

GEORGE MORGAN DAVIS (1938–2024): LIFE, WORK, AND LEGACY

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ABSTRACT

George Morgan Davis was a preeminent American malacologist of the latter twentieth 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, numerical analysis, and delicately stippled anatomical illustration, exceeded even that of his predecessor Henry Pilsbry. 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 that he wielded to shape and mold our discipline during his 40-year editorship of this journal was exceeded only by Henry Pilsbry's 70-year editorship of *The Nautilus*. Here we review Davis' distinguished career, his 200 publications, the 46 taxa that he named, and the 11 taxa named in his honor.

Key words: biography, obituary, schistosomiasis, Southeast Asia, China, Japan, freshwater gastropods, bivalves, Hydrobiidae, Pomatiopsidae, Unionoidea, electrophoresis, immunology.

INTRODUCTION

In the eyes of many, George Morgan Davis was a malacologist without peer (Fig. 1). During the summer of 1976, the American Malacological Union (now Society) held its 42nd annual meeting in Columbus, Ohio. During one particular session, many of the well-established American malacologists—kindly old Bill Clench, dour Leslie Hubricht, prickly Joe Morrison, portly Alan Solem, and rockstar Tucker Abbott—reviewed various systematic and taxonomic treatments, illustrated by photographs of the shells of their research subjects. Next to the podium that afternoon was George Davis, Pilsbry Chair of Malacology at the Academy of Natural Sciences of Philadelphia (ANSP). 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 rabbits to create antibodies, comparing mussel species A to mussel species B by precipitin arcs drawn through small agarose gels cast onto microscope



FIG. 1. George Morgan Davis, Ann Arbor, Michigan, 1972, taken by R. Robertson. Courtesy of the Academy of Natural Sciences of Drexel University, Library & Archives.

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slides. This was something new. Later, over coffee, in the view of one budding scientist (the senior author, then an undergraduate student seeking a graduate program and a potential advisor), Davis was most receptive, indeed charming, and artfully steered that student to the University of Pennsylvania and the ANSP.

PERSONAL LIFE

George Morgan Davis was born in Bridgeport, Connecticut, on May 21, 1938, the son of William Earle Davis and Amelia Morgan Davis. His father died when he was only two years old. George attended Northfield Mount Hermon [Preparatory] School in Gill, Massachusetts, earned his B. A. (1960) from Marietta College in Ohio, and his M. S. (1962) and his Ph. D. (1965) from the University of Michigan (Fig. 2). He married Harriet (Happy) Hopkins (later Robertson) on June 17, 1961, in Hanson, Massachusetts. He had two daughters with Happy, Lynne Davis Anderson of Spotsylvania, Virginia, and Julia Davis Lockwood of Clayton (near Spokane), Washington. Julia graduated from Marietta College in 1989; George was awarded an honorary doctorate at that event.

Davis reported for duty as chief malacologist at the U. S. Army's 406th Medical Laboratory at Camp Zama, Japan, in the summer of 1965. In Japan, he rescued Kuro, a stray dog with a broken leg. In 1970, he accepted the position of Associate Curator and Chair of the Department of Malacology at the Academy of Natural Sciences in Philadelphia, and moved the family, plus Kuro, back to the U. S. to Haddonfield, New Jersey. He became Full Curator at ANSP in 1978. Following separation from Happy about 1975, he married the malacologist K. Elaine Hoagland. In addition to Elaine, Happy, and his two daughters, he is survived by five grandchildren (Becca Morgan Anderson, Timothy Anderson, Jonathan Anderson, Neill Lockwood III, Dean Lockwood), a brother William E. Davis, and a niece, Robin Burns.

George played the cello for most of his life. He played in orchestras and chamber music groups in Ohio, Japan, Haddonfield, and Philadelphia. His father played cello and three of his grandchildren also played cello in middle school and high school. He fenced as a hobby in college and in Japan and taught fencing to people who were interested in learning. He also had a passion for sailing (Fig. 3), and more than once traveled by sailboat to scientific meetings on the East Coast.



FIG. 2. With his mother at the University of Michigan commencement, 1965.

