Niche partitioning in late Miocene/early Pliocene hyenas from 'E' Quarry, Langebaanweg, South Africa.

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The late Miocene/early Pliocene 'E' quarry deposits at Langebaanweg, South Africa (Fig. 1), have yielded fossil material of at least four hyena species (*Ikelohyaena abronia*, *Hyaenictitherium namaquensis*, *Chasmaporthetes australis*, *Hyaenictis hendeyi*). The co-occurrence of four closely-related hyaenids at Langebaanweg raises interesting questions about niche partitioning which have not been sufficiently addressed in previous research.

Extant bone-cracking hyenas exhibit a close correspondence between molar and premolar crown morphologies and feeding ecology (Van Valkenburg et al., 2003). In this project, premolar and molar crown form (occlusal view) was examined in the four recognized 'E' Quarry hyena species with the aim of shedding light on their dietary niches. Geometric morphometric techniques were used to quantify crown form (shape+size) of unworn or minimally worn P2s, P3s, P4s and M1s. A dental sample from two extant hyenas (*C. crocuta* and *P. brunnea*) was also included in the analysis for comparative purposes.

Crown form was digitized from digital dental images using TpsDig software (Rohlf, 1998). The landmarks chosen consisted of landmarks on the occlusal surfaces of each tooth type (biologically corresponding among specimens) and semilandmarks which tracked the crown outlines. Those on the occlusal surfaces were positioned at the bases of cusps and were thus not affected by tooth wear (Fig. 2). These varied in number from one (P2, P3) to two (P4, M1). Semilandmarks were used to track the crown outlines (Fig. 2). For all tooth types, crown form was represented by 32 sliding semilandmarks. The number of landmarks placed on each tooth thus varied between 33 (P2, P3) and 34 (P4, M1). The digitized landmarks were analyzed using thin-plate splines (TPS) (Bookstein, 1989, 1991).

Notwithstanding many similarities in feeding ecology, results indicate that the two extant bone-cracking hyenas, *C. crocuta* and *P. brunnea*, are easily separated on the basis of premolar and molar crown shape. In contrast, the 'E' Quarry hyenas display very little inter-specific variation in crown shape. In terms of P3 and P2 shape (Figs. 3 and 4), no strong inter-specific differences stand out. Minor intra-specific differences are present in the case of P4 and M1 shape. *C. australis* and *H. hendeyi* P4s and M1s (Figs. 5 and 6) tend to be slightly narrower than those of *I. abronia* and *H. namaquensis*.

The lack of any strong inter-specific differences in the shape of cheek tooth crowns, suggest that the four Langebaanweg hyena species were probably very similar in terms of their dietary requirements. The manner in which they may have avoided competition becomes clearer when one considers crown size. Results indicate that the four species exhibit even spacing of median crown size measures in three of the four studied teeth (M1, P3 and P2) (Fig. 7).

Research on modern animal communities suggests that when closely-related species are sympatric, they often exhibit selection for reduced similarity in morphological characters which place them in direct competition with one another (Lewin, 1983; Dayan et al., 1989, 1990, 1992). Since feeding niches are primarily involved, cranio-dental characters, which are closely-related to feeding ecology, are most likely to be affected. When competition driven morphological shifts occur in closely-related sympatric species, they are normally of such a nature, that they facilitate arrangement of the affected species along resource parameters. This reduces overlap in resource exploitation and thus inter-specific competition (MacArthur, 1972). Brown and Wilson (1956) termed this process of reduced morphological similarity, "character displacement". The results from this study suggest that size-related and not shape-related competitive character displacement probably played a role in reducing dietary competition between the 'E' Quarry hyenas. Crown size, particularly with regards to the premolars, would have determined the size and strength of bones that a particular hyena species would be capable of consuming. This would not only have allowed for the partitioning of prey species according to overall size, but would also have allowed for the partitioning of carcasses of large animals according to bone size and strength. Future work will use the microwear technique to further inform on patterns of niche partitioning in the Langebaanweg hyaenids.

