George Morgan Davis (1938 – 2024):
The Director's Cut

Robert T. Dillon, Jr.
Coordinator, FWGNA Project
P.O. Box 31532, Charleston, SC 29417
DillonR@fwgna.org

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Author's Note: In August of 2025 I was contacted by Dr. Chuck Lydeard in his capacity as guest editor for a special issue of *Malacologia* to be dedicated to the memory of Dr. George M. Davis, my major advisor 1977 – 1982. Chuck asked me to take the lead on a biography/bibliography for that issue, working alongside coauthors Gary Rosenberg and Paula Mikkelsen.

My first draft version, as it appeared in October, drew many parallels between Davis' 64-year career in Malacology and the career of Dr. Henry A. Pilsbry (1862 - 1957), in whose chair Davis sat at the Academy of Natural Sciences for 30 of those years. Davis, like Pilsbry, was an arrogant jackass **[1].** It is perhaps not surprising, therefore, that my first draft was heavily edited in spots. Written in the first person, it included quite a few details and insights that I felt rather sure would not pass through into publication even as I was writing them.

So, the "Director's Cut" that follows is not intended to substitute for the actual article, as it was ultimately published in *Malacologia* **[2]** in late 2025 [pdf]. It is offered as a supplement. It does not include the section on Davis' personal life, which was contributed by Gary Rosenberg with the help of daughter Julie Anderson, or the complete 200-entry bibliography of Davis' written work, which was compiled by Gary and Paula working together. It does include some figures not published in the journal article, most again thanks to Julie, and it does conclude (of course) with a section for the actual literature cited. And it's juicer. Bon appetite.

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ABSTRACT

George M. Davis was the preeminent American malacologist of the latter 20th century. Seated in Henry Pilsbry's chair at the Academy of Natural Sciences in Philadelphia, his keen eye for morphological detail, matched only by his extraordinary ability to transmit rigorous scientific observation onto the journal page in word, data table and delicately-stippled anatomical illustration, exceeded even that of his predecessor. And from a firm foundation in the classical school of descriptive biology, Davis became the first American malacologist to apply molecular techniques to address systematic questions in the Phylum Mollusca, pioneering immunological, protein electrophoretic, and sequencing technologies throughout his long career. The influence he wielded to shape and mold our discipline during his 40-year editorship of *Malacologia* was exceeded only by Henry Pilsbry's 70-year editorship of *The Nautilus*. We shall not see a third coming.

INTRODUCTION

Dr. George M. Davis was a malacologist without peer. It was in the summer of 1976 that I drove from my home in the Shenandoah Valley to Columbus, Ohio, for the 42nd meeting of the American Malacological Union, still a junior at Virginia Tech but already shopping for a graduate program and auditioning potential advisors. All that week, from a surprisingly comfortable seat in the auditorium of OSU's Independence Hall, I had watched the heroes of my youth, kindly old Bill Clench **[3],** dour Leslie Hubricht, prickly Joe Morrison **[4],** portly Alan Solem, and rockstar Tucker Abbott, as they reviewed systematic and taxonomic arcana relevant to the creatures we all loved. Mostly, they showed pictures of shells. That's what mollusks seemed to be, dateline Columbus, OH, 1976. Boogers with shells.

And then up to the pitcher's mound strode Dr. George M. Davis, Pilsbry Chair of Malacology at the Academy of Natural Sciences of Philadelphia, like a big-league ace working a rehab assignment in a Class-AA ballpark. In a peculiar inflectionless drone, he launched into a review of "current trends" in molluscan systematics, featuring his own immunoelectrophoretic technique to estimate genetic relatedness in unionid mussels. Davis was injecting lyophilized whole-protein extracts from mussel species A into bunnies to create antibodies, comparing mussel species A to mussel species B by precipitin arcs drawn through little agarose gels cast onto microscope slides. In the summer of 1976, the quality of the science being done in the laboratory of Dr. George M. Davis was unrivaled in our discipline.

I introduced myself immediately thereafter, and he was most receptive, indeed charming. Davis encouraged me to apply to the University of Pennsylvania, where he held an adjunct appointment, and invited me to Philadelphia, an invitation which I accepted in January. And after he had wined me and dined me, toured me all around the Art Museum and hosted me in his own impressive rowhouse in South Philadelphia, I was hooked. My new wife and I moved to Philadelphia in the summer of 1977, I went to work at the ANSP immediately and matriculated at Penn that fall.

EARLY CAREER

If George Davis was born with a predilection for malacology, or indeed demonstrated any special interest in natural history studies of any sort during the halcyon days of his youth, the chronicles do not record it. He seems to have arrived in Ann Arbor in the fall of 1960, freshly minted B.A. from Marietta College tucked under his arm, as something of a blank slate.

