

# Pattern formation

## Instabilities in sand ripples

Sand ripples are seen below shallow wavy water and are formed whenever water oscillates over a bed of sand. Here we analyse the instabilities that can upset this perfect patterning when the ripples are subjected to large changes in driving amplitude or frequency, causing them to deform both parallel and transverse to their crests. Our results reveal new pattern-forming instabilities in granular matter exposed to fluid flow with strong vorticity.

The formation of normal ripple patterns is driven by the 'separation zones' (regions with reversed flow) created in the troughs between ripple crests<sup>1,2</sup>. The wavelength of the ripples is set by the size of these zones, which is roughly proportional to the amplitude of the fluid oscillations and is independent of the frequency<sup>3–5</sup>. For a typical driving of amplitude 2.8 cm and frequency 0.5 Hz, for example, a ripple pattern with wavelength close to 4.0 cm is formed.

To investigate ripple patterns, we placed a thick layer of sand (spherical glass beads of diameter 250–350  $\mu\text{m}$ ) on a 0.6 m  $\times$  1 m tray inside a large, closed, stationary water tank with a transparent top lid, and pulled the tray back and forth sinusoidally. We started with completely regular patterns formed by pressing down a mould in the flat bed and then running the system (for a

short time) with an amplitude 'commensurate' with the imprinted ripple wavelength.

We 'frustrated' these perfect patterns by suddenly changing the amplitude or frequency of the oscillations. When these changes are not too large, periodic ripple patterns are stable. For example, for a frequency of 0.67 Hz, ripples of wavelength 4.2 cm are stable for driving amplitudes between 2.4 and 3.4 cm. But when the driving amplitude or frequency is quenched beyond some threshold, three distinct short-wavelength instabilities occur.

First, if the driving amplitude is increased sufficiently, the ripple crests distort along and transverse to the original ripples, and the pattern of compressed and 'bulging' regions forms a checkerboard tilted by 45° (Fig. 1a). As the deformations grow, dislocations occur until finally a new periodic ripple pattern with a larger wavelength is formed. Second, if the transition is reversed by decreasing the amplitude sufficiently, the pattern 'doubles' through the generation of small ripples between each of the original ones (Fig. 1b). Here, the separation zones become so small that they do not reach the troughs between the ripples. After the doubling, the wavelength of the system is then too small and the final state is reached through a bulging instability. Third, if the driving frequency is increased sufficiently, the ripples become unstable to the formation of stationary 'pearls' in the troughs between the ripples, which again form a tilted pattern (Fig. 1c). Unlike bulging and

doubling, pearling saturates and disappears reversibly when the frequency is decreased.

Although our system superficially resembles other classic pattern-forming systems<sup>6</sup> such as Rayleigh–Bénard convection, the transition scenarios described here have not been seen before. We believe that the theory of these instabilities must start with the separation zones, which have the shape of cylindrical vortices along the ripple troughs. These might be prone to instabilities<sup>7</sup> like the Rayleigh–Plateau 'sausage' instability (which may lead to bulging), or the centrifugal instability that gives rise to Taylor vortices whose axes are transverse to the cylinder (which may lead to pearling).

**Jonas Lundbek Hansen\***†, **Martin van Hecke\***, **Anders Haaning\***, **Clive Ellegaard\***, **Ken Haste Andersen‡**, **Tomas Bohr§**, **Thomas Sams†**

\*Niels Bohr Institute, Blegdamsvej 17, 2100 Copenhagen, Denmark

†Danish Defense Research Establishment, Ryvangs allé 1, 2100 Copenhagen, Denmark

‡ISVA, Danish Technical University, 2800 Kgs, Lyngby, Denmark

§Physics Institute, Danish Technical University, 2800 Kgs, Lyngby, Denmark

e-mail: tbohr@nbi.dk

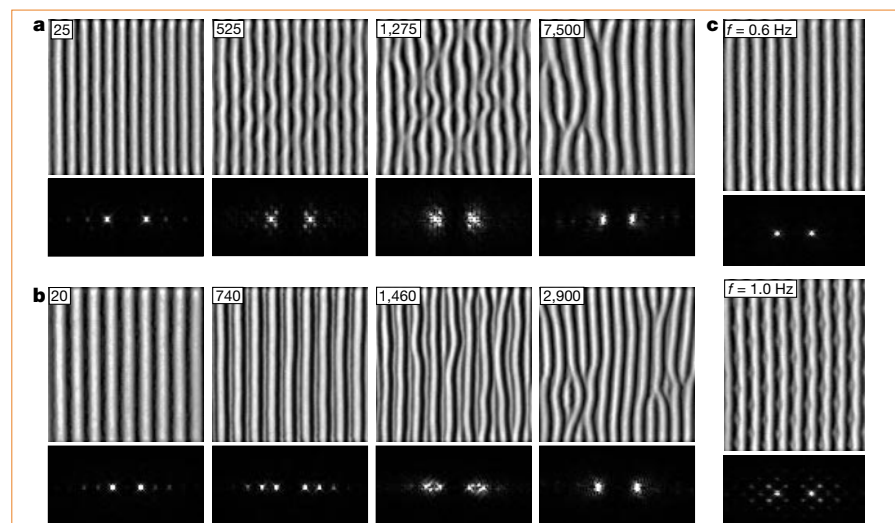
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## Palaeoanthropology

