IN REMEMBRANCE OF DONALD WILLIAMSON (6 JANUARY 1922-29 JANUARY 2016),
PLANKTOLOGIST, CARCINOLOGIST, AND EVOLUTIONIST: A METAMORPHOSIS

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THE LARVAL PHASE

Donald Williamson was born on 8 January 1922 at Alnham, Northumberland, England. Perhaps he was Donald to his mother, but to us all he was always Don, and will be so here. His father was the village schoolmaster, and they eventually moved to Seahouses on the Northumberland coast where Don spent much of his childhood, and developed a love of marine life. His father was a keen naturalist, and amongst Don’s papers I found his father’s annotated copy of *The Voyage of the Beagle*. Clearly an interest in evolution ran in the family.

In 1940 Don entered Kings College, Newcastle upon Tyne (then part of the University of Durham, now the University of Newcastle) to study zoology. Because he was studying, his call-up for World War II was deferred, and in 1942 he graduated with a B.Sc. in Zoology. He immediately joined

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the Royal Navy, having already attended radio courses whilst a student. He trained as a radar officer, and after a short spell at HMS Valkyrie, a shore-based establishment on the Isle of Man (a place he must have liked), commenced active service at sea in the Mediterranean. He served first on the cruiser-minelayer HMS Abdeil, sadly sunk by a mine with great loss of life shortly after he left, and then on HMS Antwerp, which acted as a floating headquarters for the invasion of Sicily. Not long afterwards Don was diagnosed with tuberculosis, invalided back to the UK, and in 1944 discharged to a sanatorium. He recovered after some lengthy treatment, which continued to near the end of his Ph.D. studies. The TB proved a mixed blessing, in that he was no longer accepted for teacher training (his original intention), so decided to become a marine biologist: their loss was our gain. He resumed his studies at Newcastle, completed his B.Sc. to Honours level, and carried out Ph.D. studies on talitrid amphipods, predominantly their behaviour, successfully completed in 1948. His thesis generated six papers. Thus, at the end of this rather tumultuous era, a 26-year-old Dr Williamson was turned loose, a marine biologist seeking a mission.

At this time the University of Liverpool was developing the Marine Biological Station at Port Erin in the Isle of Man. It had been predominantly used by scientists based in Liverpool, but a locally based scientific team was being recruited. There was a vacancy for a planktologist, which Don obtained. With seagoing facilities available he embraced the offshore environment, and never knowingly touched another amphipod! As well as sampling in the Irish Sea he participated in a number of North Atlantic cruises in the seventies on National Environmental Research Expeditions. He was on the Editorial Board of Crustaceana. On retirement Don continued to work from the laboratory, accommodated in the ‘Geriatric Wing’ where he and several other retired staff members had small rooms, the scientists’ equivalent of the garden shed. When the laboratory closed in 2006 he worked actively from home up to his death.

The Post-Larval Phase

On his retirement in 1987 Don could look back upon a scientific career that was fulfilled and productive, but Don did not look back, he looked forward. He metamorphosed, as did the larvae which he had studied so intensely. Don the planktologist became Don the evolutionist. In print it appeared a sudden transformation, but in fact it was hemimetabolous, rather than holometabolous.

Don’s ideas on the transfer of larvae were not the result of a sudden revelation, but were long in gestation. They started early, when he described a peculiar zoea from off Scotland (Williamson, 1960b), which combined majoid and homolid characters. Twenty years later this larva was finally confirmed as that of the majoid crab Dorynychus thompsoni by Wyville Thompson, 1873 after various studies outlined in Williamson (1982b). In that publication Don was clearly struggling to accept that the complex of homolid and majoid larval characters were the result of parallel/convergent evolution, the parsimonious explanation. Nevertheless, he decided that ‘It must be concluded that the conspicuous differences between the zoea of D. thompsoni and other zoae of the Inachidae are the result of recent evolution’ (Williamson, 1982b: 741). This theme was revisited in Hartnoll et al. (1987). At that time Tony Rice and I were coincidentally studying the post-larval stages of Dorynychus from the Porcupine Sea Bight. Don quizzed me as to whether it was a ‘proper’ spider crab: I assured him it was, despite it hav-
ing few postlarval instars, and a pelagic first postlarval in-
star. So in this 1987 paper Don again addresses the prob-
lems of parallel/convergent evolution, but almost as an aside
suggested the alternative possibility of gene transfer between
unrelated lineages, perhaps this tentativeness being a consid-
eration to his co-authors (we did not all wish to be burnt at
the stake!). These ideas had nevertheless been clearly well
developed in his mind, and had been already aired in a brief
note (Williamson, 1986b), though this was probably written
after the 1987 paper, which was presented at a conference in
1985. His 1986 paper extended beyond the crustaceans, fo-
cussing on the echinoderms, with a brief reference to other
phyla. Then from 1988 his series of substantial publica-
tions presenting his novel evolutionary ideas commenced.
The first paper was rejected by seven journals, before ac-
ceptance. These publications embraced the origin of larval
stages by genetic transfer in many invertebrate taxa, notably
echinoderms and tunicates. I recall my only significant con-
tribution to the argument as being “worms may well do that,
but crabs know better.” Perhaps I could have been more con-
structive at the time! It may appear that the presentation of
Don’s novel ideas was precipitous, but at 66 he had good
reason for concern. His father, brother, and three uncles had
all died of heart attacks before 66. Don had already had a
mild heart attack, and TB, as mentioned above, and realis-
tically considered that time was not on his side. He could
not afford the 20 years of contemplation and data collection
which Darwin had spent between the initiation of his ideas
during the voyage of the Beagle and the publication of The
Origin of Species. In retrospect Don’s concern regarding his
mortality was to prove misplaced (94 is a good age to have
reached), but with yet another twist.