George M. Davis 1938-2024

But at the University of Michigan, he was immediately recruited into the bustling Museum of Zoology laboratory of the legendary Dr. Henry van der Schalie, and there drawn into a long-running research program sponsored by the Armed Forces Epidemiological Board to assess the risk that North American freshwater gastropods might serve as hosts for Oriental schistosomiasis. Davis' 1965 dissertation, "The systematic relationship of *Pomatiopsis lapidaria* (Say) and *Oncomelania hupensis formosana* (Pilsbry and Hirase) (Gastropoda: Hydrobiidae)" was published in *Malacologia* in 1967 **[5].**

In the first section of his dissertation research, spanning 95 journal pages as published, we see classical malacology, sown by Linnaeus in the 18th century, cultivated by Say, Lea and Gould in the 19th, brought to flower by Pilsbry and F. C. Baker in the 20th century, gathered into the harvest by George Morgan Davis. Davis' talent as a scientific illustrator was stunning. His lavish charcoal drawings, delicately stippled, spilled across 32 pages, profusely labeled A, B, Cl, Ct, O, Og, Om, Op, Opi, Opo, Ov, Ov2, and On and On and On. His observations and descriptions were exquisite in their detail, as for example, "white granular units of about 25 microns diameter were especially crowded in the posterior part of the foot, becoming sparse along the sides." Davis' keen attention to the fine details of mollusk morphology, and his ability to transmit such detail vividly through both image and word onto the printed page, were the first hallmark of his career.

In the second section of his dissertation, spanning just two 1967 journal pages, we find George Davis hoeing weeds in the fields the Modern Synthesis of Darwin + Mendel. Here Davis reviewed the details of an elaborate and heroic laboratory culture effort, prosecuted over many

months, to hybridize *Pomatiopsis* and *Oncomelania*, "in order to obtain hybrids for anatomical studies." That these efforts ultimately failed cannot be counted a failure. For in those two pages, the question that had actually prompted the entire twenty-year research effort of the Van der Schalie team, involving dozens of collaborators and millions of grant dollars from the U.S. Government, was at last answered. Everybody could have gone home at that point. But no.

In the third section of his dissertation, spanning 6 pages as published in 1967, George Davis planted the seeds of contemporary malacology, as our science is practiced today. In 1964 he and Gene K. Lindsay had presented a paper at the annual meeting of the American Malacological Union describing the technique of disc gel electrophoresis, advocating it as one of the earliest applications of a molecular technique to the study of molluscan systematics **[6].** And in the previous issue of *Malacologia*, he and Lindsay **[7]** had formally evaluated the densitometric tracings of protein bands as yielded by that technique for their stability, as well as their intrapopulation, interpopulation, and intraspecific variability.

Now here in his dissertation, George Davis compared the foot muscle proteins of *Pomatiopsis* and *Oncomelania* by their densitometric tracings upon disc gel electrophoresis, resolving (rather remarkably) 17 protein bands in both. Although the assignment of homologies among those bands may have been a bit speculative, it is possible to see in George Davis' Rf values the germination of the contemporary science of malacology. A hunger for more and finer molecular tools, and better ways to analyze the data they generate, became the second hallmark of George Davis' distinguished career.

And as if that were not enough. Davis finished his dissertation research with a 13-page study entitled "Laboratory Ecology," in which he compared *Pomatiopsis* and *Oncomelania* by their biology in culture. He experimented with five types of vivaria over a range of temperatures and light regimes, focusing primarily on survivorship but gathering data on somatic growth and reproduction in those treatments where observed.

On their face, such controlled comparisons of ecology and life history yield data every bit as systematically valuable as classical morphology or contemporary molecular techniques, and I am personally no less inspired by George Davis' efforts on his final 13 pages than on any of the previous 130. As I reread my major advisor's dissertation today, I am vividly reminded of what American Malacology once was, and pointed to what it became, glancing wistfully left and right, down paths we did not take.

The conclusions from Davis' dissertation research were mild, given the five years of intense effort he had invested in them. Oriental *Oncomelania* and North American *Pomatiopsis* turned out to be two entirely different things, with no reason to be concerned that populations of *Schistosoma* adapted to the former might infect the latter.

Concurring with the general consensus of the day, Davis placed both genera in the subfamily Pomatiopsinae of the large and diverse family Hydrobiidae. And although his dissertation

research did not bear directly on the question, Davis also endorsed the growing consensus that regional shell variants of *Oncomelania hupensis* might be allocated to four subspecific nomina: the typical form in China, *formosana* in Taiwan, *quadrasi* in The Philippines, and *nosophora* in Japan.

In a follow-up paper published in 1969, however, Davis redescribed a fifth subspecies, *Oncomelania hupensis chiui*, from an isolated basin in northern Taiwan **[8].** In addition to 24 pages of artistically lavish and technically detailed anatomical illustrations and observations, 8 pages of disc electrophoretic comparison, and a single page review of his laboratory hybridization results, Davis added 10 pages describing two trailblazing immunological techniques he had picked up in the laboratory of his colleague and mentor Lindsay.

Antisera were developed from whole homogenized foot muscle of *Oncomelania hupensis formosana* (A) and *O. hupensis chiui* (B), injected into white rabbits according to an elaborate schedule over a period of two months, bled ten days subsequently. Davis' micro-Ouchterlony double diffusion comparisons were conducted in four-well agarose slides, comparing the precipitin arcs that developed between Anti-A antiserum, anti-B antiserum, A extract and B extract over a period of 12 hours. For immuno-electrophoretic comparison, Davis first separated his A-extract by disc gel electrophoresis, laying the polyacrylamide tube onto a slide, pouring agarose around it, and applying anti-A and anti-B antisera by filter paper strip. Squinting at the fine white precipitin arcs that developed after 3 – 5 days under such conditions, Davis was able to divine some measure of genetic similarity between A and B.

