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Lesniak, Kirsty

*Published in:*  
Veterinary Journal

*Publication date:*  
2013

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*The final published version is available direct from the publisher website at:*  
[10.1016/j.tvjl.2013.09.032](https://doi.org/10.1016/j.tvjl.2013.09.032)

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*Citation for published version (APA):*

Lesniak, K. (2013). Directional asymmetry of facial and limb traits in horses and ponies. *Veterinary Journal*, 198(Supplement 1), e46-e51. <https://doi.org/10.1016/j.tvjl.2013.09.032>

1 **Directional asymmetry of facial and limb traits in horses and ponies**

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4 Kirsty Leśniak \*

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6 *Centre for Performance in Equestrian Sports, Hartpury College, Hartpury, Gloucester GL19*

7 *3BE, England, UK*

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12 \* Corresponding author. Tel.: +44 1452 702488.

13 *E-mail address:* [kirsty.lesniak@hartpury.ac.uk](mailto:kirsty.lesniak@hartpury.ac.uk) (K. Leśniak).

14

15 **Abstract**

16 Current published data referring to directional asymmetry (DA) of horses refer to  
17 racing Thoroughbreds. The aim of this study was to identify whether horses and ponies  
18 exhibit directionality of trait asymmetries. Eleven functional (limb) and four non-functional  
19 (facial) bilateral traits were measured on left and right sides in a cohort of 100 horses and  
20 ponies using callipers. The population was investigated as pooled data and as horse (withers  
21 height > 148 cm) and pony (withers height  $\leq$  148 cm) sub-groups. Within the pooled data,  
22 functional traits were longer on the right for the third metacarpal (MCIII, 73%) and metatarsal  
23 (MTIII, 65%) bones and wider on the left for the forelimb proximal phalanx (54%), MCIII  
24 (40%), MTIII (51%) and hind limb proximal phalanx (55%). Dimensions of the intercarpal  
25 and tarsocrural joints were larger on the right side. Differences in DA were present between  
26 horses and ponies within non-functional traits, but not functional traits. The results suggest  
27 that DA within horses and ponies is more likely to be a species trait rather than one exclusive  
28 to racing as a result of pressures from directionally orientated training or from selective  
29 breeding strategies.

30

31 *Keywords:* Equine; Conformation; Asymmetry; Skeletal; Laterality

32

### 33 **Introduction**

34 Symmetry within nature is thought to reflect the ability to defend against  
35 environmental or genetic stressors (Moller, 1990, 1993; Hosken, 2001). The ability of an  
36 individual's genotype to defend against these stressors is depicted through the symmetry of  
37 their phenotype (Tuytens, 2003). Within bilaterally paired traits, fluctuations from the ideal  
38 symmetrical state, with no directional bias, are known as fluctuating asymmetries (FA) or  
39 phenodeviants (Van Valen, 1962; Moller 1993; Wilson and Manning, 1996). FA has been  
40 used to measure the level of developmental stability within populations and within individuals  
41 (Thornhill and Gangestad, 1994). Although the optimum state for an individual is unknown, it  
42 is generally assumed that this should be perfect symmetry (Houle, 2000).

43

44 Within a population, a mean of zero and a normal distribution around this mean  
45 should be observed for differences between left and right sides (Van Valen, 1962). FA in the  
46 region of 1-2% of character size is usually exhibited by a population (Gangestad and  
47 Thornhill, 1999). A further indicator of imbalanced development is the measure of directional  
48 asymmetry (DA), which identifies a skewed distribution of asymmetry to the left or right side.  
49 DA has not been linked to developmental stability, but has been suggested to depict an  
50 adaptive or functional asymmetry (Tuytens, 2003).

51

52 The athletic phenotype affects performance, with influential features including  
53 intermandibular width and length of the third metacarpal bones (Delahunty and Webb, 1991;  
54 Mostert and Householder, 2000). Symmetry of bilateral traits influences performance  
55 capabilities, especially for Thoroughbred racehorses. Dalin et al. (1985) correlated  
56 performance and asymmetries of sacral tuber height in racehorses and demonstrated that  
57 greater asymmetry was associated with decreased performance. However, the study by Dalin

58 et al. (1985) did not consider the origin of asymmetry. The relationship between asymmetry  
59 of skeletal dimensions and performance in horses has not been studied.

