

In memoriam: John S. Dugdale (5 Apr 1934–4 Sep 2020)

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John Dugdale, who died on 4th September 2020 aged 86, was a towering figure in New Zealand entomology for the last 60 years. He was a well-known and very frequently consulted expert on Lepidoptera, tachinid flies and cicadas, but his interests and knowledge extended far beyond these groups. He will always hold a unique place in the entomological history of this country and he also made significant contributions on the world stage; the breadth and depth of his expertise and the advances he made in our understanding of the New Zealand Lepidoptera fauna are unlikely to be equalled by any one person in future.

Born in Christchurch on 5th April 1934, John attended Christchurch Cathedral Grammar School and Canterbury University. John's interest in insects began at an early age. A holiday job at the Forest Research Institute (FRI) in Rotorua studying insects in forests east of Taupo became a full-time position, and he soon became a tireless and highly successful field entomologist. He built up an impressive collection for the FRI in the 1950s and 60s, not confined to forest insects. His major contribution, however, was to the New Zealand Arthropod Collection (NZAC), following his move to the DSIR in 1967. From that year onwards, on innumerable expeditions throughout the country, he gathered an immense amount of material. He did not confine his attentions to his favoured groups, but collected most insect orders. He collected from sea level to the alpine zone, and visited offshore islands including the Chathams, the Poor Knights and the Auckland Islands. Many of the remote localities he and his colleagues collected in have never since been visited by entomologists. The New Zealand drawers of the Lepidoptera collection in NZAC now contain about 105,000 specimens; those added by John have not been counted, but it is safe to assume that without him, the collection would be much less than half this size. Apart from collecting adult insects by day and by night, John reared many species, especially of Lepidoptera, and worked out the life histories and host-plant associations of a large number of taxa for the first time. This biological information is crucial for conservation and biosecurity. He took a particular interest in the early stages of Lepidoptera and preserved these to form a remarkable voucher collection, often linked to reared adults. He had a rare level of understanding of larval classification and identification, one of the most difficult branches of Lepidoptera study. During one of his visits to Canberra, where I was a PhD student, I can remember him identifying an Australian larva he had never seen before as a depressariid; extraordinarily, he did the identification in his head, without recourse to any written key. (He was right: rearing proved the larva to be *Eutorna eurygramma* Meyrick).

His regular Canberra sojourns point to another important aspect of John's persona as a lepidopterist: his enthusiasm for putting the New Zealand fauna in context by studying the diversity of the wider Australasian-Pacific region. Not only did he take New Zealand specimens to Canberra to compare the morphology of endemic forms with possible Australian counterparts; he also collected intensively in the Pacific region. He made productive expeditions to the Cook Islands, Tonga and Niue (all in 1975), Fiji (Viti Levu, Lakeba and Moce) in 1977, Vanuatu in 1983 (with K.J. Fox) and Western Samoa in 1994. He had an especial fondness for New Caledonia, an island he once described to me as "fluttering her eyelashes from across the Pacific Ocean", such was the allure of her entomological riches! He made extensive collections there in 1978, 1988 and 1990; these holdings, in the Pacific collection at NZAC, have been very little studied, and doubtless hold remarkable new taxa for future workers to discover. Although John published relatively few papers on 'exotic' Lepidoptera, his interest in the Australian and New Caledonian faunas did result in revisionary work specific to those countries (Dugdale 1980, 2005), and, having participated in the 1977 Royal Society expedition to Tonga and the Lau group, he contributed a scholarly account of Lepidoptera of Lakeba and Moce Islands, Fiji, to the subsequent report (Dugdale 1978). As ever, his extensive notes and correspondence in NZAC ensure that his knowledge of Pacific Lepidoptera has by no means been lost to the world. Friendships made overseas lasted a lifetime, and John is especially missed by his Canberra colleagues Marianne Horak and Ted Edwards.