Davis could cite exactly four previous applications of immunological methodologies to malacological research prior to the 1969 publication of his paper on *Oncomelania hupensis chiui*. To the rest of the American malacological community, leafing through pages 17 – 70 of *Malacologia* Volume 7, Davis' tour de force must have seemed the Dawn of The Space Age.

ARMY YEARS, 1965 - 1970

I clocked in for my first day as an hourly employee in the Malacology Department at the Academy of Natural Sciences on July 1, 1977. And just a few weeks thereafter, was pleased to accept an invitation from George to accompany him as native bearer and interpreter on a field trip to Lake Waccamaw, deep in the jungles of eastern North Carolina. And so it was that I found myself that next Friday afternoon, tossing my duffle bag into the trunk of his decrepit Plymouth Duster, jumping into the shotgun seat beside him, and plummeting south down I-95. At some point in our southbound journey, I turned over my left shoulder and saw a beautiful three-piece suit, freshly pressed, hanging in a garment bag across the seat behind me. And I inquired of George about it. And this is the story that he told.

He said that earlier in his career he had spent many weeks travelling by Jeep through the jungles of southeast Asia, in vehicles fitted with gun racks mounted directly overhead, for easy access to

firearms should bandits threaten. His team had travelled through areas so remote that often they had no idea through what country they drove, and the inhabitants of the local villages couldn't tell them, either.

So, at some point in one of these expeditions his team had broken through the undergrowth onto an airstrip. And parked in an airplane at the end of this airstrip was the King of Siam.

The King was American born, and upon hearing that an American scientist was visiting this remote corner of his realm, invited Davis to dinner. Had Davis not been able to assemble the proper attire at that critical juncture, an important opportunity for international diplomacy would have been sacrificed.

"We talked about jazz, and sailing, and so forth," said my major advisor. "Something similar could certainly happen anywhere south of Richmond," I offered, mildly.

Dr. George M. Davis had reported for duty as chief malacologist at the U.S. Army's 406th Medical Laboratory, Camp Zama, Japan, in the summer of 1965. Most of his research effort, at least initially, was directed toward *Semisulcospira* (then considered a pleurocerid) and a variety of thiarids (e.g. *Brotia*), hosting the lung fluke *Paragonimus* in Japan and southeast Asia.

He was also most certainly involved in at least one expedition to Thailand, yielding the descriptions of two new species of *Tricula* and what turned out to be a pivotal insight into the evolution of the entire East Asian hydrobioid fauna **[9].** Previously, *Tricula* had been widely confused with *Oncomelania*. But in 1968, based on a variety of anatomical, shell-morphological, and ecological distinctions, Davis split *Tricula* out into its own monogeneric subfamily, the Triculinae.

Speaking in Manila at the Fourth Southeast Asian Seminar on Parasitology and Tropical Medicine in February of 1969 **[10],** Davis focused entirely upon *Schistosoma japonicum* and its intermediate host, *Oncomelania hupensis*, in Japan, China, Taiwan, and The Philippines. *Tricula* he mentioned only in passing, to distinguish it from *Oncomelania*. That would change.

For even as early as 1967, Iijima and Garcia **[11]** had confirmed the natural transmission of human schistosomiasis in Laos, on the Mekong River Island of Khong, far outside the range of any population of *Oncomelania*. And by 1969, WHO teams were mounting epidemiological surveys to learn more.

FROM THE ORIENT TO THE ACADEMY, 1970 – 1997

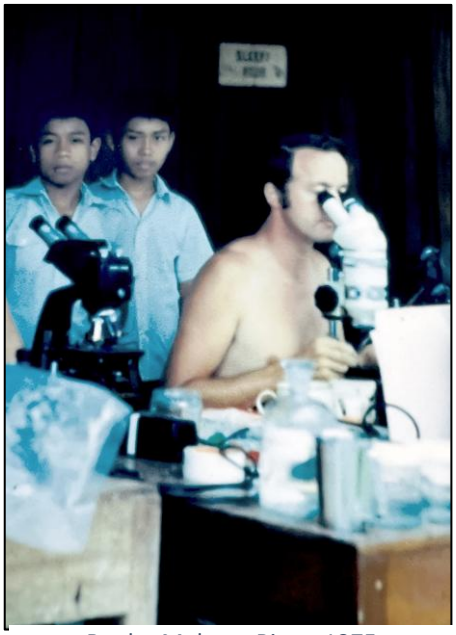
> *"On the banks of the unruly Mekong River, near the shallows of an island just above the Cambodian border in Laos, Philadelphia biologist George M. Davis sits, scalpel in hand, peering through a microscope, deftly carving up a succession of tiny snails. On the horizon, a plane is landing to help him escape the danger that surrounds him. It is 1975, Southeast Asia is in turmoil, Phnom Penh has fallen, and in a matter of days Saigon will follow. But Davis is oblivious to the packing going on around him. He will not, damn it, he will not be disturbed by the vagaries of some cursed war. For eight years, he has looked under boulders and sifted through leaves and sand for a secrete contained in this wild river, and he will not give up now. He keeps his generator light going. He keeps dissecting snails. He doesn't know precisely what he is looking for but he knows enough to keep looking."* **[12]**