Figures

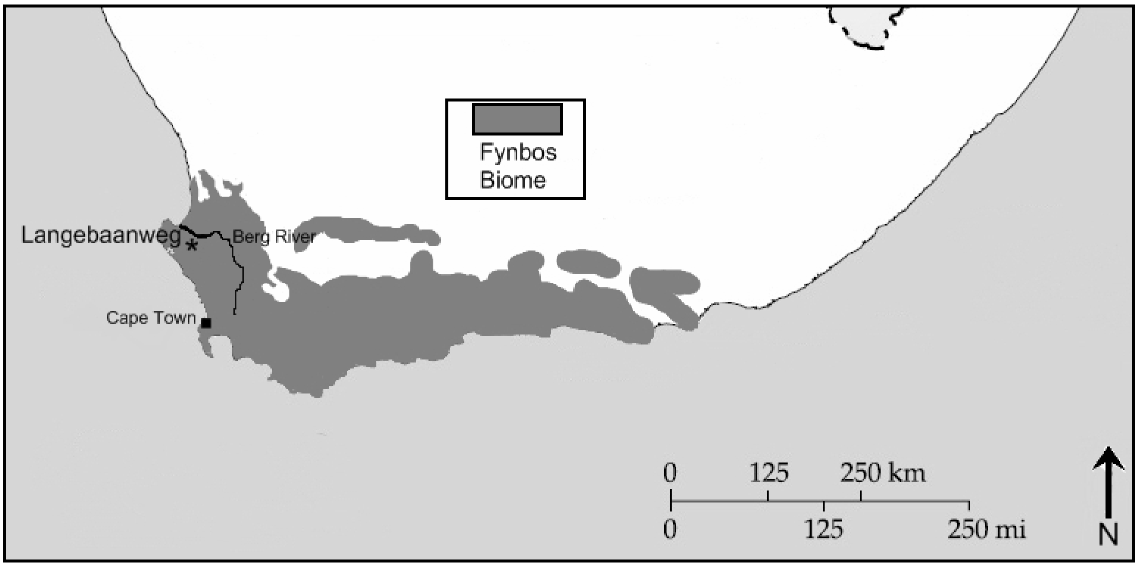

Figure 1: The location of Langebaanweg and the current path of the Berg River.

