A networked approach to the analysis of integration and modularity in the primate shoulder and thoracic skeleton

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Method 1: Networks
- All anatomical connections are quantified between bones of interest.
- Here I demonstrate the technique with 2 approaches-1 where all bony articulations are calculated, and 1 where muscular and tendinous connections are calculated.
- Modularity of the resulting network is then calculated and visualised using the package igraph in R.
- Each colour represents an anatomical module (where connections between bones in the module are more dense than those outside the module)
  - Left = Homo sapiens bony network
  - Right = Pan troglodytes bony network
  - A more user friendly display is as a false colour rendered skeleton (below).

Method 2: GMM
- 3d coordinate data for all elements in the network was obtained from CT scans from a modern patient sample (NCIA) and primate sample (KUPRI)
- All individuals were registered to a target mesh in Geomagic.
- Bony shape was quantified through a series of type 1.2, & 3 landmarks using Landmark and Geomagic.
- Landmark dataset of 905 landmarks per individual on the left hand side.
- Semilandmarks were slid and the subsequent dataset was subjected to Procrustes superposition and PCA in R using the packages Morpho and Geomorph.
- The RV coefficient, EMMLI and covariance ratio were used to analyse modularity in the thoracic skeleton, following the modules predicted by network analysis. For brevity, only results from the covariance ratio are shown below.

Applied to:

<table>
<thead>
<tr>
<th>Homo sapiens</th>
<th>Pan troglodytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bone</td>
<td>Bone</td>
</tr>
<tr>
<td>Muscle</td>
<td>Muscle</td>
</tr>
</tbody>
</table>

GMM
- CR = 0.9156 at p = 0.001
- CR = 0.8861 at p = 0.002
- CR = 0.55 at p = 0.001
- CR = 0.73 at p = 0.001

Applied to fossil hominin reconstructions

- Homo erectus
- Au. afarensis
- Au. sediba

- Homo like
- Homo like?
- Pan like?

Discussion
- H. erectus appears more like Homo in morphology, so would be expected to follow the same patterns of modularity.
- Au. afarensis is part way between, but thorax is more like Homo in morphology.
- Au. sediba is part way between but thorax is more like Pan in morphology.
- As both Afarensis and Sediba are proposed to be partially arboreal, this is a novel result, but costal remains are more fragmentary at present for Sediba. All are subject to the vagaries of preservation/reconstruction!

Conclusions
- Combining Network analysis and GMM is a fruitful way of exploring modularity of structures based upon real anatomical data
- It can help us to ‘put flesh on to bones’ on fossil hominin reconstructions.
- Pan and Homo have very different results, and further work is needed on other hominoids.