In 1970 George Davis accepted a position as Associate Curator and Chair of the Department of Malacology at the Academy of Natural Sciences and moved to Philadelphia. In 1971, WHO and USAID medical teams were able to identify the intermediate host of the Mekong schistosome as *Lithoglyphopsis aperta*, a hydrobioid snail newly described by Prasong Temcharoen **[13].** And what followed was George Davis' most important contribution to science, from a biomedical standpoint in any case – his 1976 "Monograph on *Lithoglyphopsis aperta*," coauthored with Temcharoen and Viroj Kitikoon **[14],** together with his larger "Origin and Evolution of the Gastropod Family Pomatiopsidae," published three years later **[15].**

The 1976 paper was a masterful description of that single species of hydrobioid snail implicated in the transmission of schistosomiasis in the Mekong River, which Davis argued could not be assigned to *Lithoglyphopsis*. The data he presented in evidence were entirely morphological, but wonderful in their quality and quantity; the anatomical drawings lavish, the observations detailed to the count of the mantle spot. By 1976 Davis was tabulating mean, standard deviation, and range, for measurements taken on such elastic characters as osphradium, prostate and verge, with 11 lengths and widths from the ganglia of the central nervous system alone. And newly added to his 1976 paper were four pages of histological sections showing microscopic details of reproduction and nerve.

Davis and his coauthors described three races of *L. aperta*, differentiated primarily by shell shape. Hypotheses about the higher-level systematic relationships between the host of the Mekong River schistosome and any other gastropod taxon worldwide were, however, surprisingly circumspect. They rejected a congeneric relationship with Thiele's type for the genus *Lithoglyphopsis* on the basis of shell shape and what would seem a minor character to independent researchers reading the work today, "the structure of the central tooth of the radula."

In 46 journal pages of morphological observations, minute in their detail and as broad in their scope as the 57 chapters in my freshman biology textbook, was but a single distinction in the structure of a radula tooth all there was to be found between the old *Lithoglyphopsis* and some new genus, yet to be named? Apparently, yes. Davis and his coauthors declined to name that new genus, however, punting with "It is not possible to assign *aperta* to a named genus until the morphologies of numerous other hydrobiid taxa in the Mekong River are known."



By the Mekong River, 1975

It was in the 120 glossy pages of the *Academy of Natural Sciences Monograph* 20, published in 1979 **[15],** that those morphologies became known. In that highly synthetic work, Davis as single author reported the results from five years of studies in makeshift laboratories at Khemarat, Ubon Ratchathani, and Khong Island, hunched over a Wild dissecting scope, peering at the microscopic anatomy of hundreds of tiny snails pinned into 9 cm Petrie dishes. Ultimately, he recorded observations on 27 shell characters and 23 anatomical characters for 69 hydrobioid species collected from 14 sites in the upper Mekong drainage of Thailand and Laos 1970 – 1975.

Efforts to catalog the exuberantly diverse hydrobioid fauna of the Mekong had begun in the nineteenth century, with the pioneering studies of Deshayes, Poirier and Bavay, and had quite recently been reviewed, expanded and updated by R. A. M. Brandt, with local collaborator Temcharoen. Brandt's (1974) monograph on the non-marine aquatic Mollusca of Thailand **[16],** allocating 92 Mekong species to 11 genera, and those 11 genera to the hydrobiid subfamily Lithoglyphinae, was sitting like a 423-page brick on Davis' plywood bench as he worked.

To relay just his observations on *Lithoglyphopsis aperta*, George Davis had required 46 journal pages. Punching a couple buttons on his calculator, he must have paused briefly to consider publication options for a 69 x 46 = 3,174 page monograph to answer Brandt's 423. Instead, he opted for a synthesis merely 120 pages in length, containing but 11 lovely and detailed anatomical illustrations, 4 schematic diagrams, and 4 plates of shell photos, all judiciously selected to emphasize the most important systematic differences alone.

That monograph also contained 7 phylogenetic trees or treelike diagrams, a first for Dr. George M. Davis. Davis analyzed his 50-character dataset with NT-SYS, the package of numerical taxonomy programs published by F. J. Rohlf and colleagues in 1972, calculating taxonomic distances for UPGMA cluster analysis. The classification he ultimately proposed allocated 69 Mekong species (6 to be newly described) to 10 genera (2 newly described), and those 10 genera into 3 newly-described "tribes," all three allocated to the subfamily Triculinae. Temcharoen's *Lithoglyphopsis aperta*, the host of the Mekong River schistosome, went to

Tricula aperta, along with the two *Tricula* Davis had described from Thailand in 1968. So, there's your answer.

And here is the headline, which I confess as I write now 47 years later, I have buried under an entire journal page of tedious review, but which my major advisor most certainly did not bury under his 120 pages of 1979. Davis proposed that his Triculinae, newly expanded and characterized by him, be joined together with a subfamily Pomatiopsinae and separated from the Hydrobiidae into a new worldwide family Pomatiopsidae.

A fascination with the extraordinarily diverse triculine faunas of east Asia would guide George Davis' research program for the remainder of his career. For among other newsworthy items to make worldwide headlines in 1979, beyond the publication of his monograph, was the establishment of formal diplomatic ties between the USA and the People's Republic of China, a gusher of grant funding to promote collaborative research following on its heels.

