

Garth Underwood (1919–2002): A Vision of Reptile Systematics

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Molecular Systematics of Dwarf Boas

The Tropidophiidae includes about 21 species of New World snakes in four genera. The relationships of these snakes within the family and to other families is not well resolved because of considerable disagreement about the relationships of basal snake lineages. The authors tested three previously proposed hypotheses: 1) the Ungaliophiidae clade (*Exiliboa* + *Ungaliophis*) is not closely related to the Tropidophiidae clade (here including *Trachyboa* + *Tropidophis*); 2) the latter clade is sister to Caenophidia; and 3) Ungaliophiidae is part of a monophyletic Booidea. The authors sequenced 1.9 kb of mtDNA (12S, 16S, and intervening valine t-RNA genes) from 23 species of snakes representing most major snake lineages and all four genera of dwarf boas. Aligned sequences were analyzed in PAUP* 4.0b8 with maximum likelihood; branch support was assessed with bootstrapping and Bayesian analysis. A single best tree indicated that dwarf boas are not monophyletic. Support was found for a clade including *Trachyboa* + *Tropidophis*, and another clade of *Exiliboa* + *Ungaliophis*. The former group was rejected as the sister taxon to Caenophidia, and the monophyly of Booidea was not supported. Bayesian support values estimated true probabilities of recovering respective clades more accurately than bootstrap values. One consequence of this phylogeny is that relatively kinetic skulls emerged early in snake evolution, and secondary reductions in skull flexibility occurred in fossorial lineages.

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Garth L. Underwood, the systematic herpetologist, died in the early hours of the morning on the 15 October 2002 after a brief spell in hospital. He was 83 and still making a useful contribution to the area that so fascinated him (Underwood 2002). Garth was much loved by those who knew him and he will be deeply missed, both as a herpetologist and as a friend.



Garth was born in Isleworth, Middlesex, after the First World War (16 July 1919), the eldest son of the renowned artist Leon Underwood and Mary (nee Colman). He went to University College London in 1938, but was conscripted into the Army (Royal Engineers) on the outbreak of World War II in 1939. He must have had an unpleasantly active first part of the war and was a survivor of Britain's worst maritime disaster. He was in France as part of the British Expeditionary Force after Dunkirk. In June 1940 the troopship (*HMT Lancastria*) on which he was returning to England was bombed and sunk off St Nazaire, Brittany with massive loss of life (estimated by some to be around 5000; see http://www.bbc.co.uk/history/war/wwtwo/lancastria_1.shtml). Garth described to me the bravery of his comrades who could not swim as the ship finally sank under them. Later in the war (1943) he went to India where he had an "intelligence" role. He helped develop a system to play sounds of tank battles in the jungle to amuse the Japanese. He kept the secrecy he was sworn to until, to his amusement, he saw it described in all its bizarre detail on a television programme. India had a very considerable impact on Garth. It was there where his interest in zoology focussed into an interest in reptiles, where he started publishing, and where he met his wife Molly.

He continued his studies at UCL after the war (1946), being taught by the eminent geneticist J.B.S. Haldane. He took a First Class Honours in zoology (Special genetics), with subsidiary pure mathematics, in 1948. He chose pure mathematics because he could spend the least time on it, and hence more time on zoology.

After graduating Garth took a the post of Demonstrator in Zoology at what was the University College of the West Indies at Jamaica, and what later (1962) became the University of the West

Indies. He was rapidly promoted through the system from Demonstrator to Assistant Lecturer (1949), Lecturer (1953), and Senior Lecturer (1958). Garth did not do a PhD, but submitted his publications in 1960 to the University of London, for which he was awarded a DSc for his "Systematic and evolutionary study of reptiles." In 1960 he also became Professor of Zoology in the Faculty of Agriculture, University of West Indies, Trinidad. He served as Dean of that Faculty from 1961 to 1963. During his time in the West Indies he maintained an association with the Museum of Comparative Zoology, Harvard University.

Garth decided to return to Britain for his daughter's education, and in 1964 he took the post of Principal Research Fellow at the British Museum (Natural History) in London, now the Natural History Museum (NHM). After his temporary fellowship at the museum (1964-67) he took the post of Senior Lecturer and later Principal Lecturer at what was Sir John Cass College and later became the City of London Polytechnic (currently London Metropolitan University). Although he retired from the City of London Polytechnic in 1984 he was still actively researching and was based in the Natural History Museum in London. Initially, this was an informal arrangement, but he was recognized as an Honorary Research Fellow in the Natural History Museum in 1994. He continued to work in the museum and inspire his younger colleagues until his death.

Garth's publications extend across seven decades (1945-2002). In general, his work has been marked by its lasting value rather than by a large volume of ephemera. For example, both Garth's original 1959 publications on anole evolution (Underwood 1959; Underwood and Williams 1959) and his 1967 work on snake classification (Underwood 1967) are still heavily cited in this millennium. The early 1950s saw three major contributions from Garth. His influential work on the evolution of reptilian retinas, inspired by G. L. Walls (1942), was published in *Nature* (Underwood 1951), as was his work on gecko taxonomy and evolution (Underwood 1955). Moreover, in this period he and Angus Bellairs developed their ideas on the fossorial origin of snakes (Bellairs and Underwood 1951). To my mind this remains the benchmark paper, and only convincing hypothesis, for the origin of snakes. Garth's interest in reptilian retinas continued through the next two decades (Underwood 1966, 1968, 1970) and an appreciation of their role in snake systematics, as expressed in his classic work "A Contribution to the Classification of Snakes," endured (Underwood 1967a,b, 1997).