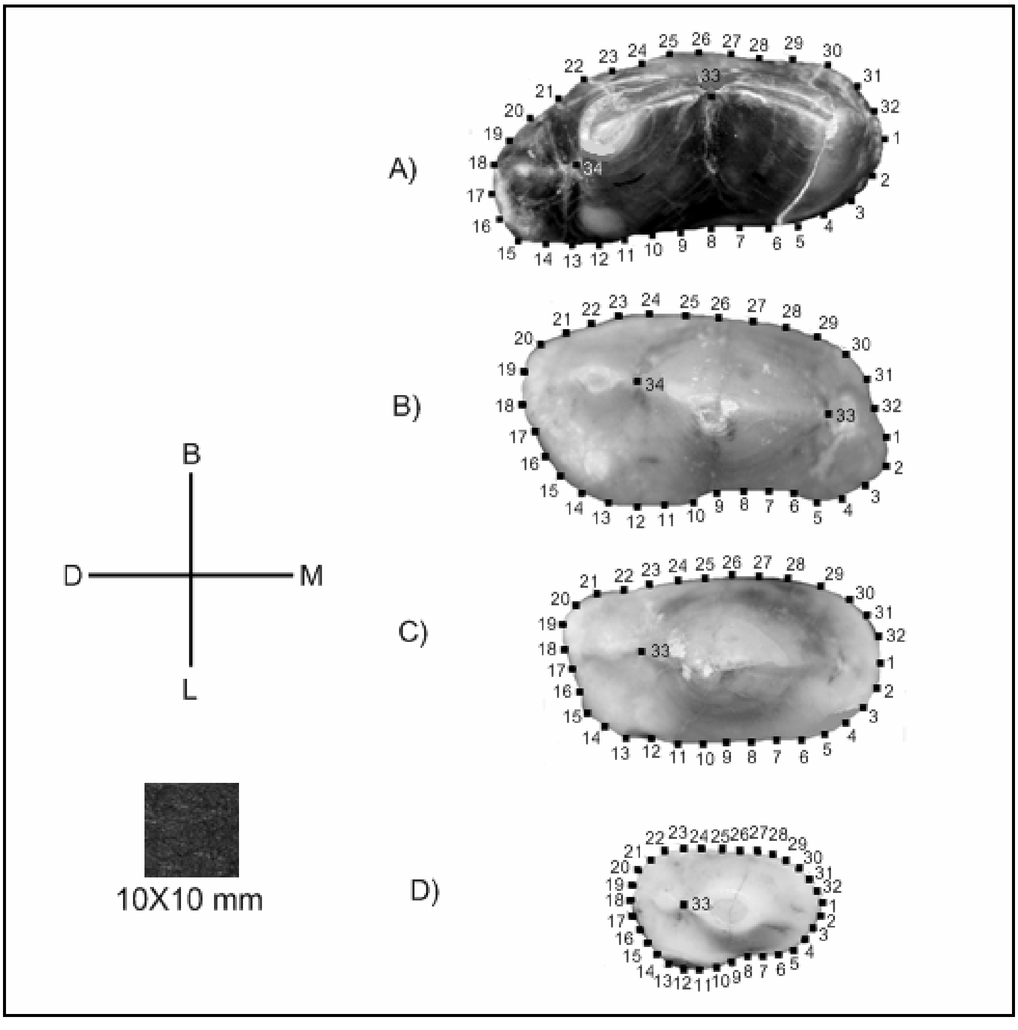

Figure 2: The locations of landmarks and semilandmarks recorded on each of the four teeth under investigation. A) M1, B) P4, C) P3, D) P2. B = buccal, L = lingual, M = mesial, D = distal.