Over the course of his long career, he held adjunct professorships at Jefferson Medical College (1971–1980), University of Pennsylvania (1972–1983), and University of Delaware (1982–1987). He was an advisor to the U. S. Education Commission in Japan (1966–1967) and received the U. S. Government Superior Performance Award in 1968. He served as President of the Association of Systematics Collections (1982–1984) and the American Malacological Union (now Society) (1976–1977). He held memberships in the Malacological Society of Japan, Ecological Society of America, American Association for the Advancement of Science, American Institute for Biological Sciences, American Society of Zoologists, Japanese and Korean Society of Parasitology, and the Philadelphia Shell Club.

EARLY CAREER

Entering graduate studies at the University of Michigan in 1960, Davis joined Henry van der Schalie's laboratory and was immediately recruited into a long-running research program sponsored by the Armed Forces Epidemiologi-



FIG. 3. At the Woods Hole dock with his sailboat, *Earendil*, 1990.

cal Board to assess the risk that North American freshwater gastropods might serve as hosts for schistosomiasis in Asia. Davis' 1965 dissertation, "The systematic relationship of *Pomatiopsis lapidaria* (Say) and *Oncomelania hupensis formosana* (Pilsbry & Hirase) (Gastropoda: Hydrobiidae)" was published in *Malacologia* in 1967 (Bibliography, #16). That work reviewed classical malacology, summarized failed attempts to hybridize the two species in the laboratory (an effort continued in the Van der Schalie lab in following years), and described the technique of disc gel electrophoresis, one of the earliest applications of molecular techniques to the study of molluscan systematics (#5). The final section was a 13-page study entitled "Laboratory Ecology," in which he compared *Pomatiopsis* Tryon, 1862, and *Oncomelania* Gredler, 1881 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 when observed.

Already evident in his dissertation, Davis' keen attention to the fine details of molluscan morphology, and his ability to transmit such detail vividly through both image and word, were the first hallmark of his career. Another hallmark became evident as he 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 (#16, plate 32). Although the assignment of homologies among those bands might have been a bit speculative, it is possible to see in 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 that they generate, became the second hallmark of George Davis' career.

The conclusions in Davis' dissertation were minor, given the years of intense effort he had invested in them. Asian *Oncomelania* and North American *Pomatiopsis* are now recognized as two entirely different entities, with no reason to

be concerned that populations of *Schistosoma japonica* Katsurada, 1904 (the only parasitic trematode then known to cause the human disease schistosomiasis in Asia) adapted to the former snail might infect the latter.

Concurrent with the consensus of the day, Davis placed both genera in the subfamily Pomatiopsinae of the large and diverse family Hydrobiidae. Although his dissertation research did not bear directly on the question, Davis also endorsed the growing consensus that regional shell variants of *Oncomelania hupensis* Gredler, 1881, might be allocated to four subspecific nomina: the typical form in China, *O. h. formosana* (Pilsbry & Hirase, 1905) in Taiwan, *O. h. quadrasi* (Möllendorff, 1895) in the Philippines, and *O. h. nosophora* (G. C. Robson, 1915) in Japan. In a follow-up paper published in 1969 (#28), however, Davis redescribed a fifth subspecies, *O. h. chiui* (Habe & Miyazaki, 1962), from an isolated ba-

sin in northern Taiwan. In addition to 24 pages of artistically lavish and technically detailed anatomical illustrations and observations, eight pages of disc electrophoretic comparison, and a single-page review of his laboratory hybridization results, Davis added ten pages describing two trail-blazing immunological techniques picked up in the laboratory of Gene K. Lindsay, another of his influential mentors at the University of Michigan.

Antisera were developed from whole homogenized foot muscle of *Oncomelania hupensis formosana* (A) and *O. h. chiui* (B), injected into white rabbits according to an elaborate schedule over a period of two months, then 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 immunoelectrophoretic 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. Analyzing the fine white precipitin arcs that developed after 3–5 days under such conditions, Davis was able to deduce some measure of genetic similarity between A and B. Only four previous applications of immunological methodologies to malacological research had been presented prior to this 1969 publication.

