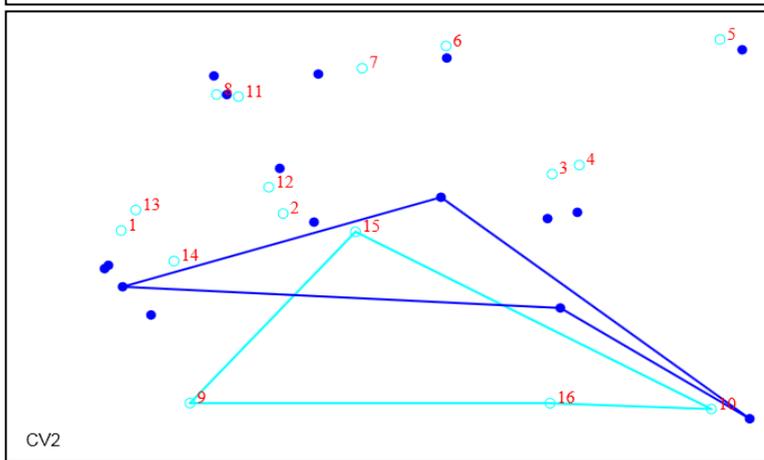
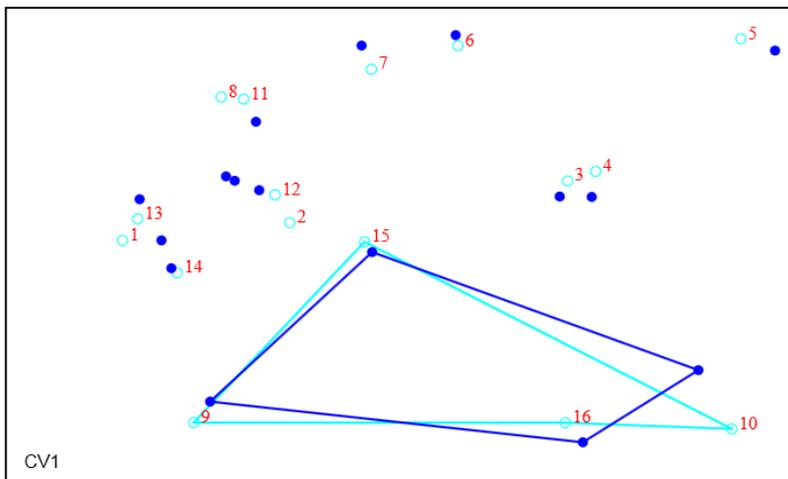
Appendix 5. Wireframe graphs of articular surfaces with cuboid (CV 1, 2 & 3)

Ectocuneiform

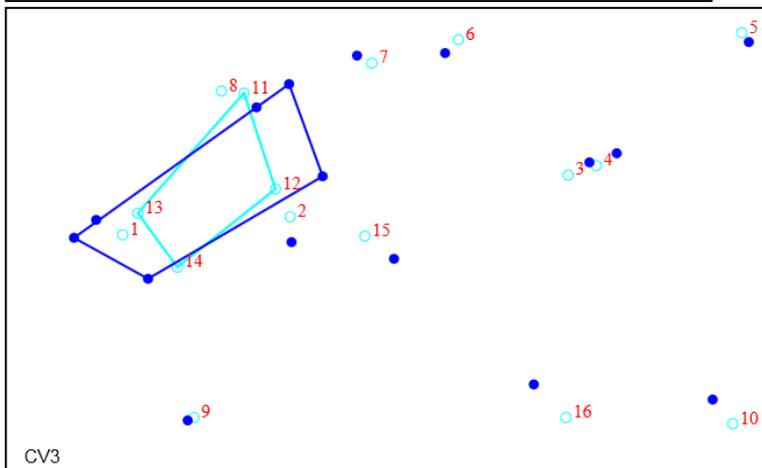
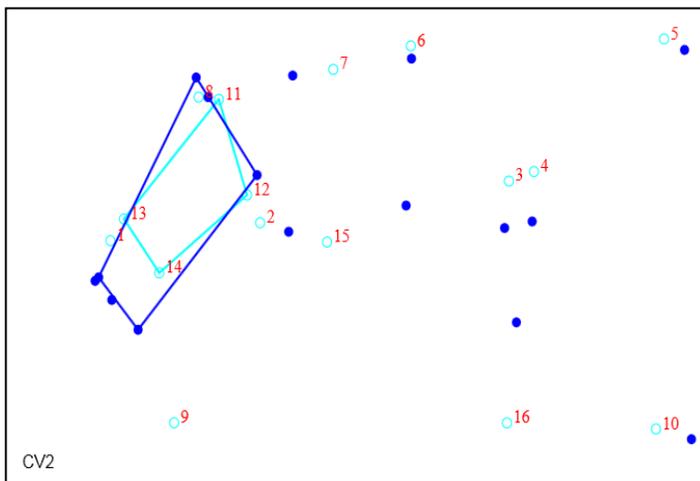
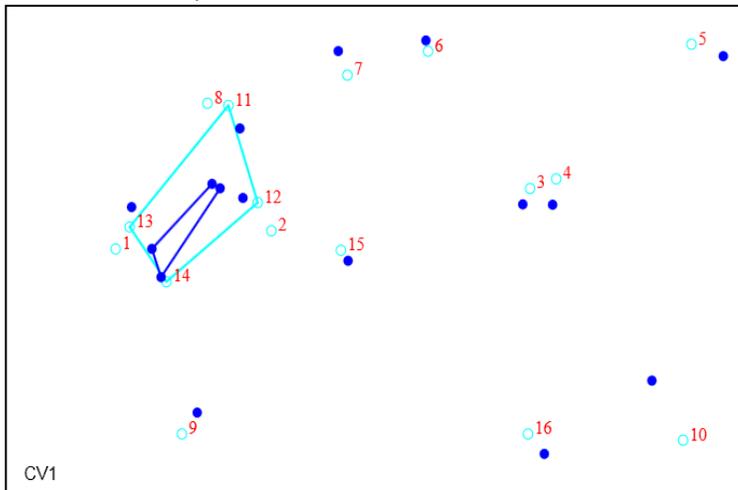
Mesocuneiform

Entocuneiform

Talocrural Joint



Cuboid facet



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