A fly in the biogeographic ointment

A tiny fossil provides a clue as to how things were in Antarctica millions of years ago.

the have discovered a fossil of a higher Antarctica, a finding that goes against the long-held belief that the continent was never inhabited by these insects¹. The fly must either have colonized Antarctica during a warm interval in the Neogene epoch, between 3 million and 17 million years ago, or it was an original member of the Gondwana fauna that survived in Antarctica for tens of millions of years before becoming extinct.

In a biogeographic study of the flies of New Zealand, Australia, southern South America and the sub-Antarctic islands², the great cladist Willy Hennig concluded that although more primitive flies might have inhabited the Mesozoic and Tertiary forests of Antarctica, there was no evidence that the higher flies had ever done so. His analysis suggested that the more derived clades of cyclorrhaphans had evolved on Laurasia after Pangaea had broken up. He postulated that the existing cyclorrhaphans of the southern continents had been derived from different northern stocks. No new evidence³ has been available until now to test his hypothesis.

The fossil has several features that enable us to identify it with confidence as a cyclorrhaphan puparium (Fig. 1). These include a single pair of round spiracles, an integument with circular patterning that reflects the way in which chitin was secreted, spines on the ventral welt (Fig. 1b) and the ecdysial scar from the second-instar stage of development. We estimate that the specimen is from a puparium that was about 5.0–7.5 mm in length. The characteristics of the fossil enable it to be assigned to one of the more highly derived clades (Schizophora) of the Cyclorrhapha, but we are unable to assign it to a family.

The fossil is from a siltstone collected by one of us (A.C.A.) from the Meyer Desert Formation, which outcrops on the margins of the Beardmore Glacier at latitude 85° S, about 500 km from the South Pole. A mid-Pliocene age⁴ has been assigned to the formation, although some consider an older minimum age of mid-Miocene more likely⁵. The siltstone was deposited on the margins of a glacier at the head of a wide fjord. The landscape was sufficiently stable to contain a lake, ice-free for long enough during the summers to support algae, freshwater molluscs⁶ and a species of fish. On the better-drained morainic soils, a shrub and herb tundra with cushion plants, Ranunculus (buttercups) and patches of dwarf Nothofagus (southern beech)7



Figure 1 Scanning electron micrographs of the Antarctic fly fossil puparium compared with a modern puparium. The puparium is the hardened integument of the 3rd (last) instar (maggot) from which the adult fly emerges. **a**, Posterior view of the fossil puparium, which is partly crushed and has silt grains embedded in the chitin. The posterior spiracles are indicated by the pair of white arrows. Scale bar, 0.5 mm. **b**, Enlarged view of a ventral cuticular welt on the fossil, showing the presence of spines. **c**, Posterior segment of a modern puparium of a blowfly (*Cochliomyia macellaria*; Fabricius: Calliphoridae). Spiracles are indicated by arrows. Scale bar, 0.5 mm. **d**, Drawing of a puparium to show the location (arrow) of the posterior spiracles in both the fossil (**a**) and a modern specimen (**c**).

was inhabited by listroderine weevils⁸ and other insects.

By the Neogene, Gondwana had fragmented and even the closest land in South America was separated from Antarctica by 1,000 km of ocean. Pollen analysis of cores from the Ross Sea indicates that an impoverished tundra vegetation existed in the Ross Sea area from the Oligocene to the Miocene, and possibly the Pliocene9. Nothofagus from the Meyer Desert Formation was probably a descendant from the early Cainozoic Gondwana forest, rather than a colonizer during the Neogene⁷. Climatic cooling and the formation of ice sheets, associated with either the opening of the Drake Passage and the formation of the Circumpolar Current between 34 million and 22 million years ago¹⁰ or a decline in atmospheric CO₂ levels¹¹, could ultimately be the cause of the extinction of most Antarctic terrestrial organisms.

In proposing that the Cyclorrhapha had never inhabited Antarctica, Hennig was astute enough to add the caveat "in the absence of a fossil record". The critical question now is whether the fossil was from a South American population that colonized Antarctica during an especially warm period during the Neogene or from a relict Gondwana population that had inhabited tundra coastal habitats for millions of vears in isolation in Antarctica. If betterpreserved fossils are found in Antarctica, a radical revision of the age and place of origin of the Cyclorrhapha might one day be necessary. Until then, dipterists need to re-examine the taxonomy of southern cyclorrhaphan fly taxa to see whether any trans-Antarctic relationships among the more derived clades have been overlooked. Allan C. Ashworth*, F. Christian Thompson† *Department of Geosciences, North Dakota State University, Fargo, North Dakota 58105-5517, USA e-mail: allan.ashworth@ndsu.nodak.edu †USDA Systematic Fntomology Laboratory, Smithsonian Institution, Washington DC 20560, USA