Back in New Zealand, John's collecting and rearing revealed a level of diversity in the Lepidoptera unsuspected by earlier workers. It was through his desire to summarise that diversity and bring the classification of the fauna onto a modern footing that he achieved what is probably his landmark publication, the annotated catalogue of New Zealand Lepidoptera eventually published as *Fauna of New Zealand* volume 14 (Dugdale 1988). This work forms the springboard for all subsequent publications on the Lepidoptera of this country. A vital portion of the research on which it is based was carried out by John during a year-long 'sabbatical' in London in 1980–81, where he was able to study the New Zealand type specimens in the Natural History Museum, especially those of the many species described by Francis Walker and Edward Meyrick. By making copious notes and sketches, designating lectotypes and photographing all primary type specimens (see Dugdale 1983), John was able to resolve numerous taxonomic issues and clarify the identity of names that had confused earlier workers such as G.V. Hudson. The resulting catalogue is a model of its kind, full of additional notes and observations in support of the classification adopted. Not content with this, John also included a masterly key to Lepidoptera families, which shows his deep understanding of Lepidoptera morphology, by no means confined to the structures of mouthparts, genitalia and wing venation usually studied by taxonomists. The images of the type specimens later formed the basis of a highly useful online database, masterminded by Trevor Crosby and Dominic Thoreau: this, unfortunately, is no longer publicly accessible due to technological changes.

John's revisionary work as a taxonomist also encompassed more focussed studies relating to particular areas or taxa. An important, relatively early work was his review of the subantarctic Lepidoptera (Dugdale 1971a); in this substantial paper, he began the process of removing the 'northern hemisphere bias' from the classification of New Zealand Lepidoptera, i.e., the tendency of earlier workers to place New Zealand species in superficially similar European genera to which they are often not closely related. He thus began to reveal the true level of endemism of the fauna at genus as well as species level.

He had wide interests, and published on Geometridae (Dugdale 1961a, 1980), Tortricidae (Dugdale 1966a, b, 1990, 2005; Green and Dugdale 1982), and Plutellidae s.l. (Dugdale 1973,



Figure 1. John Dugdale on Mt Hikurangi, eastern North Island, 11 Oct 1964. (The trip was very cold and unproductive: beating produced more icicles than insects.)

1987a, 1996a), as well as several smaller families (Dugdale 1971c, 1979, 1987b, 1995). He was senior author on two chapters in the first volume on Lepidoptera in the Handbook of Zoology series: those covering the Yponomeutoidea (chapter 8: Dugdale et al. 1998a) and the smaller microlepidopteran-grade superfamilies (chapter 13: Dugdale et al. 1998b). There was also a major revision of the 30 species of New Zealand Hepialidae (Dugdale 1994), which contains his characteristically thorough treatment of early stages, and copious excellent line drawings. A notable aspect of his work during the 1990s was chemotaxonomy: he collaborated with

biochemists to elucidate the sex pheromones of various Tortricidae and Noctuidae of economic importance (Frérot et al. 1993), and used the insights to revise the taxonomy of the tortricid genera *Planotortrix* and *Ctenopseustis*. He thus revealed the existence of cryptic species-pairs that differ in female pheromone components but are barely distinguishable on morphology (Dugdale 1990). Though Tortricidae were perhaps his favourite group, much of his extensive knowledge remains unpublished: in the end, the prospect of doing justice to the diverse and complex New Zealand fauna undoubtedly became too burdensome for one with such a love of detail and thoroughness. However, in a 'Diagnostic Guide' published by The National Plant Pest Reference Laboratory (Dugdale et al. 2005), he shared many crucial insights relating to identification of the more readily encountered New Zealand taxa in this family. And for Tortricidae, as for all groups on which his interest had alighted, he left copious notes and drawings in NZAC, and these will remain a rich source of study for future workers for many years.

Three unique papers deserve special mention, as they show different and remarkable aspects of John's abilities. One is his early paper on Ennominae larvae (Dugdale 1961a). In this work, John set out to bring the level of understanding of larval structures of New Zealand geometrids up to the level of then recent work in the Nearctic region and India. Previous descriptions of New Zealand moth larvae (e.g., by Hudson 1928, 1939) had focussed largely on colour pattern, which can be variable and offers no clues to higher relationships. For this purpose, he examined in detail the



Figure 2. John Dugdale searching for larvae, Kaitorete Spit, Canterbury, South Island, August 1996.

structure of 30 species of geometrid larvae; notably, he did not confine his attentions to the final instars, but studied all instars where available. The paper is illustrated with John's characteristically superb line-drawings. It is rich with comparative details relating to larvae of other families of moths and displays a breadth and depth of scholarship exceptional for a 27-year-old entomologist.

