Tiny Jewels: An introduction to pupillid taxonomy, ecology, and collection

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Introduction

Across most of North America roughly 50% of all land snail species and almost 90% of all individuals are less than 5mm in maximum dimension, or approximately the size of Lincoln's chin on a penny (Fig. 1). Of these, the Pupillidae make an especially important contribution to biodiversity. This family (here used in the expansive, historical sense as outlined by H.A. Pilsbry) includes the genera *Bothriopupa, Chaenaxis, Columella, Gastrocopta, Pupilla, Pupisoma, Sterkia,* and *Vertigo*, and encompasses almost 10% of the entire USA and Canadian fauna (~125 species), with an unknown number of additional taxa residing in Mexico. North America represents the global biodiversity center for *Chaenaxis, Gastrocopta, Pupilla,* and *Vertigo*, harboring at least 2/3 of all known global taxa and all known morphological groups. The Pupillidae are the third most diverse family east of the continental divide (12% of the total fauna), exceeded only by the Polygyridae (30%) and Zonitidae (22%). Pupillids alone make up approximately one-third of both total species diversity and number of individuals for site-scale faunas throughout North America, with this level approaching 80% - 100% within the northern taiga and tundra, acidic wetlands and savannas of the southeastern coastal plain, and fog-belt chaparral of the California coast. In some places, such as the pocosins of the North Carolina coastal plain, the number of pupillid land snails can exceed 5,000 individuals per square meter.

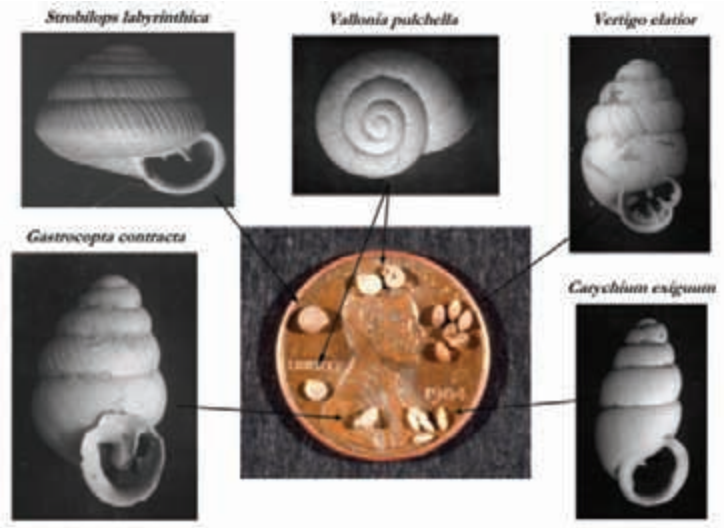

Figure 1: Representative micro-snails from a northeastern Wisconsin wet meadow.

Yet, in spite of their ecological importance, pupillids and other microsnails have been almost completely ignored by collectors. For instance, in Abbott's "*Compendium of Landshells*" only a few dozen microsnail species are included out of the roughly 2000 illustrated, with only 11 of these being pupillids. The large shells which dominate this book in actuality represent less than 2% of all individuals across not only North America, but also New Zealand, eastern Australia, western Africa, and southeast Asia as well.

Adequate documentation of land snail diversity thus requires investigators to efficiently collect and accurately identify pupillids. Unfortunately, neither has been common. Two major reasons for this exist. First, as none of the taxa exceeds 6mm in maximum dimension, accurate identification requires critical examination at 20-40x magnification. This has made even laboratory identifications suspect, with there being a high incidence of misidentification and mixed lots in museum collections. For instance, I recently found that over 90% of the *Vertigo* collections in the National Museum of Canada were incorrectly identified. Second, most species are cryptic, being found primarily in decomposed leaf litter. As a consequence they tend to be undersampled by those relying on locating individuals by eye. This has led to the lack of documentation of not only the normal range of morphological variation within and between populations and taxa but also the true geographic and ecological ranges for most species. As a result, hasty conclusions concerning specific identity, biogeography, and ecology in this family has been unfortunately commonplace.

Over the last decade, colleague Brian Coles of the Welsh National Museum and I have observed pupillid communities across most of North America, ranging from central Quebec, Hudson's Bay and the Alaskan north slope to Florida, Texas, the desert southwest, and coastal California. In this time, we have collected from over 1,700 stations, including almost 75% of North American pupillid taxa and over 200,000 total individuals. In the process we have described two new species, with perhaps another 5-6 waiting in the wings. This experience provides a unique perspective with which to introduce this important group of mollusks to the shell collecting community.