60

61 Traits of lesser functional importance often display greater asymmetry than functional  
62 traits (Markow and Clarke, 1997; Moller, 1993). In a sample of 285 children in the Jamaican  
63 Symmetry Project, upper body bilateral traits exhibited greater asymmetry than lower body  
64 bilateral traits (Trivers et al., 1999). Lower ranking Thoroughbred racehorses exhibit greater  
65 asymmetry of non-functional facial traits than the functional limb traits (Manning and  
66 Ockenden, 1994).

67

68 The effects of limb length discrepancies on gait have been investigated more  
69 extensively in humans than horses; the magnitude of the discrepancy has a strong bearing on  
70 gait kinematics and kinetics (Bloedel and Hauger, 1995). Limb length discrepancies < 15 mm  
71 rarely have clinical implications, whereas discrepancies of greater magnitude lead to  
72 dysfunction and pain (Subotnick, 1976). Limb length affects leverage during locomotion;  
73 therefore an economical and symmetrical gait is achieved only with symmetrical body traits  
74 (Vagenas and Hoshizaki, 1992).

75

76 Watson et al. (2003) reported longer right third metacarpal (MCIII) lengths than left,  
77 in 76% of racing Thoroughbreds. This was considered to be a consequence of human  
78 selection rather than imbalances induced by training stresses, since growth of the MCIII bone  
79 ceases by 7 months of age (Thompson, 1995) and therefore should not be affected by  
80 subsequent training. Femoral epicondylar dimensions in Thoroughbred racehorses run on a  
81 clockwise track are greater for the left than the right limb (Pearce et al., 2005). Runners on an  
82 anticlockwise track are presumed to have a mechanical advantage if their outside (right) limb

83 is longer (Watson et al., 2003). This finding might help explain why horses successful on an  
84 anticlockwise track may not be as successful on a clockwise track (Williams and Norris,  
85 2003). As a dynamic structure, bone responds to the forces placed upon it and alternative  
86 theories suggest that repeated directionality could also be causal in the development of equine  
87 asymmetries (Drevemo et al., 1980; Scutt and Manning, 1996).

88

89         Currently the only data that exists regarding directional asymmetry of horses are based  
90 on populations of racing Thoroughbreds. The aim of this study was to compare the magnitude  
91 and direction of asymmetry within functional and non-functional traits of non-racing horses  
92 and ponies.

93

#### 94 **Materials and methods**

95         The study population consisted of male and female horses and ponies of a variety of  
96 breeds at two equestrian centres and two livery yards in Gloucestershire, UK. None of the  
97 horses or ponies had an elite competitive record and all were > 5 years of age to eliminate age  
98 related changes in symmetry (Trivers et al., 1999). One-hundred horses and ponies were  
99 selected via a convenience sampling technique and were investigated both as pooled data and  
100 following separation into horses (withers height > 148 cm;  $n = 57$ ) and ponies (withers height  
101  $\leq 148$  cm;  $n = 43$ ). The data were reviewed as pooled data, as well as separately for horses  
102 and ponies.

103

104         Direct measurements of 11 functional and four non-functional bilateral traits (Table 1)  
105 were determined using Invicta metric callipers (1 mm accuracy), similar to previous studies  
106 (Manning and Ockenden, 1994; Manning and Pickup, 1998). The horses and ponies were  
107 made to stand squarely on level concrete while being measured; three measurements were

108 taken at each site by one assessor and a repeated measures one-way analysis of variance  
109 (ANOVA) was used to determine intra-observer variability. Two observers repeated the  
110 measurements for selected horses following the same protocol and inter-observer repeatability  
111 ( $r$ ) was calculated using the following equation (Lessells et al., 1987):

112

$$113 \quad r = s^2_A / (s^2 + s^2_A)$$

114

115 where  $s^2_A$  is the between-group variance and  $s^2$  is the within-group variance

116

117 Absolute (directional) asymmetries ( $A$ ) were calculated by subtracting the mean of the  
118 left trait ( $L$ ) from the mean of the right trait ( $R$ ) ( $A = L - R$ ) (Manning and Pickup, 1998).

119 Positive values indicated a larger left sided trait and negative values indicated a larger right  
120 sided trait. Thus, the study determined the directionality of the data rather than the magnitude  
121 of the asymmetry in terms of frequencies; outliers were not removed. The directionality of the  
122 data was examined using two-way classification  $\chi^2$  analysis with significance declared at  $P <$   
123  $0.05$  to test the assumption that, if no directional bias exists, the distribution frequency of left  
124 and right for each trait should be equal.