A CIVILIAN IN THE ARMY (1965–1970)

As chief malacologist for the U. S. Army in Japan, most of Davis' research effort, at least initially, was directed toward *Semisulcospira* O. Boettger, 1886 (then considered a pleurocerid) and a variety of thiarids (e.g., *Brotia* H. Adams, 1866), hosting the lung fluke *Paragonimus* Braun, 1899, in Japan and Southeast Asia (Fig. 4; #17, 18, 21, 22, 29, 35, 37, 46). Field expeditions during this time sometimes took the team through remote areas of "uncertain politics." As he recalled to the senior author, he spent many weeks travelling by jeep through the jungles in vehicles fitted with gun racks mounted directly overhead, for easy access to firearms should bandits or guerillas threaten (Fig. 5). At some point during one of those expeditions, his team broke through the undergrowth onto an airstrip. Parked in an airplane at the end of this airstrip was the King of Siam (Thailand). The King was American-born, and upon hear-

ing that an American scientist was visiting a remote corner of his kingdom, he invited Davis to dinner. This tale explained the presence of a three-piece suit, freshly pressed, hanging in a garment bag across the back seat of the jeep. "We talked about jazz, and sailing, and so forth," said Davis. Had he not been able to assemble the proper attire at that critical juncture, an important opportunity for international diplomacy might have been sacrificed.

He was also most certainly involved in at least one expedition to Thailand, yielding the descriptions of two new species of *Tricula* W. H. Benson, 1843, and what turned out to be a pivotal insight into the evolution of the entire East Asian hydrobioid fauna (#20). 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 (#25), Davis focused entirely upon the Japanese Blood Fluke *Schistosoma japonicum* (Katsurada, 1904) and its intermediate host, *Oncomelania hupensis*, in Japan, China, Taiwan, and the Philippines. He mentioned *Tricula* only in passing, to distinguish it from *Oncomelania*. That would change, for Iijima and Garcia (1967) had already 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*. By 1969, World Health Organization (WHO) teams were mounting epidemiological surveys to learn more.

FROM ASIA TO THE ACADEMY (1970–1997)

As a Curator at ANSP, Davis traveled extensively for field research. "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



FIG. 4. With the original illustration for plate 4 in #22, ca. 1969. Courtesy of the Academy of Natural Sciences of Drexel University, Library & Archives.

cursed war. For eight years, he has looked under boulders and sifted through leaves and sand for a secret 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" (Kirk, 1983: 20).

In 1971, WHO and USAID medical teams were able to identify the intermediate host of the Mekong schistosome as *Lithoglyphopsis* (now *Neotricula*) *aperta* Temcharoen, 1971, a newly described hydrobioid snail. What followed was George Davis' most important contribution to science—from a biomedical standpoint in any case—in his 1976 "Monograph on *Lithoglyphopsis aperta*," coauthored with Temcharoen and Viroj Kitikoon (#56), together with his larger "Origin and evolution of the gastropod family Pomatiopsidae," published three years later (#71).

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* Thiele, 1928. The data that he presented in evidence

were entirely morphological, but wonderful in their quality and quantity. The anatomical drawings and observations were superbly detailed. By 1976, Davis was tabulating mean, standard deviation, and range for measurements taken on such elastic characters as the osphradium, prostate, and verge, with 11 lengths and widths from the ganglia of the central nervous system alone. Newly added to his 1976 paper were four pages of histological sections showing microscopic details of the reproductive and nervous systems.

Davis and his coauthors described three races of *Lithoglyphopsis 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 (1928) type for the genus *Lithoglyphopsis* based on 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 detail and broad in scope, there

was but a single distinction in the structure of a radula tooth between *Lithoglyphopsis* and a new but unnamed genus. Davis and his colleagues (#56; 1976f: 241) declined to name it, 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.”

It was in the 120 pages of the 1979 ANSP *Monograph* 20 (#71) that those morphologies became known. In that highly synthetic work, Davis reported the results from five years of studies in makeshift laboratories at Khemarat, Ubon Ratchathani, and Khong Island, hunched over a Wild dissecting microscope, peering at the anatomy of hundreds of tiny snails pinned into 9 cm Petri dishes (Fig. 6). Ultimately, he recorded observations on 27 shell characters and 23 anatomical characters for 69 hydrobiid species collected from 14 sites in the upper Mekong drainage of Thailand and Laos between 1970 and 1975.