Throughout the 1980s Davis made many and lengthy field trips to China, developing collaborations with numerous researchers across the subcontinent. Also noteworthy during this period was a 1985 field trip to India, in search of *Tricula montana*, the type species of the genus *Tricula* by Benson's original 1843 description. Davis's anatomical observations on *T. montana* suggested a close match to the *T. bollingi* he had described from Thailand in 1968, but not to his *T. burchi*, or to the medically important *Tricula aperta* of the Mekong. Thus, in a paper published in 1986, he along with co-authors N. V. Subba Rao and Elaine Hoagland segregated *aperta* and *burchi* into a new genus *Neotricula* **[17].**

Expedition to China, circa 2000

Between 1983 – 1997 Davis, together with extensive teams of Chinese collaborators, published 13 papers in a series "dedicated to establishing the detailed anatomy and systematic relationships of genera of southeast Asian and Chinese freshwater prosobranch snails suspected of being members of the Pomatiopsidae." Most of these appeared in the *Proceedings* of the

ANSP. But the largest and most synthetic, his 200-page "Pomatiopsidae of Hunan, China," coauthored with 7 Chinese collaborators, was published in *Malacologia*, 1992 **[18].**

Just the table of abbreviations for Davis' 1992 monograph ran to 131 entries – 131 anatomical characters to be highlighted on the 73 beautifully-executed scientific illustrations and 14 schematic diagrams that followed. Also called into evidence were 13 plates of shell photos and (new since the mid-1980s) 19 plates of scanning electron micrographs, along with 82 tables of data. One can count 17 tables of measurements for 12 shell characters, 14 tables of measurements for 23 anatomical characters, 10 tables of measurements for 9 characters of the central nervous system, and 15 tables of measurements for 6 characters of the radula, with mean, standard deviation, range, and sample size given for all, no pause ever taken at any point during the entire blizzard of 2,824 data to test an hypothesis. Systematic analysis was both by phenetic methodology (UPGMA, PCA, minimum-spanning trees) and by Hennigian cladistics (also new since the 1980s).

To classify the 17 species of pomatiopsid snail inhabiting Hunan (4 new) ultimately required creation of a new tribe in the subfamily Pomatiopsinae and two new genera in the subfamily Triculinae, bringing the genus count for the latter subfamily up to 21. George Davis' 1992 monograph on the pomatiopsids of Hunan was the Angkor Wat of classical malacology, 30 years now overgrown by jungle, a thing of antique wonder.

FROM THE ACADEMY TO AMERICA, 1976 – 2000

George and I enjoyed a successful visit to Lake Waccamaw that long Saturday in early August of 1977 – wading about the shallows, he plucking four species of *Elliptio* off the clean white sands in the crystalline waters below, I following behind with a bucket. We finished in the late afternoon, with enough daylight ahead of us to hop back into his Plymouth and drive north as far as Emporia, Virginia. There we found lodging in a Holiday Inn.

I like Southside Virginia. I have cousins in Martinsville and Ridgeway, and as a NASCAR fan, soft spots in my heart for both the Burtons of South Boston (Ward & Jeff) and the Sadlers of Emporia (Hermie & Elliot). Pulling into the Holiday Inn by I-95 that Saturday evening 50 years ago felt like returning home. With cleaner sheets.

So, we repaired briefly to our separate rooms, washed up, and met downstairs again for supper. I do not remember what I ordered, but I do remember that George ordered the most expensive item on the menu, the filet mignon, and carefully specified to the waiter that the meat must only be cooked to a very precise and very rare temperature.

Presently the waiter returned with our meals. At which point, my advisor of two months reacted in an episode I can only describe as cool-red outrage. "Young fellow, I specifically instructed you to bring me a steak that is rare. This steak is not rare. It is overcooked. What is more, I can

detect that there is no means by which I shall obtain a rare steak from this establishment. You will take this plate away, and you will bring me a Drambuie, to compensate me, in small part, for this insult."

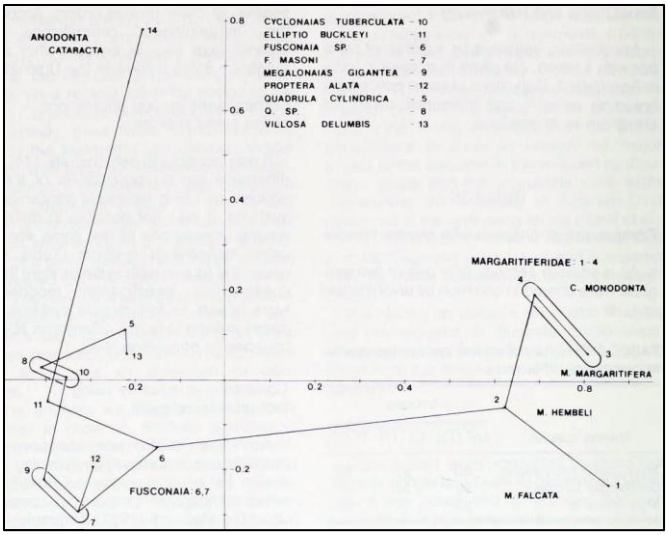
The humiliated waiter snatched up the plate and beat a hasty retreat to the kitchen. And a vessel of golden-colored liqueur appeared. And presently my advisor looked across the table, fixed me with one of his peculiar stares, brows arched over heavily-lidded eyes, and said, by way of explanation, "Microwaved. I could see that piece of meat had been frozen and microwaved." At which point it first dawned upon me that I might be in the presence of a man whose ego rivaled even my own. "In Emporia, Virginia!" I exclaimed in response. "Who could have imagined?"