125

## 126 **Results**

127 On repeated measures one-way ANOVA, there were significant variances between the  
128 three repeated measures for the length of the hind limb proximal phalanx (HPP;  $P \leq 0.05$ ).

129 However, repeatability calculations were 0.99-1.00 for all traits.

130

131 There were significant differences between the observed and expected values for the  
132 frequency of directionality of asymmetry within the pooled group data ( $\chi^2 = 39.8$ , degrees of

133 freedom,  $df = 14$ ,  $P \leq 0.05$ ) and the pony sub-group ( $\chi^2 = 31.3$ ,  $df = 14$ ,  $P \leq 0.05$ ), but not for  
134 the horse sub-group ( $\chi^2 = 18.5$ ,  $df = 14$ ,  $P \geq 0.05$ ).

135

136 Higher frequencies within bilateral facial traits were recorded for greater length and  
137 width on the left (PDA) (Table 2; Fig. 1). Mean trait values tended to be greater for the left  
138 traits within those exhibiting PDA and greater on the right for those exhibiting NDA (Table  
139 2); however, this was not seen for pinna length in the pony sub-group, where those exhibiting  
140 PDA had a greater mean value right sided trait, indicating that, although there were fewer  
141 individuals with PDA of this trait, the magnitude of the asymmetries was greater.

142

143 Left forelimb proximal phalanx (FPP) length and width dimensions were frequently  
144 larger than observed for the right for the pooled group and the two sub-groups (Table 2).  
145 Tendency for a longer right MCIII was greater in all three groups; however the pony sub-  
146 group displayed more individuals with greater width on the left whilst the horse sub-group  
147 exhibited more individuals with greater width on the right. For all groups the carpal width and  
148 depth dimensions were more frequently larger in the right limb. The mean trait values tended  
149 to be greater for the left trait within those exhibiting PDA, and greater on the right for those  
150 exhibiting NDA; however this was not seen for MCIII length in the pooled data set where  
151 those exhibiting PDA had a greater mean value right sided trait or for the carpal depth in the  
152 horse data set where those exhibiting NDA had a greater mean value left side, again  
153 indicating a lower frequency of incidence but greater individual magnitude of asymmetries.

154

155 Hind limb traits displayed high frequencies of directional asymmetry (Fig. 2). More  
156 individuals within all three groups demonstrated greater right HPP length but greater left HPP  
157 width. Similarly to the MCIII and to the HPP, a longer third metatarsal (MTIII) bone was



158 more frequently observed on the right, whilst the greater width of the same trait was more  
159 frequently observed in the left limb for all three groups. Tarsal joint width also demonstrated  
160 directionality with the right side being larger. As with some of the previous traits, although  
161 NDA was observed the mean value for the left side was larger.

162

### 163 **Discussion**

164 Asymmetries of non-functional traits may be more common and of greater magnitude  
165 than those found within functional traits (Trivers et al., 1999). Low facial trait FA has been  
166 correlated with elite performance in humans (Manning and Pickup, 1998) and horses  
167 (Manning and Ockenden, 1994; McDonald and Dumbell, 2008). Although pinna asymmetries  
168 have no direct functional significance, they potentially reflect factors negatively affecting  
169 auditory perception, such as external auditory meatus and middle ear structure malformations.  
170 Pinna asymmetries in humans have been linked to auditory canal defects and conductive  
171 deafness (Manning et al., 1997). Such developmental defects may negatively affect decoding  
172 of audio signals by influencing the passage of sensory information to the cerebral  
173 hemispheres and co-ordination of voluntary and involuntary activities. The combination of  
174 inadequately functioning cerebral hemispheres and inner ear dysfunction, important for  
175 aptitude of balance, may be sufficient enough for the individual to lack optimal balance and  
176 co-ordination for high performance potential.

177

178 Pinna length exhibited NDA in both the horse sub-group and the pooled group but not  
179 the pony sub-group. PDA of pinna length in female human beings has been linked to  
180 increased symmetry of offspring (Manning et al., 1997). However, NDA has been reported in  
181 a group of elite male athletes, although the possible implications of this finding have not been  
182 discussed (Manning and Pickup, 1998). Composed of soft tissue and cartilage, asymmetry of

183 soft tissues in the human pinna is affected by hormonal fluctuations (Scutt and Manning,  
184 1996) unlike the more cartilaginous pinna of horses. Human findings suggest a link to both  
185 sex and performance; these factors were not considered in our study. However, sex  
186 differences have been associated with equine laterality previously (McGreevy and Rogers,  
187 2004; Murphy and Arkins, 2004); lateralisation of the horse is linked to cerebral hemispheric  
188 lateralisation and therefore a link could exist between motor laterality, pinna symmetry and  
189 brain lateralisation.

