Some brief notes on John Dugdale, ghost moths (Lepidoptera: Hepialidae), and radical biogeography

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Among the many research accomplishments of John Dugdale is his comprehensive revision of the New Zealand ghost moths (Hepialidae). This multi-year project provided a taxonomy for the family that included a much-needed classification of the pasture *Porina* moths, as well as describing nine new species of *Aoraia* and establishing the new genus *Heloxycanus.* The taxonomy was, complemented by detailed morphological description of adults and immature stages and extensive documentation of species biology (Dugdale 1994). This project remains one of the few major regional studies of Hepialidae, comparable only to that of Nielsen & Kristensen (1989) on the Australian *Fraus*, Nielsen & Robinson (1983) on southern South America Hepialidae, and most recently Simonsen's (2018) monograph on several Australian genera.

John's New Zealand ghost moth project nicely coincided with my decision in 1978 to study the ecological biology of the puriri moth, *Aenetus virescens* (Doubleday, 1843). This species was one of New Zealand's most prominent insects but much of its life cycle was then unknown. As there was very little foundational work on this species, or indeed most Hepialidae, I was to benefit greatly from the knowledge and insights that John kindly provided during my research project and also later as I became engaged in the broader questions of biogeography and evolution.

My initial research led to the discovery of a detritus and fungal-feeding stage for the early instars, which was received by John with great

enthusiasm as it provided a solution to a long-standing problem. He also provided corroboration of the larval morphology for identification purposes and also for morphological changes that occurred during transition to live plant hosts (Grehan 1981). In order to establish a comparative context for this larval feeding pattern I expanded my research scope to encompass the biology of ghost moths in general. This extended interest led me to participate in a field expedition to the Rock and Pillar Range in 1983 (**Fig. 1**). This was literally a ghost moth paradise for me. As we were driving along a ridge on a fine sunny afternoon my attention was drawn to what looked like bumblebees zipping rapidly over the tussock grasslands. I was told that these were the diurnal males of *Aoraia senex* searching for the flightless females on the ground. But my primary purpose was to examine the larval habits of the sphagnum bog species recently discovered by Brian Patrick (Grehan & Patrick 1984). John was already experienced with collecting this new and as yet unnamed species. He brought a portable florescent lamp and a pressure lantern which were placed before a collecting sheet on the edge of a sphagnum bog. Even though conditions were cool, perhaps around 5ºC, moths started to arrive soon after dark. By 11:30 pm over 50 specimens turned up! This, along with finding larvae within the sphagnum moss made for a very successful expedition.

As my thesis progressed, I began to broaden my interests to encompass ghost moth systematics and biogeography, which were then very poorly known beyond some general aspects of taxonomy and distribution. The latter subject was fast becoming a central research focus as I became aware of how animal and plant distribution patterns, in concert with phylogeny, could provide evidence about their biological and geographic evolution. This was a field fraught with controversy, and the idea that animal and plant geography was historically informative was widely and intensively opposed by almost all established researchers both within and beyond New Zealand. My involvement was influenced by the research efforts of entomologist Robin Craw and botanist Michael Heads under the heading

of ‘panbiogeography’. Positive reception to this approach was largely limited to a small group of student researchers. John Dugdale was one of only three established institution-based researchers to directly test the geographic method for their specialty group.

A symposium on panbiogeography was held in May 1988 at the National Museum (later Te Papa) which was open to participation by both supporters and critics (Matthews 1989). John presented an overview of the various external relationships in the New Zealand Lepidoptera and examined their biogeographic implications (Dugdale 1989). His acceptance of the panbiogeographic approach represented a major shift (as he acknowledged to me) to a viewpoint that, while broadly corroborated (Heads 2017), remains an anathema for many, some of whom called for a publication ban (Waters *et al*. 2013). This goes to show that science can sometimes be just as much about withholding knowledge as about its discovery! But John was never fazed by controversy, and what counted for him was the nature of the evidence as he noted in the introduction of his symposium paper:

“*It [panbiogeography] is also useful in that it helps us gauge whether or not a group is in a fit systematic state for biogeographic analysis. That is, it would direct our attention to land areas that, under other biogeographic modes, we might not otherwise have considered in our systematic analysis of a group. It makes us aware of possible solutions to seemingly paradoxical situations, such as the “paradox” in which some of our most “primitive” Lepidoptera (Hepialidae, Tortricidae) have close Australian, but not South American affinities, whereas our “more advanced” Lepidoptera (Geometridae, Noctuidae) have groups which have close American affinity but are not found in Australia*.”

John was also able to take a step back and look at the issues from different perspectives as he continued to provide me with insightful feedback to

avoid the landmines of perception, saying “I don't think you should shoot yourself in the foot in public, and I know from experience that people magnify the bad or poor points you make, never the good.” Following completion of my thesis in 1987 our communications became less frequent as I moved to the US and my hepialid interests were increasingly marginalized by other work priorities. Although we met up again all too briefly in early 2002 (**Fig. 2**) it was not until 2015 that I was again able to focus on ghost moth systematics and taxonomy, made possible by the collaboration of Carlos Mielke of Brazil. Again, John willingly provided important feedback and commentary on our efforts. In recognition of his help and his New Zealand studies we established the new genus *Dugdaleiella* Grehan & Mielke, 2019 for a group of ghost moths restricted to the high elevations of the northern Andes (**Fig. 3**).