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Electronic paper

Flexible active-matrix electronic ink display

Utrathin, flexible electronic displays that look like print on paper are of great interest¹⁻⁴ for application in wearable computer screens, electronic newspapers and smart identity cards. Here we realize the fabrication of such a display on a bendable active-matrix-array sheet. The display is less than 0.3 mm thick, has high pixel density (160 pixels \times 240 pixels) and resolution (96 pixels per inch), and can be bent to a radius of curvature of 1.5 cm



Figure 1 Flexible active-matrix electronic-ink displays. **a**, Operating principle of electronic ink. The relative movement of negatively charged black and positively charged white particles inside their microcapsules is controlled by the direction of the applied voltage. **b**, A backplane thin-film transistor measured *in situ* under compressive stress. The transistor is bent to three different radii of curvature: green, 2.0 cm (0.19% strain); blue, 1.3 cm (0.29% strain); and red, 1.0 cm (0.38% strain). The thin-film transistor has identical characteristics when measured without bending (black curve) and at a radius of curvature of 2.0 cm; degradation is minimal even at 1.0 cm. Results were similar under tensile stress. **c**, Text image shown on a bent display whose resolution is 96 d.p.i. and which has a white-state reflectance of 43% and a contrast ratio of 8.5:1. Askin, R. A. & Raine, J. J. Terra Antartica 7, 493–501 (2000).
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without any degradation in contrast. This use of electronic ink technology on such an ultrathin, flexible substrate should greatly extend the range of display applications.

Thin (0.4-mm) but inflexible liquidcrystal displays have been made on plastic by using a diode-matrix array⁵ and an amorphous-silicon, thin-film transistor (TFT), active-matrix array⁶. To create a flexible display, we used a TFT array (backplane) with microencapsulated electrophoretic material (electronic ink)⁷, which consists of millions of microcapsules containing charged pigment particles in a clear fluid. A negative voltage applied to the top surface causes the positive white particles to move to the top of the capsule and the surface to appear white; reversing the electric field causes the negative black particles to appear at the top surface and create a dark spot (Fig. 1a).

We used a 75- μ m-thick steel-foil substrate to build the TFT backplane because steel foil is lightweight, mechanically stable and compatible with existing fabrication processes for active-matrix liquid-crystal displays^{8,9}. Before the array fabrication, an insulating layer was applied onto the foil to render the substrate passive. The amorphous-silicon TFTs were made in the bottomgate, back-channel etch configuration. The gate and source/drain metal were deposited by sputtering. A ductile composite of aluminium and refractory metal was used for the gate metal to enhance the backplane's flexibility.

Silicon nitride, amorphous silicon and a doped amorphous-silicon layer were deposited as the gate insulator, the channel and the contact layer, respectively, by plasmaenhanced chemical-vapour deposition. The metal, semiconductor and insulator layers were patterned by photolithography. The display was made by laminating a sheet of electronic ink onto the backplane. The electronic ink consists of a layer of electrophoretic microcapsules and a polymer binder, coated onto a polyester/indium-tin oxide (common electrode) sheet. The total display thickness is less than 0.3 mm.

A typical TFT has a threshold voltage of 4.0 volts and a linear mobility of $0.50 \text{ cm}^2 \text{ V}^{-1} \text{ s}^{-1}$. The drain off current is about 1.0 pA at 10 V drain voltage. The current on/off ratio is 5×10^6 , which is sufficient for high-resolution displays. The TFT performance does not degrade after first being bent for 120 seconds around a cylinder that is 2 mm in radius (1.9% strain) and then released.

We also measured TFTs in situ under compressive stress at three radii of curva-

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ture (Fig. 1b). Because steel has a large Young's modulus, our selection of a thin substrate decreases the distance of the TFT circuit from the display neutral plane¹⁰, reducing the in-plain strain of the circuit. As a result, the display can be repeatedly bent 20 times to a radius of curvature of 1.5 cm without any degradation.

Bias temperature stress on the TFT backplane was performed at a gate voltage of 25 V and up to 80 °C. The results indicate that the flexible backplane has a threshold voltage shift comparable to that of conventional glass TFT backplanes in laptop computers, and possibly a similar reliability and lifetime. The row electrode is driven between 0 and 24 V, and the column electrode is driven between 0 and 20 V.

Figure 1c shows the bent display of a text image of 96 d.p.i. resolution; the display has a viewing angle of almost 180°. The ink-switching speed is 250 ms, which is sufficient for electronic paper. For wearable computers, a reduction to 15 ms would be required for video-rate switching; in addition, the substrate thickness would need to be reduced for foldable displays. We suggest that electronic ink combined with flexible amorphous-silicon active-matrix back-planes will provide a viable pathway to 'e-paper' and wearable computer screens.

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Comparative genomics

Insecticide resistance in mosquito vectors

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Resistance to insecticides among mosquitoes that act as vectors for malaria (Anopheles gambiae) and West Nile virus (Culex pipiens) emerged more than 25 years ago in Africa, America and Europe; this resistance is frequently due to a loss of sensitivity of the insect's acetylcholinesterase enzyme to organophosphates and