190

191 An almost equal split of PDA and NDA was demonstrated for nostril width within all  
192 three groups. Although the anatomical markers used to measure this trait were chosen to  
193 reduce the influence of flare, this physiological response to novel stimuli was considered to  
194 have an impact on the results for this trait, as was indicated by the standard deviation values  
195 in comparison with the means. PDA was observed at a greater frequency for nostril length and  
196 width within the pooled and the horse sub-group, but only for nostril width in the pony sub-  
197 group. Lateralised nostril use has been identified in species such as the domestic fowl where  
198 the young respond to imprinting odours through head shaking after using their right nostril  
199 (Vallortigara and Andrew, 1994; Olka and Turkewitz, 2001); a lateralisation link may also  
200 exist within the current study. Mixed sex populations of horses have previously demonstrated  
201 right nostril preferences during olfactory stimulus tests to novel objects (McGreevy and  
202 Rogers, 2004); no sex or age bias for nostril preference was reported, although males were  
203 deemed to be more strongly lateralised than the females. Nostril use may be an indicator of  
204 sensory lateralisation to novel stimuli (McGreevy and Rogers, 2004), and dominance of the  
205 right cerebral hemisphere, involved with processing novel stimuli. The link between nostril  
206 asymmetry and the neurological processing of novel stimuli has yet to be confirmed but given  
207 similar findings for other sensory organs and motor structures, a link between nostril

208 asymmetry, nostril laterality and right-side cerebral dominance is proposed for the current  
209 results.

210

211 A higher frequency of PDA was demonstrated for length and width of the FPP within  
212 all three groups. For all three groups, the right MCIII was more frequently greater in length  
213 whilst the left MCIII was greater in width. The NDA of MCIII length reflects previous  
214 findings, including the results of Watson et al. (2003), where the right MCIII was longer than  
215 the left for 76% of Thoroughbred racehorses studied. The longer right limbs were suggested  
216 to provide a locomotory advantage over PDA due to the mechanical requirements involved in  
217 running in an anti-clockwise direction; as seen on most racecourses. The tendency for the  
218 right limb to be longer was present regardless of the direction in which the horses raced. This  
219 supports the findings of the current investigation, further intimating that DA is a species trait  
220 rather than one developed through selective breeding of racehorses. The difference between  
221 the measurement techniques and the individual observers used in the current study and the  
222 study by Watson et al. (2003) study potentially mean the magnitude of the data would differ;  
223 however, the directionality should not, enabling the directionality of the two sets of data to be  
224 compared.

225

226 The dimensions of the femoral epicondyle in Thoroughbred racehorses run on a  
227 clockwise track are greater on the left than the right (Pearce et al., 2005). Although this  
228 potentially indicates bone adaptation due to increased loading of the outside limb during  
229 clockwise racing, similar PDA of bone widths were found in the current study and could  
230 demonstrate a normal DA within the species rather than the adaptive response to exercise  
231 suggested previously (Pearce et al., 2005). Predisposition for injury is greater in the shorter  
232 left limb due to potential compensatory gait mechanisms, whereby the horse shortens the

233 stance phase and lengthens the break over-phase of the longer limb to prevent excess bending  
234 of the longer left bone; consequentially landing is heavier on the shorter limb (Davies and  
235 Watson, 2005; Perttunen et al., 2004).

236

237 McGreevy and Rogers (2004) investigated motor and sensor laterality in  
238 Thoroughbreds and identified a preference for advanced left limb placement during grazing;  
239 this trend strengthened with age. They suggested that the non-advanced limb bore more  
240 weight; however, this could be argued, depending on the individual's stance. The non-  
241 advanced limb is often stretched under the body, with weight borne through the dorsal aspect,  
242 but the advanced limb often carries the majority of the horse's bodyweight and is therefore  
243 under greater compressive forces. As an alternative theory, horses may naturally advance the  
244 shorter limb and angle the longer limb under the body to attain the grazing position. This  
245 differing hypothesis would support the finding of the longer right limb in the current study.  
246 The additional compressive strain on the shorter left limb would result in thickening of the  
247 bone over time due to remodelling of this dynamic structure, again reflecting the wider bone  
248 dimensions seen within the current study. Lateralisation may be determined in utero (Murphy  
249 and Arkins, 2004) and has been suggested, alongside gait habits, to influence bone thickness;  
250 however this appears to be in spite of limb asymmetries rather than as a synergistic effect of  
251 the asymmetry (Davies and Watson, 2005)