It had not been George Davis' exquisitely detailed renderings of East Asian hydrobioid anatomy that had brought me to the dining room of a Holiday Inn by I-95 that memorable summer evening in 1977. It had been the gee-whiz space-age immunological methodology he had been promoting as a tool to understand the evolution of the North American unionacean mussels. The results of that research began to reach publication four years later.

In 1981 Davis and his colleague Sam Fuller published their 34-page "Genetic relationships among recent Unionacea of North Amercia" in *Malacologia* 20(2), with an endearing typographic error in the title of a journal article he not only wrote but edited **[19].** The coauthors tabulated ten different classification systems that had been proposed for the North American unionacean mussels as of that date, noting the "profound influence" of Ortmann's classic **[20, 21]** two-family system, Margaritiferidae and Unionidae, with four subfamilies in the latter: Anodontinae, Lampsilinae, Gonideinae, and Unioninae. Their own analysis, involving 52 species representing 27 genera, was based primarily on immunological comparison, supplemented by a small set of morphological characters added in discussion.

Whole homogenized extracts of both foot muscle and gravid gill were pooled from 12 to 60 individual mussels of each species and injected into rabbits according to an elaborate schedule over six weeks, antisera tested for effectiveness by the resolution of at least 10 precipitin arcs in homologous reactions upon immunoelectrophoresis. Counting arcs generated on comparison of antisera to homologous and heterologous antibodies yielded a percent difference between the pairs of taxa involved. And matrices of pairwise differences (calculated under several assumptions) were visualized using the multi-dimensional scaling routine of NT-SYS.

Davis and Fuller's analysis suggested to them three co-equal groups, which they elected to classify as subfamilies of the Unionidae: the Margaritiferinae, the Anodontinae, and the Ambleminae. Then calling up a small set of six morphological character traits, they recognized 4 "tribes" in the Ambleminae: Amblemini, Pleurobemini, Lampsilini, and Gonideini.



Davis & Fuller **[31]** Fig 1.

Also appearing in 1981 was Davis' not-quite-first application of the emerging technique of allozyme electrophoresis to address questions in molluscan systematics, his "Molecular genetics and speciation in *Elliptio*" with Bill Heard, Sam Fuller, and Caryl Hesterman **[22]**. Davis and colleagues analyzed genetic variation at 14 allozyme-encoding loci in 22 populations of *Elliptio*, including the four species we had collected together at Lake Waccamaw in August of 1977, along with 8 outgroup populations of other unionacean genera, calculating a matrix of Nei's genetic distances, depicting the results by two-dimensional scaling with a minimum-spanning tree.

That 1981 population genetic survey of *Elliptio* was the only full paper that George Davis ever published listing Caryl Hesterman as a coauthor. Caryl held a soft-money position in the Davis lab for many years, developing and refining most of the molecular techniques upon which his research program was based. She also served as Managing Editor of *Malacologia* 1986 – 2016. Caryl Hesterman's manifold contributions might perhaps have warranted better acknowledgment during Davis' lifetime than they were ultimately granted.

I have stipulated "not-quite-first" two paragraphs above, because I had (of course) invited my advisor to co-author my first paper on the genetics of the North American pleurocerid snails, performed entirely in his laboratory, using his own electrophoretic equipment and his own reagents, published in *Malacologia* the previous year **[23].** On page 92 we reported a Spearman rank correlation of 0.70 between intraspecific shell morphological divergence and genetic distance, significant at the p = 0.05 level. This, to my knowledge, was the only value of p George Davis ever published in his 60-year career.

Davis went on to author or collaborate on two additional studies of genetic variation at allozyme-encoding loci in the unionaceans, both in 1984, one expanding his coverage to include populations of *Uniomerus, Megalonaias, Quadrula, Elliptoideus* and *Quincuncina* **[24],** the other focusing on the genetics of peripheral populations in Nova Scotia, with his student Pieter Kat

[25]. In the late 1980s Davis also applied allozyme electrophoretic techniques in several collaborative studies addressing genetic relationships among brackish-water populations of *Hydrobia* on the US Atlantic coast **[26, 27].** And in 1994, he and coauthors Dave Strayer and Tom Bianchi shocked the world **[28]** with a demonstration that an Atlantic drainage population of *Pleurocera virginica* might be hybridizing with a Great Lakes population of *P. semicarinata livescens* through the Erie Canal **[29].**

Ever in the vanguard, by 1990 George Davis was becoming involved with pioneering applications of new DNA sequencing technologies to address deep and longstanding questions in molluscan systematics. His name was listed third in a team of six authors, headed by his student Ken Emberton, in an effort to sequence 150 nucleotides from the D6 region of the 28S rRNA molecule in 10 pulmonate gastropods **[30]** and third in a team of four coauthors, headed by Gary Rosenberg, to sequence the same gene for 20 unionoid bivalves and 13 marine gastropods shortly thereafter **[31].** Lydeard **[32]** has reminisced about his 1992 collaboration with Davis on a sequencing study of the unionid mussels of the Savannah River Ecology Lab in Georgia, ultimately published in 1996 **[33].**