## Did our ancestors knuckle-walk?

All African apes walk on their knuckles. There is no evidence for this behaviour in the earliest hominids, however, which conflicts with molecular DNA evidence suggesting that chimpanzees are more closely related to humans than to gorillas. On the basis of a multivariate analysis of four traits of the proximal wrist joint, Richmond and Strait<sup>1</sup> claim that African apes and early hominids do share a common knuckle-walking ancestor. I propose that these traits are not uniquely associated with knuckle-walking and question the basis of their conclusion. It is still possible that no human ancestor knuckle-walked and that this behaviour evolved independently in different species.

Although such an ancestor would counter objections to an exclusive human–chimpanzee clade, it would not prove that knuckle-walking evolved only once in the ancestry of African apes and



**Figure 1** Patterns obtained by changing the driving parameters for a tray of sand oscillating in a water tank. **a, b**, Sequences of pictures from two experiments in which the amplitude of the drive was changed. The tray area in each is 53 cm  $\times$  53 cm; the light source was on the left and the sand tray was oscillated in the left–right direction; the camera was directly above the sand bed. Below each picture is shown the central region of the corresponding power spectrum,  $2.32 \text{ m}^{-1} \times 1.16 \text{ m}^{-1}$ . Numbers in the corners show the period at which the pictures were taken. For the top row (**a**), the initial wavelength was 4.2 cm, then the amplitude was 4.0 cm and the frequency 0.41 Hz. The power spectrum shows clear evidence of the bulging modulations mentioned in the text. For the bottom row (**b**), the imprinted wavelength was 5.6 cm, the driving amplitude was 2.8 cm and the frequency 0.68 Hz. The initial doubling is evident. **c**, The pearling transition and the corresponding power spectra in the range  $1.88 \text{ m}^{-1} \times 0.94 \text{ m}^{-1}$ . Each picture shows an area of 43 cm  $\times$  53 cm. The ripples have a wavelength of 4.2 cm; the driving amplitude was 2.8 cm; frequencies ( $f$ ) are indicated. Top, state well below the transition; bottom, fully developed pearling state. The pearls are new small ripples and not distortions of old ripples, because only the troughs and not the crests are deformed. Both states are stable at their respective driving parameters, so no period number is shown.

humans. Richmond and Strait<sup>1</sup> discount the possibility that knuckle-walking evolved independently in gorillas and in a common human–chimpanzee ancestor, an idea supported by the different ontogenetic development of gorilla and chimpanzee carpal load-bearing morphology<sup>2</sup> and by terrestrial orang-utans who normally walk on the dorsum of their fingers, albeit in a less efficient<sup>3</sup> fist-walking posture<sup>4,5</sup>, and occasionally knuckle-walk<sup>6,7</sup>. The entire great-ape lineage may thus be predisposed towards knuckle-walking when terrestrial quadrupedalism becomes a major selective factor<sup>6,7</sup>, undermining the claim that the four cited traits can resolve the phylogenetic relationships of chimpanzees, humans and gorillas<sup>1</sup>.

Richmond and Strait<sup>1</sup> assume that because some features of the present-day distal radius fulfil one of the mechanical requisites of African-ape knuckle-walking (limiting extension at the radiocarpal joint), then they must have arisen in response to the requirements of knuckle-walking. But it is debatable whether form, function and adaptive significance should be so linked within a modern evolutionary framework<sup>8,9</sup>. Claims for knuckle-walking adaptations in the wrist need careful evaluation as this behaviour describes a novel posture of the metacarpals and phalanges in relation to a substrate<sup>4,5</sup>. Digitigrade, semidigitigrade or fist-walking postures may make similar demands on the wrist joints to knuckle-walking<sup>4</sup> and so could also have given rise to stabilizing and extension-limiting mechanisms at the radiocarpal joint.

Extension-limiting structures allow contact between the hand and substrate to be maintained more efficiently when climbing large vertical supports<sup>4</sup> and so may have arisen in a climbing ancestor of humans and great apes<sup>10</sup>. From this perspective, Richmond and Strait<sup>1</sup> only demonstrate that behaviours requiring limited extension at the radiocarpal joint were important in hominid ancestry. Methodological considerations, however, suggest that the proposed extension-limiting mechanism of the distal radius may not have been suitably quantified.