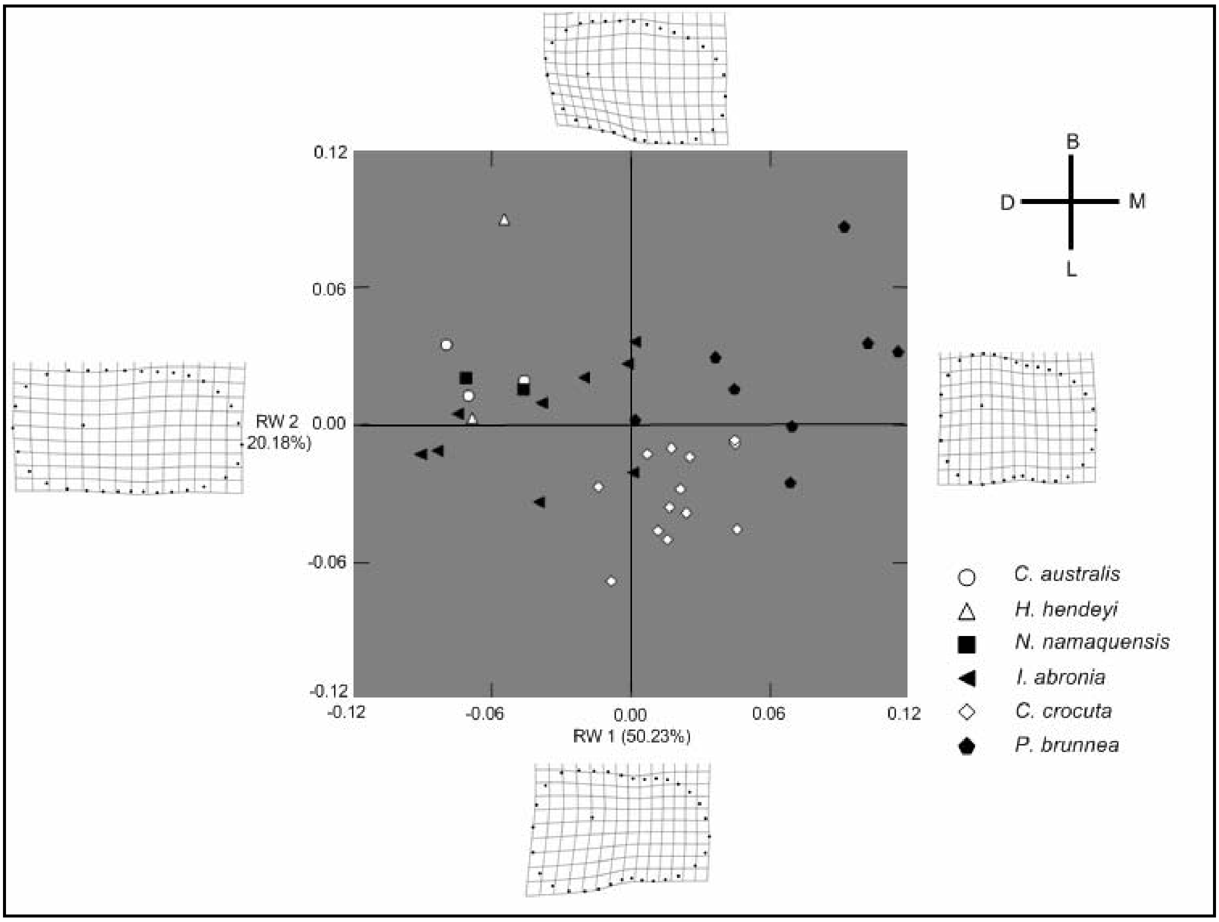

Figure 3: Plot of RW1 and RW2 of a relative warp analysis of the P2. Changes in shape at the negative and positive extremes of the RW1 and RW2 axes are illustrated as thin-plate splines. B = buccal, L = lingual, M = mesial, D = distal.