It was also in 1996 that Davis first appeared as a coauthor on sequencing studies directed toward the evolution of his first love, the oriental pomatiopsids. That collaborative study **[34],** documenting cytochrome b sequence variation among four individual *Oncomelania hupenis* (three populations, two subspecies), was augmented two years later by a larger study of CO1 sequence diversity in 13 individual rissooids: *Tricula* (1 individual), *Gammatricula* (2), *Oncomelania* (4), *Hydrobia* (3), *Truncatella* (2), and the Rissoid *Setia* (1) with three more distantly-related mollusks as outgroups **[35].** It was in the CO1 paper that the name of Dr. Thomas Wilke, then a postdoctoral associate in residence at the ANSP, first appeared in the long list of George Davis' prominent collaborators.

Wilke took the lead in 2001, at the head of a team that included Davis and four other researchers from Europe. By that time Davis was listing George Washington University as his professional address, having been forced out of the ANSP in 2000. Piling gene upon gene and taxon upon taxon, Wilke and colleagues **[36]** sequenced both CO1 and 18S for representatives of 40 hydrobioid genera, ultimately proposing that several freshly-elevated families be split out of the old diverse, equitable, and inclusive Hydrobiidae, including the Amnicolidae, the Cochliopidae, and the Lithoglyphidae.

And in 2013, Wilke and a five-man team now including heavy hitters Bob Hershler of the USNM and Winston Ponder of the Australian Museum **[37]** "pushed short DNA fragments to the limit." Using an analysis of the sequence variation in three genes over 90 hydrobioid gastropods, they dynamited the old worldwide Hydrobiidae into 21 family-level taxa, carrying the process that Davis had begun way back in 1979 to its inevitable conclusion. George Davis was not listed among the authors of that 2013 work. But in the acknowledgments section we read, "This work was largely inspired by the extensive work on the Rissooidea by George M. Davis and his life-long commitment to resolving the evolutionary history of this challenging but fascinating superfamily."

LEGACY

In 1984, George Davis, along with Mel Carriker and Arthur J. Cain, published an article in *The American Malacological Bulletin* entitled, "Report on courses advised for graduate students in the field of malacology" **[38].** According to Alan Kabat (pers. comm.), "Jack Burch came up to George in the lunch line at an AMU meeting shortly thereafter and nervously asked George whether this paper was directed towards Michigan. George quickly and loudly responded, "No, it is that *other* school in the North."

Woods Hole, 1990

The history of American malacology in the late 20th century can be read as a contest between two teams, MCZ and UMMZ, on two fields, the ANSP and the USNM. The champion of Team MCZ was for many years R. Tucker Abbott, who like Davis served as a parasitologist for the U.S. military (1944 – 46), rose to sit in the Pilsbry Chair (1954 – 69), and edited the premier journal in our field, then *The Nautilus* (1959 – 1995). When in 1969 Abbott was hired away by the wealthy John E. du Pont to help found the Delaware Museum of Natural History, a vacancy was created at the ANSP that George Davis seemed almost predestined to fill. No further curatorial positions were to open in the malacology departments of any other major American museum until 1977.

Seated in Henry Pilsbry's high and exalted chair for 40 years, George Davis became the most valuable player of Team UMMZ, taking the ball from van der Schalie and Burch, carrying it to the end zone in Philadelphia. The game ball in this metaphor was *Malacologia*, the editorial offices of which moved south from Ann Arbor in 1975 **[32].** Davis' 42-year editorship of *Malacologia*, and the influence to shape and mold our discipline that came with it, is rivaled only by that of Henry Pilsbry's 70-year editorship of *The Nautilus* 1889 – 1957.

It was from Philadelphia that George Davis rose to dominate the American Malacological Union, serving as its president 1976 – 1977, and on its council perennially thereafter. And from Philadelphia he sent his own star player, Bob Hershler, onward to Washington, spreading the UMMZ scientific ethos into the marble halls of the USNM **[39].** From Philadelphia too I was sent, bearing an appreciation for that ethos, albeit to ground less contested.

To an aspiring young malacologist, 21 and fresh out of college in the summer of 1977, the Academy of Natural Sciences was a Big Rock Candy Mountain, descended to earth from a hobo's dream. The collections were superb, of course, best in the nation, competently maintained by

Dr. Art Bogan, a unionid guy from Tennessee, with a small army of hourly employees and volunteers, including a talented young high school student named Gary Rosenberg. Shy and kindly Dr. Robert Robertson was curated into the north corner of the expansive collection floor. Frequent visitors included Dr. Elaine Hoagland down from Lehigh, Bob Hershler up from Johns Hopkins, cigar-chomping Hal Lewis, and the aristocratic Prof. Arthur J. Cain, who ultimately had more influence on my thought in five minutes than George Davis had in five years **[40].**

But the magic was to be found in a modern three-story addition hidden Harry-Potter style, Diagon Alley behind the historic museum. My new advisor led me through a dark and cavernous room filled with fossils, boxes, and dust, and opened the steel door to a wonderland of glistening laboratories dedicated to the advancement of knowledge in all specialties – ecological, organismal and molecular – and scientists who knew how to make walls of elaborate and exotic equipment work. He toured me through an animal room stacked with cages of bunnies, poked, stuck, and bled, smelling like science, and into the spacious and well-appointed laboratory he called his own. And there I met the petit and lovely Ms. Caryl Hesterman, very kind and very firm, who would be my hostess and guide for the next four years.