Efforts to catalog the exuberantly diverse hydrobiid fauna of the Mekong began 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 nonmarine aquatic Mollusca of Thailand, 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 describe just his observations on *Lithoglyphopsis aperta*, Davis required 46 journal pages. Punching a couple buttons on his calculator, he might have paused briefly to consider publication options for a 3,174-page monograph to answer Brandt’s 423 pages. Instead, he opted for a synthesis merely 120 pages in length, containing only 11 detailed anatomical illustrations, four schematic diagrams, and four plates of shell photos, all judiciously selected to emphasize the most important systematic differences. That monograph also contained seven phylogenetic trees or tree-like diagrams, a first for Davis. Davis analyzed his 50-character dataset with NT-SYS, a package of numerical taxonomy programs published by Rohlf et al. (1972), calculating taxonomic distances for UPGMA [Unweighted Pair Group Method with Arithmetic Mean] cluster analysis (Sokal & Michener, 1958). The classification that he ultimately proposed allocated 69 Mekong species (six newly described) to ten genera (two newly



FIG. 5. In a military vehicle, 1965–1970.

described), and those ten genera into three newly described “tribes,” all allocated to the subfamily Triculinae. *Lithoglyphopsis aperta*, the host of the Mekong River schistosome, became *Tricula aperta*, along with the two other *Tricula* species that Davis described in 1968 (#20). Davis proposed that his Triculinae, newly expanded and characterized, be joined together with the 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. The establishment of formal diplomatic ties between the USA and the People’s Republic of China, prompted an abundance of grant funding to promote collaborative research. Throughout the 1980s, Davis made many and lengthy fieldtrips to China, developing collaborations with numerous researchers across the subcontinent (Fig. 7). Also noteworthy during this period was a 1985 field trip to India, in search of *Tricula montana* W. H. Benson, 1843, type species of the genus *Tricula*. Davis’ anatomical observations on *T. montana* suggested a close match to *T. bolingi*, which he had described from Thailand in



FIG. 6. Dooley Foundation Hospital, by the Mekong River in Laos, 1975.

1968 (#20), but not to his *T. burchi* (also #20) or to the medically important *T. aperta* of the Mekong. Thus, in 1986, along with coauthors N. V. Subba Rao and Elaine Hoagland, he segregated *T. aperta* and *T. burchi* into a new genus *Neotricula* (#106).

Between 1983 and 1997, Davis and an extensive team 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” (Davis, 1992b: 143) (Fig. 7; #86, 96, 100, 103, 117, 120, 121, 122, 129, 136, 143, 144, 151). Most of these appeared in the *Proceedings of the ANSP*. But the largest and most synthetic, his 200-page “Pomatiopsidae of Hunan, China,” authored with seven Chinese collaborators, was published in *Malacologia*, 1992 (#129).

Just the table of abbreviations for Davis’ 1992 monograph included 131 entries—anatomical characters 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. Systematic analyses were both by phenetic methodology (UPGMA, PCA, minimum-spanning trees) and (also new since the 1980s) by Hennigian cladistics.

To classify the 17 species of pomatiopsid snails (four of them new) inhabiting Hunan ultimately required creation of a new tribe in the subfamily Pomatiopsinae and two new genera in the subfamily Triculinae, bringing the number of genera for the latter subfamily up to 21.

FROM THE ACADEMY TO AMERICA (1976–2001)

In 1981, Davis and Sam Fuller published their “Genetic relationships among Recent Unio-nacea of North America [sic]” in *Malacologia* (#80). This was the culmination of research that began years earlier, and that attracted the senior author to Davis as a mentor. He recalled:

“George Davis and I enjoyed a successful visit to Lake Waccamaw on a 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



FIG. 7. Expedition to China, 2000s.

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. We repaired briefly to our separate rooms, washed up, and met downstairs again for supper. 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 injustice.' The humiliated waiter snatched up the plate and beat a hasty retreat to the kitchen. A vessel of golden-colored liqueur appeared. 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."

Davis & Fuller (#80) tabulated ten different classification systems proposed for the North American unionoidean mussels to that date, noting the "profound influence" of Ortmann's classic (1910, 1913) 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 12–60 individual mussels of each species and injected into rabbits according to an elaborate schedule over six weeks, with the antisera tested for effectiveness by the resolution of at least ten 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. Matrices of pairwise differences (calculated under several assumptions) were visualized

using the multidimensional scaling routine of NT-SYS.

Davis & Fuller's analysis suggested three coequal groups, which they elected to classify as subfamilies of the Unionidae: Margaritiferinae, Anodontinae, and Ambleminae. Then calling up a small set of six morphological characters, they recognized four "tribes" in the Ambleminae: Amblemini, Pleurobemini, Lampsilini, and Gonideini.

