

WHERE IT ALL BEGAN (NEARLY)



Julian Dow discusses Simon Maddrell's 1969 paper entitled: Secretion by the Malpighian tubules of *Rhodnius*. The movements of ions and water.

A copy of the paper can be obtained from <http://jeb.biologists.org/cgi/content/abstract/51/1/71>

It is a happy coincidence that this paper was selected for this volume, which celebrates the distinguished career of Simon Maddrell. This is by no means his most heavily cited paper, though it has attracted over 220 citations since its publication. Nor was it Maddrell's first publication on *Rhodnius* Malpighian tubules – for that we have to look back to 1963 (Maddrell, 1963). Nor was it the first publication on *Rhodnius* tubule physiology – that honour goes to the father of modern insect physiology, Sir Vincent Wigglesworth, who published a triple salvo in 1931 (Wigglesworth, 1931a; Wigglesworth, 1931b; Wigglesworth, 1931c) – also in *J. Exp. Biol.* What makes this particular paper worthy of a JEB classic is the breadth, comprehensiveness and experimental virtuosity which it displays in 29 pages.

Maddrell's earlier work had focused on the neurohormonal control of diuresis, and had convincingly shown the basic properties of release into the haemolymph (Maddrell, 1963). In this paper, based on his postdoc in Bill Harvey's lab at the University of Massachusetts, he turned his attention to the ionic basis of secretion using a battery of techniques which have since become the staple of insect transport physiologists, though I suspect few can do them all as

well today as they were done back then (Maddrell, 1969).

The paper's introduction makes a clear, compelling case for the blood-sucking insect *Rhodnius* as a suitable model for transport studies, citing the large size of the tubule, the high secretion rates required to clear the massive fluid intake associated with each blood meal, and the remarkable thousandfold stimulation of secretion by neurohormonal extracts. This can be seen as a friendly riposte to the work being done on *Calliphora* tubules at the same time by Berridge (Berridge and Oschman, 1969). Berridge's fly tubules were also productive models, but lacked the blood-sucker's extraordinary ability to ramp up their secretion. In particular, the composition of the *Rhodnius* tubule as a homogeneous epithelium of a single cell type was seen as an advantage. Maddrell started by showing that the whole of the upper length of the tubule was uniform in its secretory properties, so validating the use of any or all of the tissue. He did this by dividing the upper tubule into as many as six or eight pieces, and measuring secretion rates from as few as 12 cells at a time. I don't think this virtuosity has been matched since! He then went on to test the tubule in a range of 14 now-standard ion substitution salines and showed that, unlike that of most insects, the tubule could perform perfectly well without potassium, reflecting this species' sodium-rich blood-sucking lifestyle. Potassium could be transported well when present, but the tubule failed quickly without sodium. Surprisingly, the tubule also did a very good job of transporting ammonium, apparently through the same pathway as potassium, so providing valuable information on the nature of the potassium transport pathway. The impression was thus obtained that sodium and potassium were handled distinctly by the tubule, and that different species had differing preferences for the two ions.

Maddrell then rattled through the anions, showing that chloride was necessary for secretion, and that bromide made a fairly good job of replacing chloride. Although sodium and chloride were normally both absolutely required for secretion to take place, ammonium nitrate worked too! This is probably the only case where a transporting epithelium can be so comprehensively fooled. Over a phenomenal range of osmotic pressures, he showed that the upper tubule produced an iso-osmotic urine, although the secretion rate was extremely sensitive to the osmotic pressure of the bathing solution. This was followed by a survey of the effects of the major metabolic poisons and transport inhibitors of the day

(and indeed of this day). The metabolic inhibitors azide, cyanide and 2,4-dinitrophenol all knocked out fluid secretion, confirming that it was an active process, whereas acetazolamide and ouabain were apparently without effect, suggesting that carbonic anhydrase and the Na^+, K^+ -ATPase were not significant (though this view was later revised). Interestingly, copper ions were about the most toxic solute tried, though the target of inhibition was not clear.

There are further goodies buried in the paper; for example, this seems to be the first time that a peritracheal innervation of the tubule is described. Although the nerve endings in the tubule were loaded with neurosecretory vesicles, Maddrell showed by grinding up tubules and applying the extract to further tubules

in a secretion assay that these terminals did not contain appreciable diuretic activity. The neurosecretory terminals were thus probably doing something different.

In the current climate of only reading papers from the last couple of years, it's nice to take the opportunity to read such a classic again. The discussion went into some detail on the nature of the transport processes. The best view of the day was that there was an apical potassium pump; as several papers in this volume attest, we now know this to be an apical V-ATPase and a closely coupled exchanger. However, the overall paper remains a gem and helped to establish the field of insect osmoregulation.

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