All this Dr. George M. Davis made available for my use, no further permission needed, no questions asked. And the bulldog had rubber teeth. Yes, certainly he barked; yes, certainly he blustered. When he entered the room, all stood at attention for orders. And indeed, I myself was on the receiving end of more than one GMD directive during my sojourn in the City of Brotherly Love. But after a private meeting or two in the early years, my advisor and I came to an understanding. We had in common the UMMZ scientific ethos, an ethos to which I never subscribed, but which I appreciated, nonetheless.

And what was that ethos? Quoting Davis verbatim, from the introductory paragraph of his 1994 essay on taxonomic discrimination **[41]:**

> "If we could call back to the present some of the early fathers of morphology-based malacology, for example Cuvier, Bouvier, Troschel, Stimpson, Pelseneer, Thiele, Johansson, and Pilsbry to name a few, and bring them up to speed on the vast accumulation of literature since their time, they would readily understand and be enthusiastic about the modern day potential for sophistication in taxonomic discrimination. They would say that it is about the recognition of, and the definition of species, genera, and higher taxa. They would be in agreement, and I with them, that the fundamental basis for taxonomic discrimination was then, and is today, the comparative anatomical data set."

Davis was, first and most fundamentally, a malacologist of the classical school. Sitting in Henry Pilsbry's chair, he carried his predecessor's Baroque fascination with the attachment of tubes to sacks, their twistings fore and aft, to Rococo perfection in hundreds of journal pages overflowing with delicately-stippled illustration.

But over the entire span of his career, Davis directed the evolution of malacology from classicism to neoclassicism. The full title of the 1994 essay from which I have quoted above was, "Molecular genetics and taxonomic discrimination." And Davis went on to observe,

> "Molecular techniques have long been used as an aid for discriminating among taxa… The use of immunology in systematics is over four decades old; the use of allozymes, three decades. The now-generation is scrambling to sequence RNA and DNA aided by PCR and cloning."

So then onward, after a nod back to classical methodologies in paragraph number one, the remainder of Davis' 20-page essay was directed toward the shiniest tools in the toolbox of systematic biology, 1994. And on the ninth of those 20 pages, he paused to address the concept of the species.

Davis considered the biological species concept "not acceptable as it stands because the emphasis is on isolating mechanisms." He observed that "the problem is not one of distinguishing species that occur in sympatry, but those that are allopatric," pointing out – quite rightly – that application of the biological species concept is difficult in such cases. And of course, the most important consideration in science is the convenience of the scientist. "The process of speciation in allopatry" he concluded, "has nothing to do with isolating barriers."

Rather, Davis endorsed a variant of the "Cohesion Species Concept" of Templeton **[42],** species being "a group of populations of a monophyletic lineage" demonstrating "phenotypic-reproductive cohesion," that cohesion being unmeasurable, a subjective construct of the taxonomist. The classical school of systematic biology, where species had been defined subjectively on the basis of the visible phenotype, had become the neoclassical, species defined subjectively on the basis of the invisible genotype.

And so was the Modern Synthesis of Darwin + Mendel bridged over. Born a scion of the Classical School, George Davis had been baptized Presbyterian-form in modernity with his early laboratory experiments on hybridization, sprinkled not dunked. Then finding objective, hypothesis-driven science too constraining, he jumped over the deeper waters of Fisher, Mayr, Dobzhansky and Simpson to the Neoclassical now, drawing our discipline along with him. Today it has become our job, as professional malacologists, to distinguish the species, a job much too important to be left to the untidy whim of the animals themselves.

Dr. George M. Davis was the greatest American malacologist of the age just past, an age that sent Thomas Say sailing west from Philadelphia down The Ohio with his boatload of knowledge, bound to gather up the bugs and slugs of our frontier and tell us what we were just beginning to step upon, light dawning from The East. In just such a fashion, seven generations later, did George Davis of Philadelphia don his own pith helmet, drop a finger onto The National Geographic, and mount his own expeditions to the most remote corners of the 20th century world, gather up their bugs and slugs, and tell the naïve inhabitants thereof what they had been stepping upon for millennia, light now dawning from The West.

And Dr. George M. Davis was the first American malacologist of the age in which we live today, an age that opened in 1964, when he himself coaxed the first homogenate of mollusk through a tube of polyacrylamide, and peering at protein bands as they developed, looked for clues to the evolutionary relatedness of the bugs and slugs that he himself had homogenized.

His was the commanding presence in our discipline when our discipline turned. Just as Thomas Say begat Isaac Lea **[43],** and Lea begat Tryon, and Tryon prepared the way for The Coming of Dr. Henry A. Pilsbry **[44],** so too did Tucker Abbot prepare the way for a Second Coming, that of Dr. George M. Davis, descending from the clouds, at the sound of a trumpet. We shall not see a third.

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