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 (#82). Davis and colleagues analyzed genetic variation at 14 allozyme-encoding loci in 22 populations of *Elliptio* Rafinesque, 1819 (including the four species that we collected at Lake Waccamaw in August 1977), along with eight outgroup populations of other unionoidean genera, calculating a matrix of Nei's genetic distances and 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* from 1986 to 2016. Caryl Hesterman's manifold contributions might perhaps have warranted better acknowledgment during Davis' lifetime than they were ultimately granted.

Davis went on to author or collaborate on two additional studies of genetic variation at allozyme-encoding loci in the unionoideans, both in 1984, one expanding his coverage to include populations of *Unio*merus Conrad, 1853; *Megaloniaias* Utterback, 1915; *Quadrula* Rafinesque, 1820; *Elliptioideus* Frierson, 1927; and *Quincuncina* Ortmann, 1822 (#93), the other focusing on the genetics of peripheral populations in Nova Scotia, with his student Pieter Kat (#97). In the late 1980s, Davis also applied allozyme electrophoretic techniques in several collaborative studies addressing genetic relationships among brackish-water populations of *Hydrobia* W. Hartmann, 1821, on the U. S. Atlantic coast (#112, 116). In 1994, he and coauthors Dave Strayer and Tom Bianchi shocked the malacological world with a demonstration that an Atlantic drainage

population of *Pleurocera* (previously *Goniobasis* or *Elimia*) *virginica* (Gmelin, 1791) might be hybridizing with a Great Lakes population of *P. semicarinata livescens* (Menke, 1830) (previously *Goniobasis* or *Elimia livescens*) through the Erie Canal (#133).

By 1990, Davis was becoming involved with pioneering applications of new DNA sequencing technologies to address deep and long-standing 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 ten pulmonate gastropods (#118) 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 (#139). Davis collaborated with Chuck Lydeard in 1992 on a sequencing study of unionid mussels while Lydeard was a post doc at the Savannah River Ecology Lab in Georgia. This work was ultimately published in 1996 (#148; Lydeard, 2025).

In 1996, Davis appeared as a coauthor on sequencing studies directed toward the evolution of his first love, the Asian pomatiopsids. That collaborative study (#149), documenting cytochrome b sequence variation among four individual *Oncomelania hupensis* (three populations, two subspecies), was augmented two years later by a larger study of *cox1* sequence diversity in 13 individual rissooids with three more distantly related mollusks as outgroups (#155).

The *cox1* paper marked the first appearance of Thomas Wilke, then a postdoctoral associate at the ANSP, among 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 listed George Washington University as his professional address, having been pushed out from the ANSP in 2000. Piling gene upon gene and taxon upon taxon, Wilke and colleagues (#173) sequenced *cox1* 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, Cochliopidae and Lithoglyphidae.

In 2013, Wilke and a five-man team, now including Robert Hershler of the National Museum of Natural History and Winston Ponder of The Australian Museum, "pushed short DNA

fragments to the limit" (as the title implied). Using an analysis of the sequence variation in three genes over 90 hydrobioid gastropods, they split the old worldwide Hydrobiidae into 21 family-level taxa, carrying the process that Davis had begun in 1979 to its inevitable conclusion. Davis was not listed among the authors of that 2013 work, but the acknowledgments section 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" (Wilke et al., 2013: 723).

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" (#99). 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." He meant the Museum of Comparative Zoology (MCZ) at Harvard University.

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 (1944–1946), rose to sit in the Pilsbry Chair (1954–1969), 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 (Lydeard, 2025). 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 (now Society), serving as its President (1976–1977), and on its Council perennially for decades thereafter. From Philadelphia, he sent his student, Bob Hershler, on to Washington, spreading the UMMZ scientific ethos into the marble halls of the USNM.