The second is his paper on the female genitalia of Lepidoptera (Dugdale 1974). This classic work was based on very careful three-dimensional study of the delicate membranous parts of female moths often damaged, discarded or squashed in conventional taxonomic slide-mounts. For this publication, John examined over 40 insect species belonging to six insect orders, to place the Lepidoptera structures in a wider context. Unravelling the homologies of the various tubes, ducts and sac-like portions was a major and intricate task, even given that there were some previous publications to offer guidance. One of the remarkable insights to emerge from this study was the realisation of the unique morphology of the 'Exoporia', a primitive moth group that includes the swift moths Hepialidae and the superficially quite different endemic New Zealand family Mnesarchaeidae. These families, which had previously been placed in separate suborders of Lepidoptera, have been recognised as closely related ever since, and are now united in a single superfamily, Hepialoidea.

The third is his key to Lepidoptera larvae inhabiting leaf-litter in southern beech forests, based on studies in the Orongorongo Valley (Dugdale 1996b). Leaf-litter has a diverse associated moth fauna in New Zealand, and several species may often be reared from a single small collection. To isolate and associate the larvae with their correct adults, as well as observe their species-specific habits required considerable patience and ingenuity. John described his technique to me as follows: he would scatter the leaf-litter sample on newspaper in a tray, and leave this in an unlit room. After dark, he would re-enter the room stealthily and turn the light on, whereupon the startled caterpillars would reveal their whereabouts by the sudden movement of jerking back into their cases or shelters. In this way he was able to produce a unique illustrated guide to the caterpillars likely to form prey items for mice in the beech litter. He thus contributed an extraordinary insight into the complex interactions between native and exotic species that become especially significant in beech mast years, when rodent abundance has a knock-on effect on stoat numbers, which in turn, can severely reduce endemic bird populations.

One of John's great strengths was his insistence on integrating taxonomic studies into a much broader framework of functional morphology, biogeography, ecology and conservation. His extensive survey work and understanding of Lepidoptera ecology and life histories was greatly supplemented from the 1970s onwards by the similarly energetic efforts of Brian Patrick, who was based in Invercargill and later in Oamaru and Dunedin. It was natural that they should eventually put together their vast combined experience to collaborate on a review of the conservation status of the New Zealand Lepidoptera (Patrick and Dugdale 2000). This publication is a landmark, greatly exceeding in scope and depth any previous attempts at listing potentially threatened species of endemic butterflies and moths; all subsequent reviews have been based firmly on this one.

In retirement, John collaborated with me on two papers describing striking new endemic Lepidoptera genera overlooked by the earlier generations of entomologists. One of these was the 'kamahi scribbler' (*Xanadoses nielsenii* Hoare & Dugdale, 2003) (Cecidosidae), whose long sinuous bark-mines John had first encountered in the 1950s when working at FRI: it was 30 more years before the maker of the mines was finally reared (Hoare and Dugdale 2003). The other was 'Fred the Thread' (*Houdinia flexilissima* Hoare, Dugdale & Watts, 2006) (now Pterolonchidae),



Figure 3. John Dugdale (with a prize ornamental specimen) at his farewell party, Landcare Research, Mt Albert, Auckland, 30 Jun 1995.

whose larva was discovered by our co-author Corinne Watts. It mines in culms of *Sporadanthus ferrugineus* in the Waikato peatlands and is possibly the world's thinnest caterpillar (Hoare et al. 2006). In both cases, John provided superb illustrations and descriptions of the larval stage, and for *Xanadoses*, of the structural characters of the adult too. I believe that for him, as well as for me, these collaborations were a source of great joy and satisfaction.

John did not by any means confine his interests to Lepidoptera, and also became a noted expert on Cicadidae (Dugdale and Fleming 1969, 1978; Dugdale 1971b) as well as on the extremely challenging fly family Tachinidae (Dugdale 1961b, 1969). He could converse with great knowledge and insight about many other insect groups, especially phytophagous groups such as longhorn beetles and weevils, many of which he had reared during his time at FRI and subsequently. And, as noted above, he always sought to place the New Zealand fauna in a broader biogeographic context. When he failed to find close relatives of endemic taxa in his studies of Australian material in ANIC, he would turn his attention to South America, and borrowed comparative material from temperate Chile and Argentina in the hope of tracking down Gondwanan connections. All of this was before the days of DNA barcoding and global molecular phylogenies, but once these phylogenies started appearing, John took a voracious interest; if New Zealand or other taxa of significance had been omitted, he could be counted on to notice!