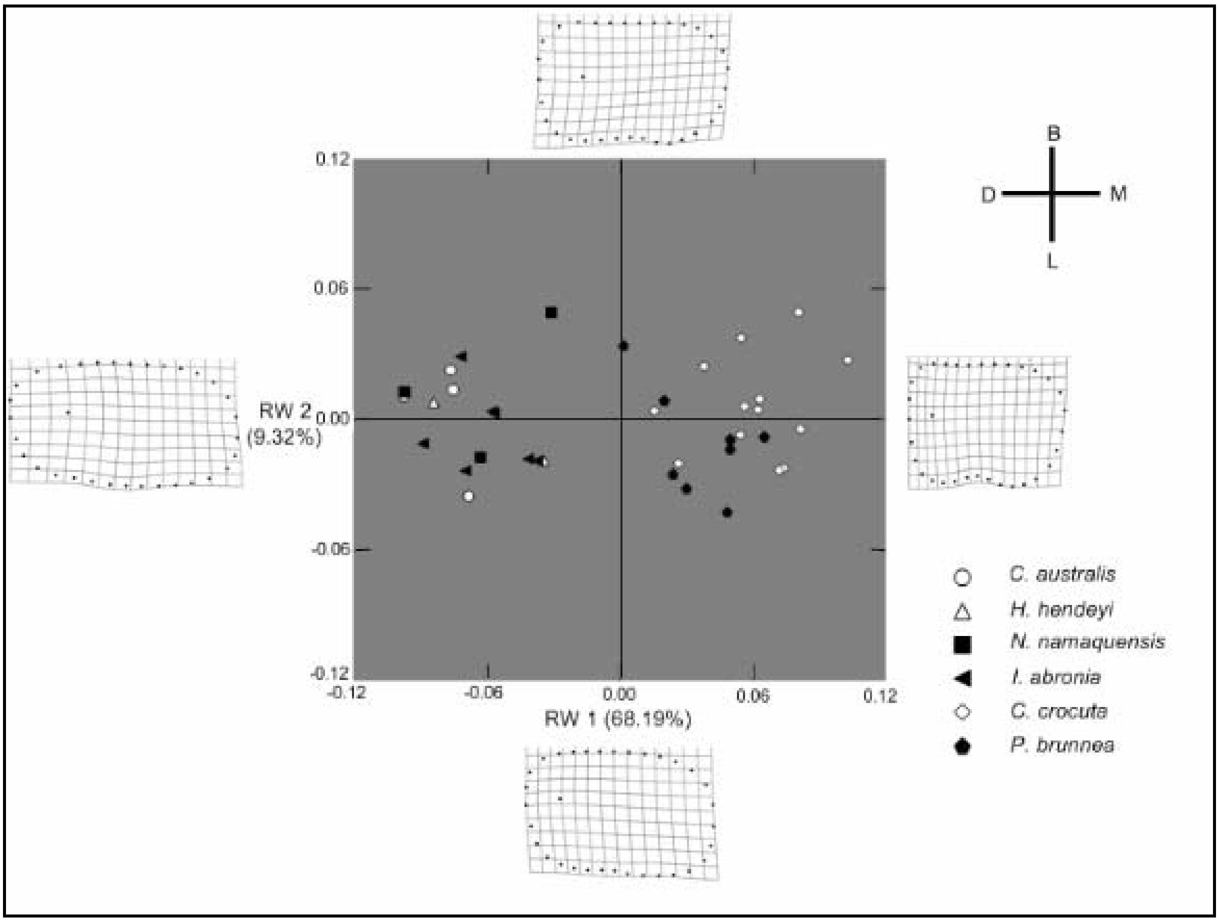

Figure 4: Plot of RW1 and RW2 of a relative warp analysis of the P3. Changes in shape at the negative and positive extremes of the RW1 and RW2 axes are illustrated as thin-plate splines. B = buccal, L = lingual, M = mesial, D = distal.