From Philadelphia too, the senior author 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 Arthur 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 Robert Robertson occupied the north corner of the expansive collection floor. Frequent visitors included Elaine Hoagland down from Lehigh University, Bob Hershler up from Johns Hopkins, cigar-chomping Hal Lewis, and the aristocratic Professor Arthur J. Cain. But the magic was to be found in a modern three-story addition hidden 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 the walls of elaborate and exotic equipment work. He toured me through an animal room stacked with cages of rabbits—poked, stuck, and bled, smelling like science—into the spacious and well-appointed laboratory he called his own. And there I met Caryl Hesterman, very kind and very firm, who would be my hostess and guide for the next four years. All of this George Davis made available for my use, with 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 meet-

ing 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 (#138):

“If we could call back to the present some of the early fathers of morphology-based malacology, for example Cuvier, Bouvier, Troscchel, 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, 1994f: 3).

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”; it was a plenary lecture at a symposium on Molecular Techniques and Molluscan Phylogeny convened during the 11th International Malacological Congress in Siena, Italy in August–September 1992. 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” (Davis, 1994f: 3).

Then after a nod back to classical methodologies, the remainder of Davis' lecture was directed toward the most modern tools in systematic biology that year. On the ninth of those 20 pages, he paused to address the concept of the species. Davis (1994f:11) 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. “The process of speciation in allopatry”, he concluded, “has nothing to do with ‘isolating barriers’” (Davis, 1994f: 11). Rather, Davis endorsed a variant of the “Cohesion Species Concept” of Templeton (1989), 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, in which species were defined subjectively on the basis of the visible phenotype, had become the neoclassical, with species defined subjectively based on the invisible genotype.

And so was the modern synthesis of Darwin + Mendel bridged. Born a scion of the classics, George Davis was brought into modernity with his early laboratory experiments on hybridization. However, finding objective, hypothesis-driven science too constraining, he jumped over the deeper waters of Fisher, Mayr, Dobzhansky, and Simpson to the neoclassical, carrying our discipline with him. It has become our job today, as professional malacologists, to distinguish the species, a job much too important to be left to the untidy whim of the animals themselves.

George M. Davis was one of the greatest American malacologists of the age just past, an age that dawned when Thomas Say of Philadelphia first gathered mollusks on our continent and told us what we had been stepping upon; an age 150 years in duration, through which American science rose from the backwater to the mainstream. In just such fashion, seven generations later, George Davis of Philadelphia mounted expeditions to the most remote corners of the 20th century world, gathered up their mollusks, and showed the inhabitants what they had been stepping upon. Davis was also the first American malacologist of the age in which we live today, an age that opened in 1964, when he coaxed the first molluscan homogenate through a tube gel, and peered at protein bands as they developed, looking for clues to the evolutionary relatedness of the mollusks that he had homogenized. He also brought the electronic database of the collection to Philadelphia in 1975 (Rosenberg

& Callomon, 2025). He was a commanding presence in our discipline when our discipline turned to molecular methods. Charming and urbane, witty and vain, ever looking for new worlds to conquer. Love him or hate him, George Morgan Davis could not be ignored. We shall not see his like again.

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- Aquidauania* Davis, 1979f: 116. (Pomatiopsidae)
- Chencuia* Davis in Davis & Subba Rao, 1997a: 297, 298. (Erhaliidae)
- Delavaya dianchiensis* Davis & Guo in Davis et al., 1986a: 468, 470–474, 477, figs. 1J–G, 2–7, tables 1–5, 50, 52. (Pomatiopsidae) China: Yunnan Province, Jinxiandeng Spring.
- Erhaia* Davis & Kuo in Davis et al., 1985a: 66, 67. (Erhaliidae)
- Erhaia daliensis* Davis & Kuo in Davis et al., 1985a: 50, 52–54, 68, figs. 1–10, tables 1–4, 9. (Erhaliidae) China: Yunnan Province, Dazhifang Village.
- Erhaia kunmingensis* Davis & Kuo in Davis et al., 1985a: 57, 60, 62, 63, 66, 68, figs. 11–17, tables 5–9. (Erhaliidae) China: Yunnan Province, Xiaolongmen Village.
- Erhaia nainitalensis* Davis & Subba Rao, 1997a: 276–280, figs. 1–13, 13A, C, E, G,