252

253 NDA of carpal joint traits was demonstrated by all three groups. Although structurally  
254 dissimilar, the human knee joint would have the most similar role within locomotion to the  
255 equine carpal joint. A similar NDA of the human knee joint width was identified by Trivers et  
256 al. (1999). Auerbach and Ruff (2006) reported NDA of the mediolateral breadth of the  
257 femoral epicondyle in the adult human; a principal structure within the human knee. Although

258 no hypotheses for these findings were given, they may reflect the increase in stability needed  
259 to compensate for the longer humeral length observed for the same limb, similar to the longer  
260 right MCIII observed in the current study.

261

262 HPP width demonstrated a tendency for PDA, as also seen in the FPP; however HPP  
263 length demonstrated greater predisposition for NDA. This supports the forelimbs results  
264 where the trait is wider on the shorter, left limb as well as previous research findings where a  
265 greater propensity for NDA has been reported for length (Watson et al., 2003). However, the  
266 measurement of this trait demonstrated significant variance ( $P \leq 0.05$ ) and therefore the  
267 results for the length of the HPP could be questioned without further analysis using a more  
268 repeatable measurement technique.

269

270 DA tendencies of the MTIII reflect those observed for the MCIII and HPP, where the  
271 right limb is longer, but the left limb is greater in width. A high percentage of individuals  
272 displayed zero asymmetry for MTIII width (pony 26%, horse 19%, pooled group 22%)  
273 compared to the other traits. McGreevy and Rogers (2004) suggest that hind limbs  
274 demonstrate a more ambidextrous nature than the forelimbs; however Meij and Meij (1980)  
275 previously reported a strong left hind limb preference within the majority (83%) of their study  
276 group.

277

278 The propensity for NDA of the tarsal width did not follow the same PDA trend  
279 observed for the widths of the previous limb traits. In humans suffering from limb length  
280 discrepancies, compensation mechanisms are observed within the knee and the ankle joints of  
281 the longer limb (Walsh et al., 2000). Whether similar compensation mechanisms exist within  
282 the tarsal and carpal joint of the horse, resulting in osteophytic changes within the joints of the

283 longer limb, is an area devoid of research; future investigation could give insight into the  
284 effect of limb length discrepancies on the degeneration of the equine tarsal joint.

285

286 In other species, reduced heterozygosity has been linked to developmental instability  
287 and an increase in bilateral trait asymmetry (Babbitt, 2006; Fessehaye et al., 2007). A  
288 reduction in the heterozygosity of the Thoroughbred population exists as a result of modern  
289 breeding strategies; thus symmetry of this breed should be reduced, as has been demonstrated  
290 in previous equine asymmetry research (Watson et al, 2003; Davies and Watson, 2005; Pearce  
291 et al, 2005). These studies have been undertaken mainly in racing Thoroughbreds, where  
292 authors have concluded that asymmetry results from adaptive stresses or as a consequence of  
293 breeding strategies (Watson et al, 2003; Pearce et al, 2005); as such, they are brought in to  
294 question by the current results which are from a population with higher heterozygosity and  
295 which should therefore, in theory, show lower asymmetry across the population.

296

## 297 **Conclusions**

298 The current findings suggest that the horse is naturally subject to a degree of DA.  
299 Further stress related asymmetry may occur in addition to, but not instead of, this naturally  
300 occurring asymmetry. It is not possible from this investigation to identify whether this  
301 asymmetry is genetically influenced, but these results support the suggestion that  
302 lateralisation is determined in utero. The bilateral traits within this study demonstrated  
303 persuasive evidence that the right side traits are generally longer, while left side traits are  
304 wider. The naturally occurring DA in this study may help to explain why many horses are  
305 reported to have an asymmetry of movement, or functional asymmetry. Regardless of the  
306 cause or the potential underlying characteristics, the findings from the current study suggest  
307 that, for horses and ponies, DA may be the optimum for certain traits, rather than the

308 presumed optimum of symmetry. A laterality preference, rather than a training influenced  
309 directionality could be influential in physical asymmetry.

310

### 311 **Conflict of interest statement**

312 The author of this paper does not have a financial or personal relationship with other  
313 people or organisations that could inappropriately influence or bias the content of the paper.