Important Concological Features for Shell Identification

Identification of pupillid shells requires careful observation and comparison of approximately two-dozen shell characteristics. While a number of these are also commonly used in identification of taxa from other families, use of some is almost completely limited to pupillids. The more important of these features are:

Apex: the uppermost 2-3 whorls of the shell
Body Whorl: the final full whorl in an adult shell
Callus: calcified thickening of the palatal wall of the aperture, often deposited between lamellae

Crest: a bowing out of the shell immediately in back of the aperture as seen in side view
Palatal Depression: indentation of the shell surface at the location of the palatal lamellae
Penultimate Whorl: the next to the last whorl in an adult shell
Sinulus: indentation of the aperture margin along the palatal wall
Suture: indentation of the shell surface where two whorls meet

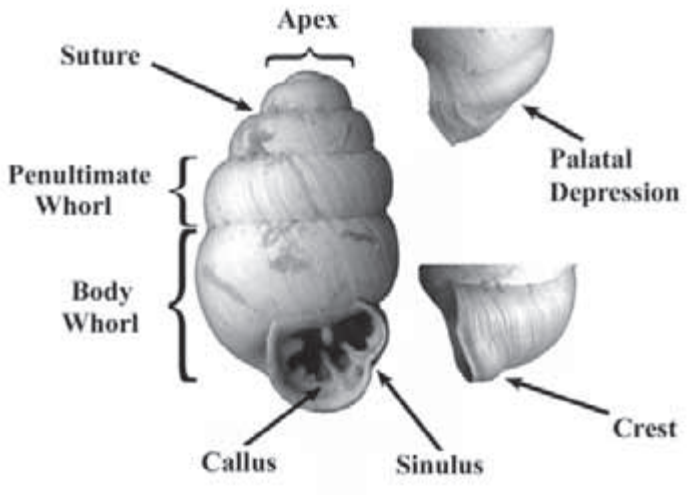

Figure 2: Major shell features used to identify pupillid taxa, illustrated through use of SEM images of *Vertigo elatior* (left), *V. bollesiana* (upper right) and *V. cristata* (lower right).

Overall shell shape is also often diagnostic, ranging from conical to ovoid to cylindrical. Also of considerable importance in pupillid taxonomy is the position and appearance of a variable number of shell thickenings often found in the shell aperture. While often colloquially referred to as 'teeth' this term is misleading as they are in no way related to the snail's gastrointestinal track. In fact, it remains unclear what function (if any) they serve. Because of their thin, plate-like appearance, it is best to refer to these as 'lamellae'. It should be noted, however, that H.A. Pilsbry made the terminology unnecessarily complex by referring to the palatal lamellae as 'lobes.' The up to seven or more lamellae in the shell aperture are designated by their position:

Angular: the plate on the parietal wall of the aperture to the right of the parietal lamella in dextral shells
Basal: the plate on the bottom left side (in dextral shells) of the aperture below the columellar lamella
Columellar: the plate on the columellar wall of the aperture
Infraparietal: the plate on the parietal wall to the left of the parietal lamella in dextral shells
Parietal: major plate in the middle of the parietal wall of the aperture
Lower Palatal: lowermost of the two major plates often found on the palatal wall
Upper Palatal: uppermost of the of the two major plates often found on the palatal wall

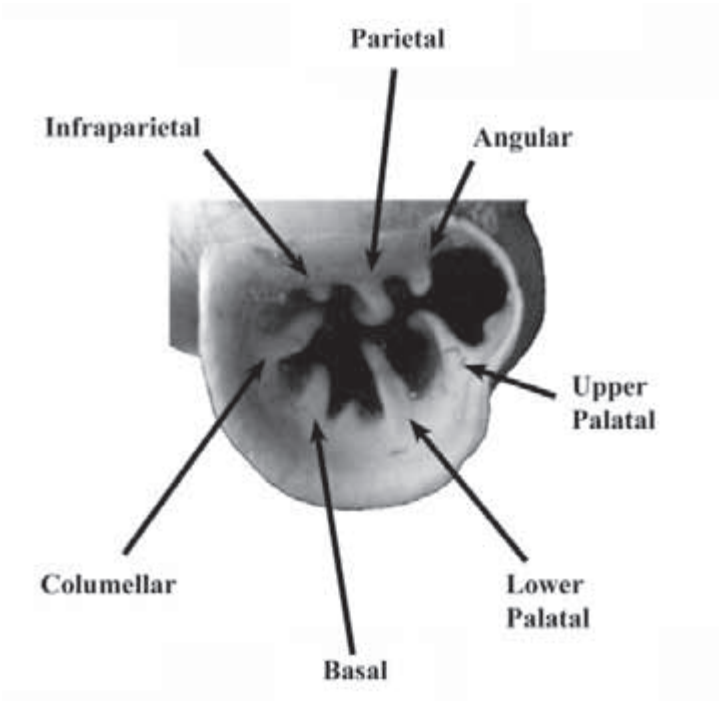

Figure 3: Location of the major apertural lamellae used in pupillid identification, illustrated through use of a *Vertigo ovata* SEM image.