- tables 1–5. (Erhaliidae) India: Nainital District, Padampuri.
- Erhaiini Davis & Kuo in Davis et al., 1985a: 69. (Amnicolidae)
- Gammatricula* Davis & Liu in Davis et al., 1990d: 145, 146. (Pomatiopsidae)
- Gammatricula chinensis* Davis, Liu & Chen, 1990d: 146–148, 151, figs. 1–13, tables 1–6. (Pomatiopsidae) China: Jianzxi Province, Gugang Town.
- Gammatricula songi* Davis & Chen in Davis et al., 1994j: 117–119, 122, 123, figs. 2–15, tables 1–14. (Pomatiopsidae) China: Zhejiang Province, Wang An Village.
- Guoia* Davis & Chen in Davis et al., 1992b: 186, 187. (Pomatiopsidae)
- Halewisia* Davis, 1979f: 111. (Pomatiopsidae)
- Helebops carrieri* Davis & McKee, 1989b: 217, 218, 220, 224, 225, 231–234, 236–238, figs. 2A–G, 3, 4, 5A–D, 6–26, tables 1–6. (Hydrobiidae) Maryland: Dorchester County, Ragged Point Road.
- Hydrobia djerbaensis* Wilke, Pfenninger & Davis, 2002a: 59, 60, fig. 10J, appendix 11A, B. (Hydrobiidae) Tunisia, Djerba Island.
- Jinghongia* Davis in Davis & Kang, 1990c: 136, 138. (Pomatiopsidae)
- Jullieniini Davis, 1979f: 23. (Pomatiopsidae)
- Karelainia* Davis, 1979f: 111. (Pomatiopsidae)
- Kunmingia* Davis & Kuo in Davis et al., 1984e: 189. (Pomatiopsidae)
- Lacunopsini Davis, 1979f: 23, 25. (Pomatiopsidae)
- Neoprososthenia* Davis & Kuo in Davis et al., 1984e: 189. (Pomatiopsidae)
- Neotricula* Davis in Davis et al., 1986d: 436–438. (Pomatiopsidae)
- Neotricula dianmenensis* Davis & Chen in Davis et al., 1992b: 218, 222, 229–231, 234, fig. 70A–D, 71–77, tables 34–38. (Pomatiopsidae) China: Hengyang Prefecture, Jiepai Village.
- Neotricula duplicata* Davis & Chen in Davis et al., 1992b: 234–236, 238, 241, 243–246, 248, figs. 70 E–I, 78–95, tables 39–45. (Pomatiopsidae) China: Yiyang Prefecture, Huang-sha-ping Village.
- Neotricula lillii* Davis & Chen in Davis et al., 1992b: 248, 252, 256, 257, fig. 70J–L, 96–102, tables 46–51. (Pomatiopsidae) China: Zhuzhou Prefecture, Chang Wang Village.
- Oncomelania hupensis lindoensis* Davis & Carney, 1973a: 4–6, 8–10, 12, 15, figs. 8, 9, 15, 16–21, tables 1–4, 6, 11. (Pomatiopsidae) Sulawesi, Lake Lindu.
- Pachydrobiini Davis & Kang, 1990c: 138, 139. (Pomatiopsidae)
- Pseudobythinellini Davis & Chen in Davis et al., 1992b: 154, 155. (Amnicolidae)
- Robertsia* Davis & Greer, 1980d: 249, 251, 253. (Pomatiopsidae)
- Robertsia gismanni* Davis & Greer, 1980d: 262–264, fig. 3D–F, tables 3–5, 9–12. (Pomatiopsidae) West Malaysia: Jelai River system, Serau River.
- Robertsia kaporensis* Davis & Greer, 1980d: 253–260, 262, fig. 3A–C, 4–8, 9B, 11, tables 2–9. (Pomatiopsidae) West Malaysia: Jelai River system, Kapor River.
- Semisulcospira habei* Davis, 1969i: 237, 239, 240, pl. 3, figs. 1–3, tables 19–21. (Semisulcospiridae) Japan: Kyoto Administrative District, Uji River.
- Semisulcospira habei yamaguchi* Davis, 1969i: 240, 243, pl. 3, figs. 4–6, tables 22–24. (Semisulcospiridae) Japan: Shiga Prefecture, Lake Biwa.
- Spurwinkia* Davis & Mazurkiewicz in Davis et al., 1982b: 162, 164–166. (Cochliopidae)
- Stenothyra huaimoi* Hoagland & Davis, 1979g: 211, 212, 227, figs. 57, 61F. (Stenothyridae) Laos: Vientiane Province, Huai Mo River.
- Stenothyra jinghongensis* Davis, Guo & Hoagland in Davis et al., 1986b: 331, 333–335, figs. 1F–H, 14–16, table 7–10. (Stenothyridae) China: Mekong River, Jinghong City.
- Stenothyra khongi* Hoagland & Davis, 1979g: 212, 213, 227, figs. 49–52, 59D–F. (Stenothyridae) Laos: Mekong River, Ban Na Village.
- Tricula bamboensis* Davis & Zheng, 1986a: 486, 490, 492–494, fig. 20A–E, 21–26, tables 11–15, 50, 52. (Pomatiopsidae) China: Yunnan Province, Kunming.
- Tricula bollingi* Davis, 1968c: 304, figs. 5–12, 18B, 19–22, tables 5–12. (Pomatiopsidae) Thailand: Chiang Mai Province, Pang Makham Pom Village.
- Tricula burchi* Davis, 1968c: 296, figs. 1–3, 13, 14, 16, 17, 18A, tables 1–4, 12. (Pomatiopsidae) Thailand: Chiang Mai Province, Huai Mae Kut at Ban Tham.
- Tricula hudiequanensis* Davis & Guo in Davis et al., 1986a: 512–516, figs. 45B–F, 46–53, tables 28–32, 50, 52. (Pomatiopsidae) China: Yunnan Province, Hudi Spring.
- Tricula ludongbini* Davis & Guo in Davis et al., 1986a: 516, 517, 520, 523–526, figs. 54–60, tables 33–36, 50, 52. (Pomatiopsidae) China: Yunnan Province, Black Dragon Pool.
- Tricula maxidens* Chen & Davis in Davis et al., 1992b: 297, 300, 301, figs. 137–145, tables 67–70. (Pomatiopsidae) China: Xiangxi Prefecture, Yantuo Village.