314

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448 **Table 1**

449 Bilateral traits measured including description.

450

Trait	Description
Third metacarpal length (MCIII) and third metatarsal length (MTIII)	Measured laterally from the 'V' formed by the overlap of the annular ligament over the superficial digital flexor tendon at the distal portion of the limb, to the protrusion of the fourth metacarpal/ metatarsal at the proximal region of the distal limb
Third metacarpal width (MCIII) and third metatarsal width (MTIII)	Measured on the horizontal axis half way between the carpometacarpal /tarsometatarsal joint and the metacarpophalangeal /metatarsophalangeal joints
Fore proximal phalanx length (FPP) and hind proximal phalanx length (HPP)	Measured laterally from the protuberance of the lateral cartilage of the distal phalanx to the lateral protrusion made by the proximal condyle of the proximal phalanx
Fore proximal phalanx width (FPP) and hind proximal phalanx width (HPP)	Measured horizontally at the narrowest point of the phalanx
Carpal joint width	Measured horizontally from the medial to the lateral aspects of the intercarpal joint
Carpal joint depth	Measured laterally from the dorsal aspect of the intermediate carpal bone to the palmer aspect of the accessory carpal bone
Tarsal joint width	Measured horizontally from the medial to the lateral aspects of the tarsocrural joint
Pinna length	Measured from the point at the summit of the pinna to the inverted point at the base of the pinna
Pinna width	Measured from the medial to the lateral aspect of the pinna at the midpoint of its length.
Nostril length	Measured from the top of the fold on the medial aspect of the nostril to the lowest point of the nostril
Nostril widths	The width of the nostrils was measured horizontally from the alar fold on the medial aspect to reduce the impact of nasal flaring, to the lateral border of the nostril

451

452

453 **Table 2**

454 Distribution of facial trait directional asymmetries as absolute numbers and percentage  
 455 values; the larger values and therefore the directional asymmetry is highlighted in bold with *P*  
 456 values to illustrate levels of significance.

	Ponies (%)			Horses (%)			Pooled (%)		
	Left larger	Right larger	No asymmetry	Left larger	Right larger	No asymmetry	Left larger	Right larger	No asymmetry
Pinna length	<b>53</b>	33	15	45	<b>49</b>	6	<b>48</b>	42	10
Pinna width	<b>65*</b>	28	8	<b>51</b>	37	12	<b>57*</b>	33	10
Nostril length	45	<b>48</b>	8	<b>55</b>	36	9	<b>51</b>	41	8
Nostril width	<b>51</b>	39	10	<b>50</b>	38	13	<b>51</b>	38	11
FPP length	<b>26</b>	16	1	<b>70***</b>	23	7	<b>66***</b>	29	5
FPP width	<b>22</b>	14	7	<b>53</b>	33	14	<b>52*</b>	33	15
MCIII length	10	<b>30***</b>	3	25	<b>68***</b>	7	24	<b>69***</b>	7
MCIII width	<b>15</b>	12	16	40	<b>42</b>	18	<b>38</b>	36	26
Carpal width	7	<b>27***</b>	9	39	<b>47</b>	14	29	<b>54**</b>	17
Carpal depth	17	<b>21</b>	5	46	<b>49</b>	6	43	<b>49</b>	8
HPP length	18	<b>23</b>	2	48	<b>50</b>	2	45	<b>52</b>	3
HPP width	<b>23</b>	14	6	<b>47</b>	40	13	<b>50</b>	37	13
MTIII length	12	<b>31**</b>	0	41	<b>57</b>	2	35	<b>64**</b>	1
MTIII width	<b>20</b>	10	13	<b>49</b>	33	18	<b>48*</b>	29	23
Tarsal width	8	<b>30***</b>	5	42	<b>46</b>	13	31	<b>55**</b>	12

457

458 One-way  $\chi^2$  analysis using Yates correction (df. 1)

459 FPP, fore proximal phalanx; HPP, hind proximal phalanx; MCIII, metacarpal III; MTIII, metatarsal III.

460 \* $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ 

461

462 **Figure legends**

463

464 Fig. 1. Asymmetry means including standard deviations for the non-functional (facial) traits  
465 of the pooled, horse and pony groupings for both the positive and negative directional  
466 asymmetry categories.

467

468 Fig. 2. Asymmetry means including standard deviation for the functional (limb) traits of the  
469 pooled, horse and pony groupings for both the positive and negative directional asymmetry  
470 categories. FPP, fore proximal phalanx; HPP, hind proximal phalanx; MCIII, metacarpal III;  
471 MTIII, metatarsal III.