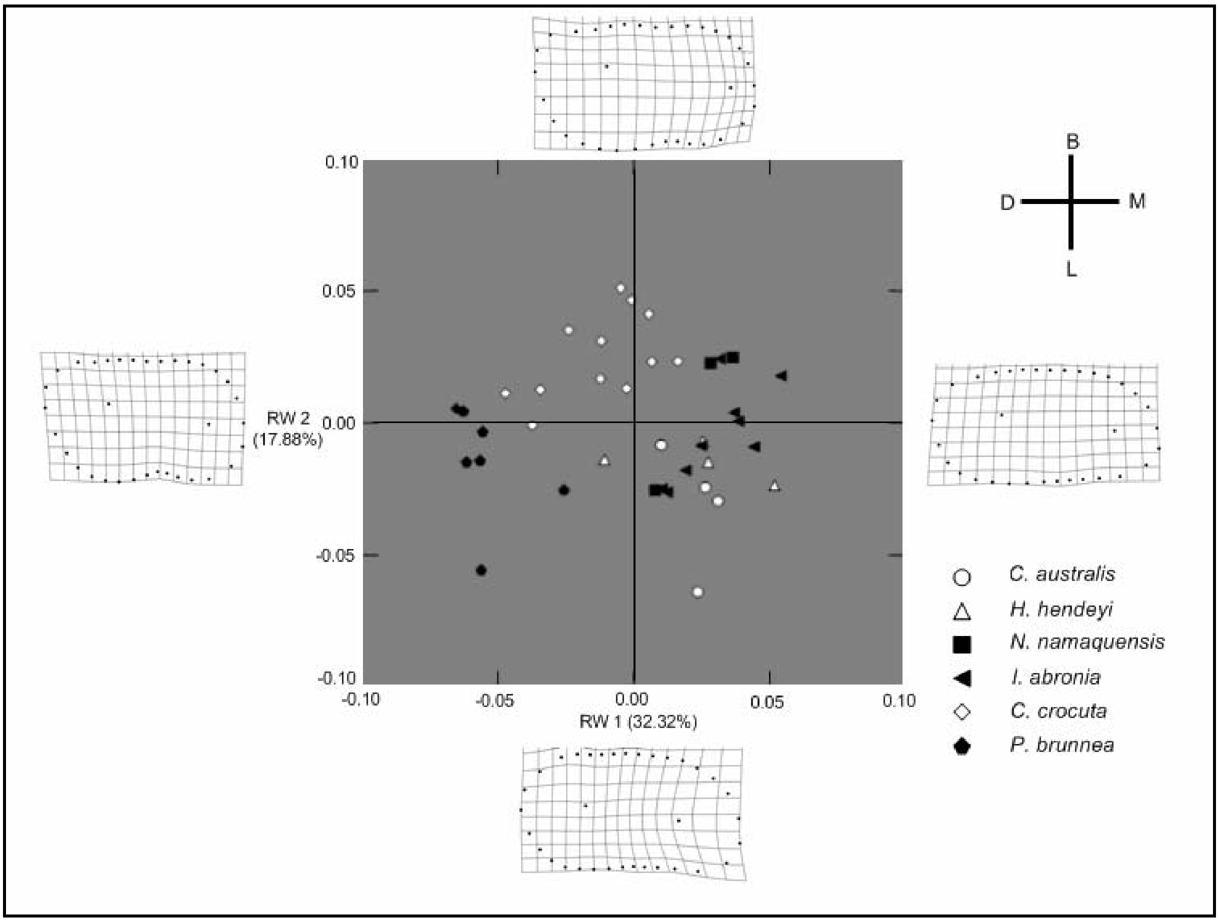

Figure 5: Plot of RW1 and RW2 of a relative warp analysis of the P4. Changes in shape at the negative and positive extremes of the RW1 and RW2 axes are illustrated as thin-plate splines. B = buccal, L = lingual, M = mesial, D = distal.