John's major contribution to his many areas of expertise was recognised in 2001, when he was elected a Fellow of the Entomological Society of New Zealand, a rare honour. He had been an active member of the society, attending many conferences and field trips, and served on the executive as librarian between 1988 and 1996. He is also remembered in the scientific epithets of a substantial number of invertebrates named after him, which are listed in Appendix 1. I am not aware of other awards or honours he received, and although John's deep knowledge and his generosity in sharing this were very widely appreciated, it would probably be fair to say that his exceptional lifelong service to his field did not earn him the full recognition he deserved.

In spite of the extraordinary energy and commitment he gave to entomology, John also found time to be a much-loved family man. One secret to his success, as described in family tributes at his funeral, was carrying a butterfly net on family outings to places of entomological interest... His beloved wife Kathy sadly died 13 years before him and her loss was deeply felt. An earlier loss that affected John keenly was that of Dr Ken Fox of Taranaki (1936–1986), a close friend and fellow lepidopterist, who had accompanied John on many a productive collecting trip (see Dugdale (1987c) for Ken's obituary).

John was an excellent, reliable and witty correspondent; his letters and e-mails are full of unusual insights and perspectives, and often exhibit a delightful and characteristic mildly grumpy stoicism. A typical example may be quoted from an e-mail he sent me in November 2019 when he was 85. He listed various Lepidoptera in ethanol that he was packing up to send to NZAC, finishing with the following item: "There is also a macerated male *Agathiphaga* but without a phallus. I felt a pang of sympathy." He remained extremely sharp and retained his huge knowledge to the end of his life.

John had begun a revision of the distinctive and spectacular endemic geometrid genus *Declana* in 1965 when at FRI, but though it reached an advanced stage it was never completed or published. Alan Emmerson (a fellow moth enthusiast and then a volunteer at NZAC) persuaded him to revive this manuscript in 2012, following recent new discoveries in this group of moths. With my additional encouragement, John agreed, and there followed a highly productive collaboration between John and Alan that lasted, with various interruptions and temporary setbacks, until his death. The manuscript is nearly complete, and I have undertaken, with Alan's help, to put the finishing touches to it and ensure its publication this time round. It should be a fitting swan-song, a revision of a remarkable group of New Zealand moths from a remarkable New Zealand entomologist. John will live on very long in our memories, and indefinitely in his vast contribution to New Zealand science.

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Appendix 1. Invertebrate genera and species named after John Dugdale

It is interesting to note that the first three species named after John were not insects, but one spider and members of two obscure groups of tiny soil-dwelling invertebrates: a pauropod (*Juxtapauropus dugdalei*) and a symphylan (*Hanseniella dugdalei*). All three were described in vol. 7 of the *Records of the Canterbury Museum*, published in 1956, when John was only 22 years old. John had collected specimens of the pauropod on 27th April 1952 at Fox's Creek, Canterbury (Remy 1956); the symphylans were from Taramakau, Westland, but no collection date is indicated in the original description (Adam and Burtel 1956). John had collected paratypes of the third species, the spider *Subantarctia dugdalei*, in Riccarton Bush, Christchurch, Canterbury in 1949 (with J. Haldane) and in 1952 (Forster 1956).

I have traced two genera and 41 species named in John's honour; one of these species has subsequently fallen into synonymy. The orders with the most '*dugdalei*' epithets are Coleoptera with seven and Araneae with six, reflecting John's extensive collecting efforts beyond the groups on which he focussed his research.

In the list below, orders are presented in alphabetical order and species are listed alphabetically within their respective orders. Names not currently regarded as valid are placed in square brackets. Subfamily placement is given only for members of highly diverse families. The type locality is in New Zealand unless otherwise stated.