A clearly delimited scaphoid notch is not always evident in the hominoid species included in the analysis<sup>1</sup>, so the measurements may not be replicable. It is unclear why the angle between the scaphoid and lunate facets of the radius may be significant in quantifying the extension-limiting mechanisms at this joint. This dimension should discriminate between African and Asian apes, with a narrower angle in the latter. The greater radio-ulnar curvature of the distal radial articulation in orang-utans and gibbons is atypical for anthropoid primates, and probably facilitates the rotary movement of the proximal carpal joint needed for forearm suspensory locomotion<sup>4,11</sup>. But it is not explained why increased rotary

movement should preclude an extension-limiting mechanism at the radiocarpal joint<sup>1</sup>. Part of the discrimination between African apes, Asian apes and hominids (their Fig. 2) may therefore reflect differences in suspensory behaviour and have nothing to do with knuckle-walking.

The first two canonical axes of Fig. 2b of ref. 1 do not separate the *A. afarensis* radii from orang-utans any more than from chimpanzees. The variables that strongly contribute to the remaining axis are not identified, so it is unclear why the Mahalanobis  $D^2$  distance is greater between orang-utans and *A. afarensis* than between chimpanzees and *A. afarensis* (their Fig. 2c, based on all canonical axes), a difference that bears on the conclusion that *A. afarensis* had a knuckle-walking ancestry.

Although hominids may have evolved from a knuckle-walker, I do not believe that Richmond and Strait's analysis<sup>1</sup> has proved this. I cannot, therefore, support related interpretations regarding the phylogenetic affinity<sup>1</sup> and locomotor mode<sup>12</sup> of early hominids, or of the chimpanzee-like characteristics of their immediate ancestor<sup>1</sup>.

#### Mike Dainton

Department of Human Anatomy and Cell Biology,  
New Medical School, University of Liverpool,  
Ashton Street, Liverpool L69 3GE, UK  
e-mail: mdainton@liverpool.ac.uk

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Richmond and Strait argue that evidence of ancestral knuckle-walking is retained in the distal radius of *Australopithecus*<sup>1</sup>, basing their conclusions on a canonical variate analysis that uses four measurements of the distal radial joint surface in higher primates. We dispute their claim that early hominids retained a specialized wrist morphology associated with knuckle-walking and question the biological and mechanical interpretations they use to attribute knuckle-walking features to the radius of *Australopithecus*.

The authors believe that in African apes there is a mechanism that 'locks' the wrist into place, which they base on their inference that the scaphoid conforms with a distally facing notch in the dorsal joint margin of the radius in full extension. They suggest that this 'locking mechanism' acts by limiting wrist extension and argue that it exists

because chimpanzees do not consistently recruit the major flexor muscles of the digits during knuckle-walking.

We question these conclusions on several grounds. First, very little motion occurs at the radioscapoid joint — Richmond and Strait's X-ray evidence shows that it takes place almost entirely at the midcarpal joint. All synovial joints conform throughout their range of motion, and would be expected to do so in full flexion. Most important, synovial joint stability derives from its muscles and ligaments<sup>2</sup>, not from its essentially frictionless joint surfaces: the primary role of joint-surface geometry is to assure that the joint reaction force remains orthogonal to rigid-body contact surfaces, and that velocity vectors remain tangential throughout the range of motion<sup>3</sup>.

Neither do normal joints lock. Locking would prevent motion and thus the performance of cartilage-sparing, negative work by the joint's soft-tissue envelope. Cartilage congruity maintains joint reaction force normality throughout the flexion–extension cycle, especially under high external loads. Neither peripheral nor edge loading occurs in normal, stable joints<sup>3</sup>. Further, neither the location nor direction of the joint reaction force can be determined from an X-ray image — comprehensive free-body analysis is required.

Finally, tendons and fascial sheaths are crucial to joint stability, particularly those of the long digital flexors<sup>4</sup>. An absence of electromyographic activity suggests that passive recruitment of the joint capsule and the muscle's connective-tissue envelope are all that is required for joint stability during light-to-moderate loading<sup>5</sup>, a possibility considered as likely in a study<sup>6</sup> cited by Richmond and Strait. It is unclear how other joints of the wrist and hand might be sustained (see the authors' Fig. 1b) during significant loading if no tendons are recruited.

This confusion extends to ontogeny. Details of surface conformity, as in Richmond and Strait's 'scaphoid notch', result from cartilage modelling (they cannot be determined by hereditary 'descriptive' specification<sup>7</sup>). Chondral modelling modulates the curvature, shape, congruence and smoothness of a joint's articular surface<sup>8</sup> and postnatal joint motion and joint reaction forces determine the final adult joint contours<sup>9,10</sup>. It is therefore unlikely that *Australopithecus* retained details of joint contours specific to knuckle-walking without performing that behaviour.

Richmond and Strait used four variables for their canonical variate analysis, of which two were the breadth and orientation of their 'scaphoid notch' — defined as the length of the portion along the dorsal margin of the distal radial articular facet that is bevelled. This 'notch' must be either a special morphological substructure of the joint