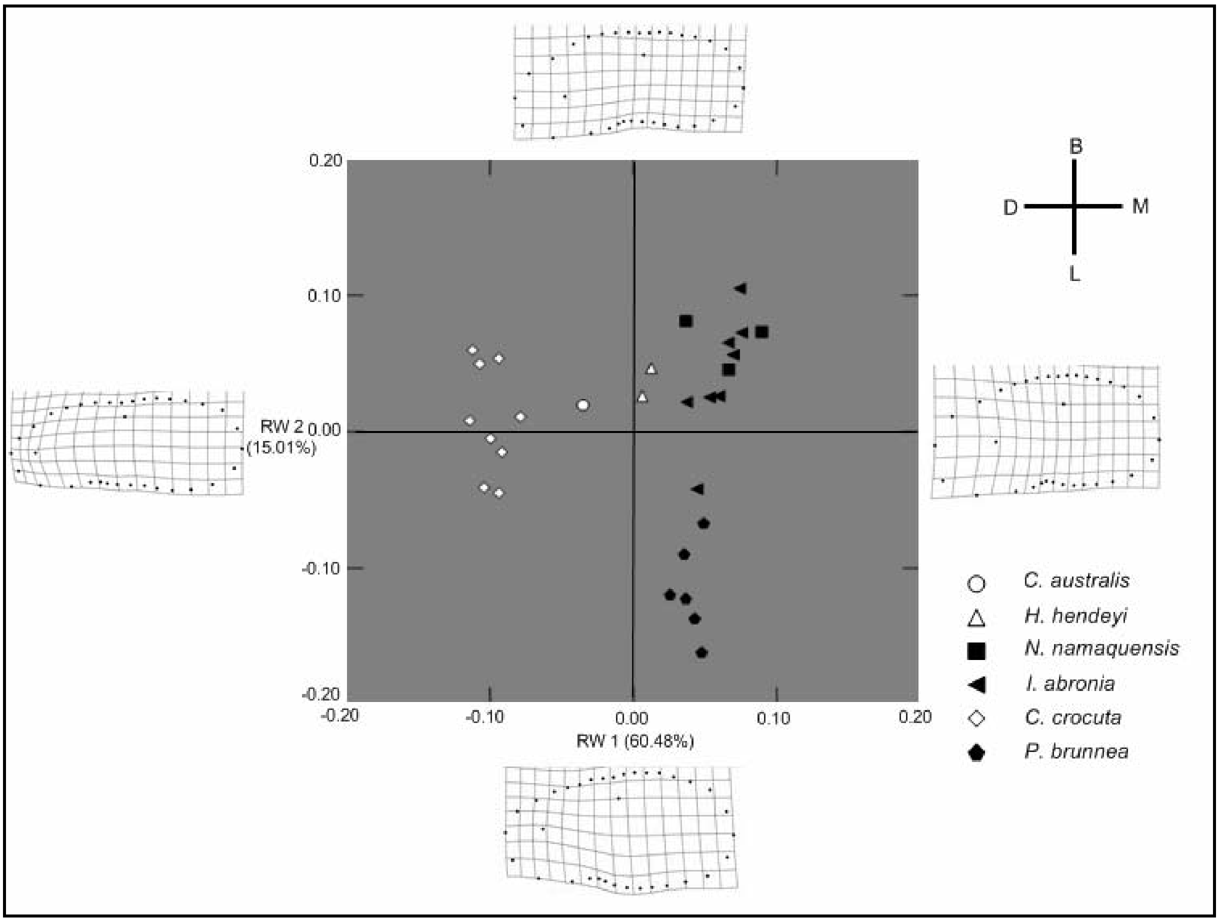

Figure 6: Plot of RW1 and RW2 of a relative warp analysis of the M1. Changes in shape at the negative and positive extremes of the RW1 and RW2 axes are illustrated as thin-plate splines. B = buccal, L = lingual, M = mesial, D = distal.

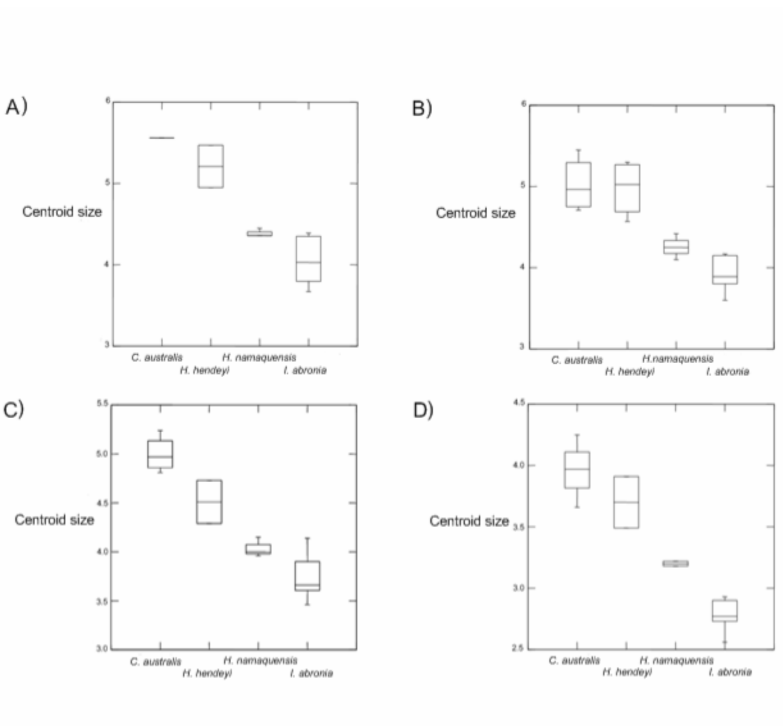

Figure 7: Box plots summarizing variation in dental crown centroid size among the four 'E' Quarry hyenas. The graphs represent the following teeth: A) M1, B) P4, C) P3 and D) P2. The vertical line in the centre of the box marks the median of the sample. The length of each box represents the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The whiskers extend to the highest and lowest values of the interquartile range.

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