In the genus *Gastrocopta*, the angular and parietal lamellae are fused into a single body, which is often referred to as an 'angulo-parietal lamella.' It is important to note that, depending upon the species, the strength of a given lamella, or the total number of lamellae, may vary between individuals both within and between populations. This level of variability can only be assessed when large numbers of shells are observed over a broad ecological and/or geographic range.

Species Concepts and Taxonomic Issues

Some believe that because their critical distinguishing features are often no larger than a tenth of a mm (or less) in size, they must be of no taxonomic merit. These researchers have tended to recommend the lumping of many taxa. On the other hand, others have felt that even the slightest differences must have taxonomic merit, and have advocated the elevation of many pupillid forms to species-level rank.

Until recently, there has been no objective way to assess these opposing viewpoints, as pupillids often demonstrate a high degree of aphallism and limited levels of anatomical variation. As a result, the level of taxonomic discourse often descended into name-calling and appeals to authority. Thanks to DNA sequencing, independent information can now be obtained. We recently completed an initial survey of DNA sequences from 25 pupillid taxa, focusing on the *Vertigo gouldii* group (Figure 4). While these analyses demonstrate that shell features should not be used to infer evolutionary relationships, they usually function well in assigning species-level differences. The beliefs of some of the most ardent lumpers can thus be shown to be false, with the former western '*V.*