In recent years John also acted as a formal reviewer of ghost moth taxonomic papers that were beginning to proliferate for the faunas of Australia, Central America and Southern America. This support was of immense value as there are so few specialists with a deep knowledge of ghost moth systematics and morphology. Although he withdrew as a reviewer earlier this year, he continued to give feedback on new developments, including incisive commentary on details of ghost moth morphology. These notes were invaluable for understanding potential similarities between various genera, as a higher-level classification of the family has remained elusive. Just two days before he passed away he expressed agreement with a new tectonic subduction model for the origin of the Pacific islands genus *Phassodes* and its phylogenetic relationship with the Australian genus *Abantiades* (**Fig. 4**) (Grehan & Mielke 2020). Even though our mutual engagement over ghost moths and biogeography was intermittent and mostly at great geographic distance, John’s kindness, generosity, and the time and effort he made for me was always greatly appreciated and will always be remembered with gratitude. The future of ghost moth research will never feel quite the same.

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Fig. 1. Searching for hepialids along a ridge line on the Rock and Pillar Range, Otago, 1983. Photo by John Grehan.

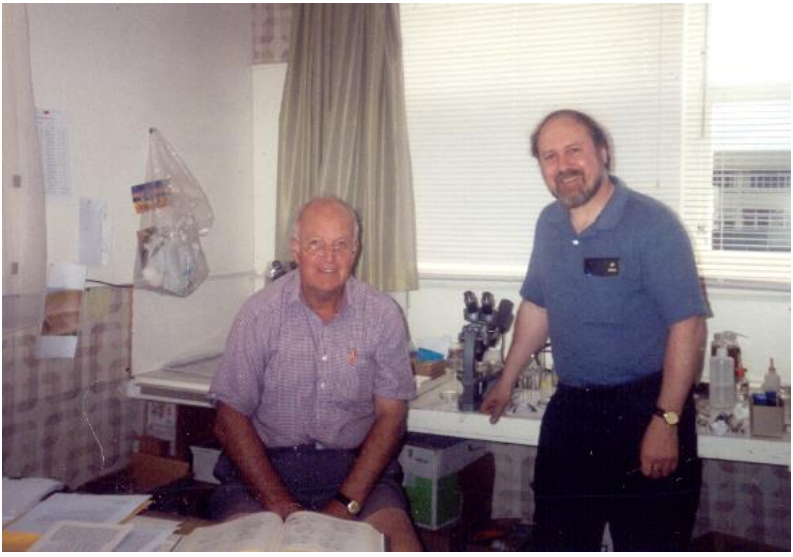

Fig. 2. John Dugdale (left) and John Grehan (right), Nelson, New Zealand, February 2002. Photo by Claudia Violette.

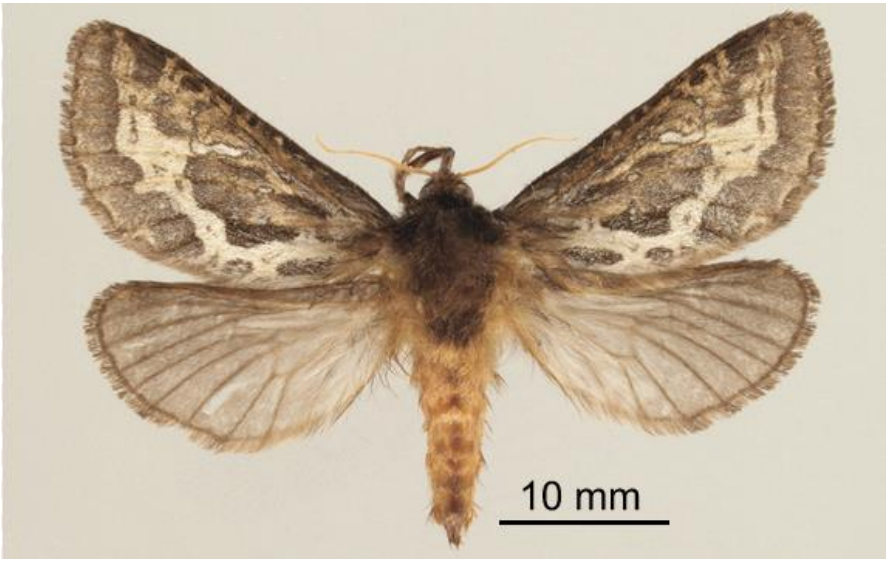

Fig. 3. *Dugdaleiella monticola*. Cotopaxi, Ecuador (Grehan & Mielke 2019). Photo by Jane Hyland.

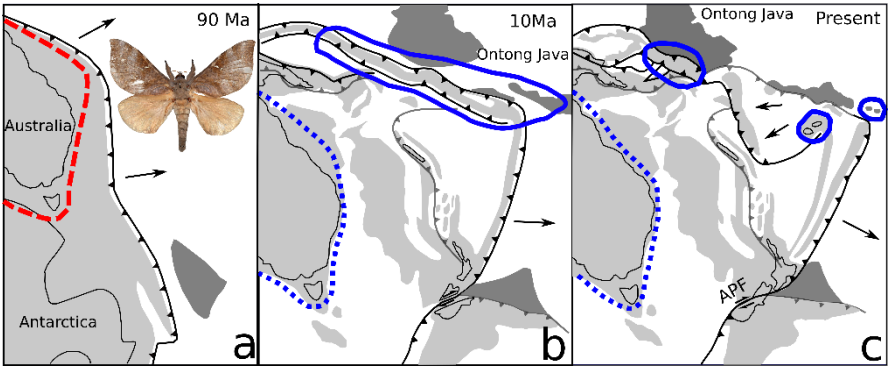

Fig. 4. Tectonic model for the divergence of *Phassodes* on oceanic islands (solid blue lines) and *Abantiades* on continental land (dashed lines) from common ancestor (red dashed line). See Grehan & Mielke (2020) for details.