Genera

Dugdalea Forster & Platnick, 1985 (Araneae: Orsolobidae) (type species: *D. oculata* Forster & Platnick, 1985)

Dugdaleiella Grehan & Mielke, 2018 (Lepidoptera: Hepialidae) (type species: *Triodia monticola* Maassen, 1890) [Ecuador]

Species

Tylenchida (phylum Nematoda)

Criconema dugdalei Wouts, 2006 (Criconematidae)

Pauropoda (phylum Arthropoda)

Juxtapauropus dugdalei (Remy, 1956) (Pauropodidae) (described in *Scleropauropus*)

Symphyla

Hanseniella dugdalei Adam & Burtel, 1956 (Scutigerebellidae)

Araneae

Marplesia dugdalei Forster & Wilton, 1973 (Amphinectidae)

Megafroneta dugdalei Blest & Vink, 2002 (Linyphiidae). [N.B. This name was published as *Megafroneta dugdaleae*, which is an incorrect original spelling according to Article 31.1.2 of the ICZN and must be emended as above under Article 32.5.1. It cannot be construed as an incorrect latinization under Article 32.5.1, since that would render Article 31.1.2 redundant.]

Orepukia dugdalei Forster & Wilton, 1973 (Cycloctenidae)

Subantarctia dugdalei Forster, 1956 (Oonopidae)

Toxopsiella dugdalei Forster, 1964 (Cycloctenidae)

Turretia dugdalei Forster & Platnick, 1985 (Orsolobidae)

Coleoptera

Asilis dugdalei Wittmer, 1979 (Cantharidae)

Chalepistes dugdalei (Barrett & Kuschel, 1996) (Curculionidae: Entiminae) (described in *Irenimus*)

Eupines dugdalei Shen & Leschen, 2020 (Staphylinidae: Pselaphinae)

Orchymontia dugdalei Ordish, 1984 (Hydraenidae)

Sagola dugdalei Park & Carlton, 2014 (Staphylinidae: Pselaphinae)

Sciacharis dugdalei Franz, 1980 (Staphylinidae: Scydmaeninae)

Stenosagola dugdalei Park & Carlton, 2013 (Staphylinidae: Pselaphinae)

Zorion dugdalei Schnitzler, 2005 (Cerambycidae)

Diptera

Anabarhynchus dugdalei Lyneborg, 1992 (Therevidae)

Austrosimulium dugdalei Craig, Craig & Crosby, 2012 (Simuliidae)

Ceratomerus dugdalei Sinclair, 2017 (Brachystomatidae)

Lapita dugdalei Bickel, 2002 (Dolichopodidae) [New Caledonia]

Tricimba dugdalei Spencer, 1977 (Chloropidae)

Hemiptera

Arawa dugdalei Knight, 1975 (Cicadellidae)

Eriochiton dugdalei Hodgson & Henderson, 1996 (Eriococcidae)

Kikihia dugdalei Fleming, 1984 (Cicadidae)

Rhopalotococcus dugdalei Williams, 2007 (Eriococcidae)

Ventrispina dugdalei Cox, 1987 (Pseudococcidae)

[*Xenophysella dugdalei* Evans, 1982 (Peloriidiidae) (now a synonym of *X. stewartensis* Woodward, 1952)]

Hymenoptera

Pseudospolas dugdalei Ward, 2015 (Ichneumonidae)

Zelostemma dugdalei Buhl, 2017 (Platygastridae)

Lepidoptera

Ischalis dugdalei Weintraub & Scoble, 2004 (Geometridae: Ennominae)

Mnesarchella dugdalei Gibbs, 2019 (Mnesarchaeidae)

Pseudocoremia dugdalei Stephens & Gibbs, 2003 (Geometridae: Ennominae)

Scoriodyta dugdalei Hättenschwiler, 1989 (Psychidae)

Orthoptera

Paprides dugdali Bigelow, 1967 (Acrididae)

Plecoptera

Vesicaperla dugdalei McLellan, 1977 (Gripopterygidae)

Zelandobius dugdalei McLellan, 1993 (Gripopterygidae)

Thysanoptera

Anaglyptothrips dugdalei Mound & Palmer, 1983 (Phlaeothripidae)

Karphothrips dugdalei Mound & Walker, 1982 (Thripidae)

Lissothrips dugdalei Mound & Walker, 1983 (Phlaeothripidae)

Trichoptera

Edpercivalia dugdalei Ward, 1998 (Hydrobiosidae)

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