Don continued to develop his ideas, as well as conducting
experimental crosses with promising but equivocal results.
In March 1990 he attended a symposium in Boston USA,
and also delivered talks at Amherst and Woods Hole. On
his return he decided to continue his experimental work to
obtain more definitive outcomes, and whilst collecting spec-
imens on a rocky shore fell and hit his head. This precipitated
a stroke, three months in hospital, and a resultant limited ca-
pacity on the right side. But Don could drive (fortunately he
gave up some years ago, to the benefit of himself and other
road users), type, lecture, and continue his work, and he did
so for a further 26 years, with his final paper published in the
year before his death. Overall he produced two books and 20
other publications on his evolutionary theories.

This is not the place, and I am not the person, to discuss
in detail Don’s hypotheses, but a brief summary here is ap-
propriate. The conventional view of larval evolution is that
larvae evolved within the life cycle of an organism as an ad-
vantangeous aspect of its development, as did other character-
istics of the species such as size or colour. Don’s alternative
hypothesis is the ‘larval transfer hypothesis,’ or hybridogene-

sis: the larvae originated as adults of other taxa, and their
genomes were likewise initially derided. So where do Don’s
ideas stand at present? Perhaps Jim Shapiro, author of Evo-
lution: A View from the 21st Century (2011) can summarise
this current status.

‘Are Some Animals Hybrid Organisms with Hybrid
Genomes? Another highly controversial (but not illogical) sym-
biogenic evolutionary proposal has been put forward by Donald
Williamson to explain the developmental history of invertebrates
that display markedly different larval and adult stages, such as cater-
pillars and butterflies. The larval transfer or hybridogenesis pro-
posal is that these organisms have combined two genomes in one
monophyletic organism, such that one genome directs larval develop-
ment and the other directs adult development. This proposal solves
the problem of why animals with clearly related adult forms differ
discontinuously in their larval forms. But it has met heated oppo-
sition from mainstream developmental biologists. Much of the evi-
dence Williamson cites in support of his ideas has not been pub-
lished, and he does not propose clear molecular criteria to validate
his proposal. So it is uncertain whether we will see another assump-
tion overturned about eukaryotic evolution based on strictly vertical
inheritance. Nonetheless, Williamson’s idea merits mention as il-
lustrating the testable new ideas that we are free to explore in 21st
Century evolutionary theory.’

So, is Don’s hypothesis testable? Jim Shapiro, who visited
Don last year and discussed his ideas, kindly offered to indi-
cate potential genomic tests: his comments follow. ‘A molec-
ular test of Don Williamson’s larval transfer hypothesis is
eminent feasible. Williamson’s proposal makes clear pre-
dictions about the distinct phylogenetic positioning of func-
tions expressed during larval and adult development. The
functions expressed in larval development should be more
closely aligned to sequences from the proposed donor clade
than to those expressed as adult functions of the putative re-
cipient organism. Relevant data can be collected in the form
of RNA sequences expressed during larval and adult morphogenesis.
Bioinformatic analysis can determine the ap-
propriate phylogenetic position of expressed larval and adult
sequences. If Williamson is correct, then the molecular phy-
logenies should reveal the larval relationships indicated in
Table 1 of his 2001 review rather than the accepted adult
taxonomies. If the larval transfer hypothesis is wrong, then
both larval and adult sequences will group together reflect-
ing the adult taxonomy.’

A fitting tribute to Don would be a rigorous testing of his
hypotheses, and a resolution of the conflicting views
currently surrounding them.

Acknowledgements
To Don: any element of levity in this tribute is a reflection of his quirky
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in 2006, and the dispersal or loss of relevant records, has made my task
so much more difficult. To those who have helped by the provision of
information for this tribute, including Paul Clark, Steve Hawkins, Richard
Nash, Ernest Nayler, Tony Rice, Jim Shapiro, and Janet Williamson.
**LIST OF PUBLICATIONS ON TALITRIDS, PLANKTON, AND DECAPOD LARVAE BY DR DONALD I. WILLIAMSON**


1967a. The megalopa stage of the homloid crab Lateillia australiensis and comments on other homolid megalopas. Australian Zoology 14: 200-211.


**LIST OF PUBLICATIONS ON THE EVOLUTION OF LARVAE BY DR DONALD I. WILLIAMSON**


**PH.D. THESIS SUPERVISED OR CO-SUPERVISED BY DR DONALD WILLIAMSON**