Tricula xianfengensis Davis & Guo in Davis et al., 1986a: 526–528, 530, 535, figs. 61–72, tables 38–43, 50, 52. (Pomatiopsidae) China: Yunnan Province, Xianfeng Village.

Tricula xiaolongmenensis Davis & Guo in Davis et al., 1986a: 535, 548, 552, 554, 556, figs. 73–79, tables 44–50, 52. (Pomatiopsidae) China: Yunnan Province, Xialongmen Village.

Triculini Davis, 1979f: 21–23. (Pomatiopsidae)

Type material of species-group taxa are illustrated by Rosenberg & Seizova (2025)

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Boetersiella davis Arconada & Ramos, 2021: 964, figs. 9A–H, 10A–D, 11A–F, 12A–D; tables 1–4. (Hydrobiidae) Spain: Durcal (Granada), Pilar del Mono spring.

Davisassiminea Fukuda, Ponder, & Criscione, 2025: 28, 29. Type species: *Rissoa (Cingula) capensis* G. B. Sowerby III, 1892.

Davishydrobia Wilke in Wilke & Stelbrink, 2025: 196–199. (Hydrobiidae) Type species: *Paludina knysnaensis* Krauss, 1848.

Fontelicella davis D. W. Taylor, 1967: 10, fig. 4. (Hydrobiidae) New Mexico.

Fontigens davis Dillon, Malabad, Orndorff & Liu, 2023: 300, 301, figs. 9.4, 9.5B. (Fontigentidae) Virginia: Giles County, Dulaneys Cave.

Heleobia davis Pons da Silva & Thome, 1985: 515–534 (Hydrobiidae) Rio Guaiba, Rio Grande do Sul, Brazil.

Paraprososthenia davis Brandt, 1968: 234, pl. 8, fig. 20. (Delavayidae) East Thailand, Bandan: Mekong River.

Potamolithus davis de Lucia, Montenegro & Gutiérrez, 2025: 174–180, figs. 4–30, Tables 1–3. (Tateidae) Argentina: La Yerba Fall, Paraíso Stream (27°14'13.1"S, 54°02'40.1"W), Misiones Province.

Semisulcospira davis Sawada & Nakano, 2021: 6–9, figs. 1, 4–7, table 1. (Semisulcospiridae) Japan: Lake Biwa.

Tricula davis Grego, 2018: 25, 26, figs. 33–36. (Pomatiopsidae) Laos: Khammouane Province, Tham Khon Dôn Cave.

Veronicella davis Thomé, Santos & Pedott, 1996: 265–274 (Veronicellidae) Brazil.

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