Later on in the 1950s Garth worked on legless lizards (Underwood 1957a,b) and the West Indian fauna (Underwood 1957c, 1959, 1964; Underwood and Williams 1959). His work on Lesser Antillean anole series proved to be of enduring importance. His interest in the West Indian herpetofauna continued, with publications on Lesser Antillean snakes until 1999 (Underwood 1993; Underwood et al. 1999).

Garth pioneered a multiple evidence approach to snake systematics, advocating the use of a wide range of morphological features from visual cells, through osteology to rictal glands. He used his Fellowship at the museum (1964-67) to develop his ideas in this area. This formed the basis of "A Contribution to the Classification of Snakes" as well as later papers (1967b, 1997, 1999), and his last paper (Underwood 2002) was on a morphological system (rictal glands) that may give evidence for snake relationships.

A more quantitative approach to taxonomy was developing around the time of Garth's museum fellowship and Garth saw this as complementing his multiple evidence approach. He learned to program a computer and wrote his own programs to pursue his ideas. He was still working on programming compatibility analysis in his later years.

Garth was a committed and dedicated teacher, publishing papers on biological teaching in *Nature* and elsewhere (Underwood 1963). He was also a conscientious administrator acting as Dean in the University of West Indies and as Head of Department in the City of London Polytechnic for a while, at a time of great transition for that Institute. I think it is fair to say that he saw administration as something that was necessary, rather than a reward in itself, and when I knew him he was most fulfilled by museum research. What little time for research his teaching in London allowed was generally spent in the museum looking at specimens. This is what he loved most and his association with the Natural History Museum lasted from his Fellowship until he died, irrespective of whether he was employed elsewhere or retired.

At the time Garth was working in London, one could be forgiven for thinking that Garth was only interested in museum studies and had little interest in fieldwork. However, this was not really the case. Garth's time in the West Indies was a period when he was able to undertake fieldwork, not only in Jamaica and Trinidad, but also throughout the Eastern Caribbean islands, and he took full advantage of this. Garth's description of his first experiences of Dominica, catching numerous *Alsophis* snakes within walking distance of the capital Roseau contrasts with my current experiences, even though these areas have been less impacted by development than some. Garth then did no fieldwork after leaving the West Indies until after the death of his wife Molly. The loss of Molly, to whom he was entirely devoted, was a severe blow to Garth. After being widowed, he recovered an interest in fieldwork and, in spite of advancing years and health problems, he made a series of adventurous trips. In 1998 he visited southern Africa collecting snakes and in 1999, at the age of 80, he went on an expedition to the Crocker Range in Sabah, Borneo. He later visited his old territory of Trinidad and Tobago, taking his grandchildren with him, and his last trip was to attend the 2002 ASIH/HL/SSAR meeting in Kansas City.

Garth was well respected as a herpetologist. He was made an Honorary Member of The Herpetologists' League in 1978 (one of only five), he had numerous species and a genus named after him, and the 1997 "Venomous Snakes, Ecology, Evolution and Snakebite" volume (edited by R. S. Thorpe, W. Wuster, and A. Malhotra) was dedicated to him. Currently, The Natural History Museum is preparing a special issue of the *Bulletin* in his honor, and a retrospective will soon appear in *Copeia*. Sadly, the latter two will now be posthumous.

Garth's achievements may explain why he was a respected herpetologist, but they do little to explain the enduring loyalty of his students or the affection with which he was held. For this one needs to understand Garth's character. Garth had his gentle, and entirely unaffected, eccentricities. I first met Garth 35 years ago when I tried to convince him he should take me on as a PhD student once I had graduated. This was at the stage at which his Museum Fellowship had just ended. The pre-meeting telephone calls had led me to expect a much older man, but Garth was still in his

forties at this time. He came across as someone with some old mannerisms, but with a youthful, quick, and flexible mind, readily open to new ideas. This open, flexible mind stayed with him throughout and he was always very receptive to new ideas, even when they contradicted his own. He was, for example, very complimentary about the hypothesis of a marine origin for snakes.

I used to see Garth when he came into the museum for his weekly dose of research. There was a constant flow of notable researchers through the museum that Garth would delight in meeting, but he always took time to talk to encourage those that were starting out their academic journey. A very young Harry Greene (yes, even Harry was young once) turned up one day from his military posting in Germany to talk about his tail display-injury hypothesis. Harry was dressed smartly, with a severe military haircut, and bristling with respect for authority. However, Garth, in spite of (or perhaps because of) his own time in the military, was entirely non-authoritarian and non-status orientated in his approach to everything and everyone. Harry must have used the address "Sir" more times than I had heard since my schooldays. In spite of being non-plussed by this, Garth soon got Harry to relax, address him as Garth, and have a sensible conversation about bite marks on sand boas' rears.

He was a great teacher, not just directly, but also by example. He always expected the best possible effort in everything and impartial objectivity when considering evidence. The flow of visitors gave plenty of opportunity to air various viewpoints. His approach to academic debate was completely non-confrontational, and when faced with overconfidence he could be crushingly reasonable. Garth was an excellent model: un-opinionated without being opinion-less, open-minded without being mindless, and highly principled without being a prig. It reflects our limitations, and not Garth's, if we were not always able to learn from him. He cared about doing and publishing good science, and providing quality teaching. He never mentioned the paraphernalia of "citation rates," "grant capture," and "quality assurance" that so burden academia, and are so loved by those who administer because they can no longer do. Such a person was not always well-adapted to life in today's academia, but Garth was almost entirely free from cynicism. He enjoyed herpetology, he enjoyed systematics, he enjoyed teaching, and he enjoyed talking to others and encouraging them.

His daughter Vivienne, an architect, survives Garth. We extend to her our congratulations on having such a father and deepest sympathy for the loss.

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