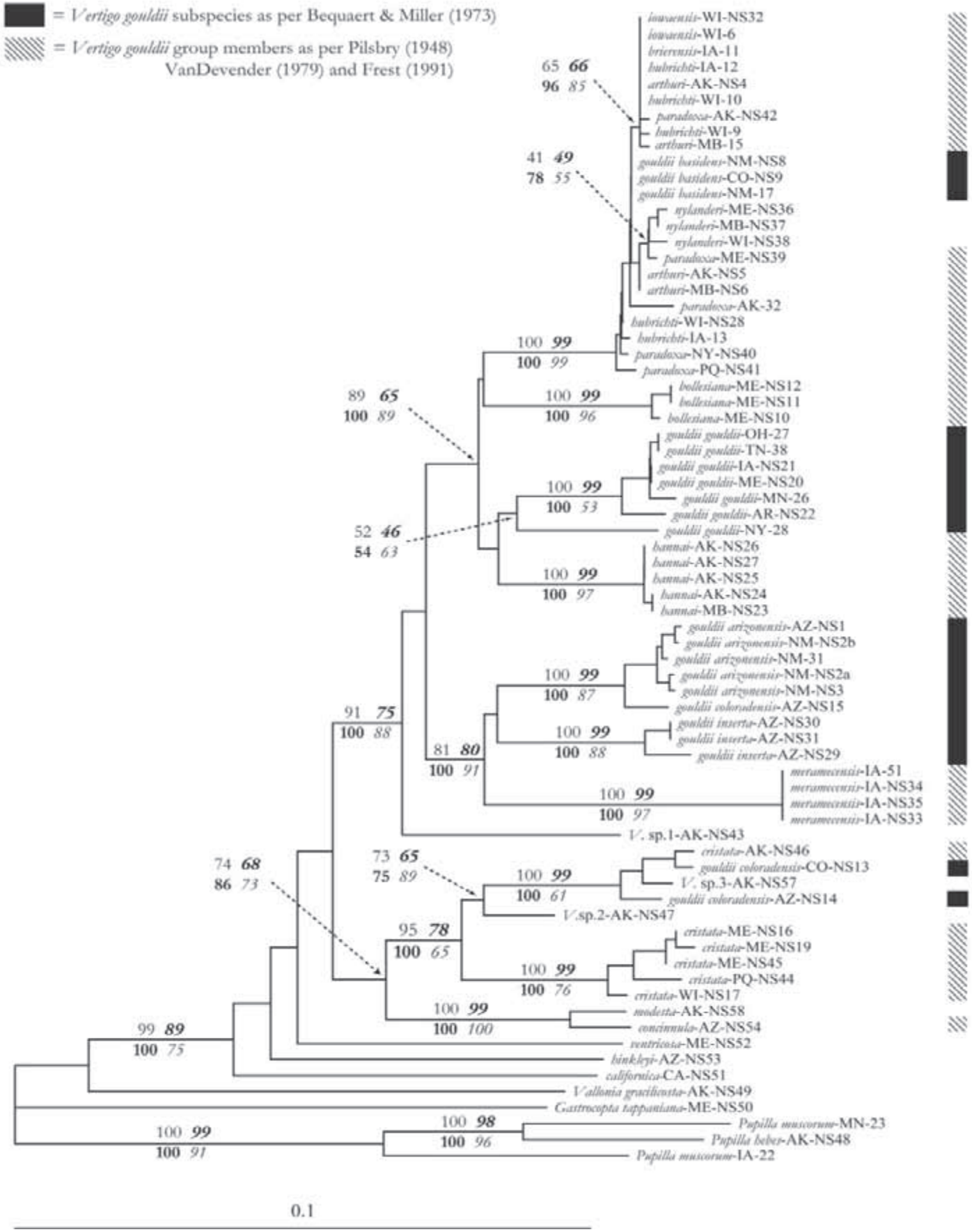

Figure 4: Phylogenetic tree of the *Vertigo gouldii* group and other various pupillids. Nodes with strong to moderate support based on four different analytical approaches have been provided to the left of each node.

gouldii' subspecies actually representing five highly distinct species-level taxa. Ardent splitters were also shown to be wrong, particularly in the case of the *Vertigo arthuri* clade which some had suggested to represent up to six species. This did not surprise us as we had already observed complete conchological intergradation between these forms across much of North America. These analyses also demonstrated that some species assumed to be shared between North America and Eurasia actually represent species complexes. In the case of *Pupilla muscorum* the distinct Eurasian lineages have escaped and become naturalized across eastern North America. These analyses also help us understand more about their origin. Assuming a 1% sequence divergence per million years, it appears that modern species originated during a rapid speciation event approximately 7 million years ago. This not only is approximately the same time that elephants and mastodons diverged, but also roughly the time that the major hominid groups differentiated. We and pupillids species appear to be of about the same age.

Biology, Ecology, and Biogeography

While most land snails are hermaphrodites, what sets the pupillids apart is the commonness by which single individuals fertilize their eggs with their own sperm. This allows pupillids (and many other microsnails) a great advantage in migration: the movement of only a single individual is required to found a new population. This greatly increases the likelihood of long-range migration. Potential vectors for these movements include not only birds and other large vertebrates, but also water and even wind, with it being possible for small taxa to be blown across the open ocean from one island to the next. Recent genetic evidence also demonstrates that small land snails have been able to migrate from Western Europe to Tristan da Cuna (isolated islands in the South Atlantic) and back, likely on migrating shore birds. Such long-range passive dispersal is aided by their adhesive mucus, which makes it easy for them to adhere to passing vertebrates. This can be easily demonstrated for pupillids by noting the individuals that commonly stick to a hand run through damp sedge or grass leaves.

As a result, North American pupillids are characterized not only by having large ranges, but also by almost completely saturating potential habitats within that range. Because of their small size, it is common for population densities to exceed hundreds, if not thousands of individuals per square meter. For this reason, most are not highly endangered, being found not only across large extents but also at large population sizes within many sites. For instance, even though it may only actively move a few meters within its lifetime, the 1.8mm *Vertigo arthuri* extends from Newfoundland to the Alaskan interior, south to New York, Iowa, the Black Hills, and northern New Mexico. Within this range it is not uncommon for it to be found in all potential habitats, such as in northwestern Minnesota where it occurs in aspen parkland or in the New England states where it is restricted to upland white cedar forest.

Another vital aspect to pupillid ecology is their high rates of small-scale sympatry. It is not uncommon to find a half-dozen species co-occurring at sub-meter scales! The highest co-existence levels appear to be with *Gastrocopta* in the southern Plains and

Figure 5: Standard field collection techniques for documenting pupillid biodiversity, using pictures taken during recent field work in the Alaskan interior.

Figure 6. Collection information is as follows: ***Bothriopupa variolosa***, Cuba, CM 62.21311 (color has faded in long-term storage); ***Columella simplex*** Haywood Landing, Jones Co., North Carolina, 34°49'10"N, 77°11'2"W; ***Gastrocopta ashmuni***, Canyon del Agua, San Miguel Co., New Mexico, 35°29'45"N, 105°3'24"W; ***Gastrocopta clappi***, Cedars of Lebanon State Park, Wilson Co., Tennessee, 36°20'40"N, 92°6'25"W; ***Gastrocopta contracta***, Rowley Fen, Buchanan Co., Iowa, 42°22'26"N, 91°51'7"W; ***Gastrocopta corticaria***, Canton Glade, Jones Co., Iowa, 42°10'46"N, 90°59'52"W; ***Gastrocopta pentodon***, Lebanon State Forest, Burlington Co., New Jersey, 39°52'29"N, 74°30'58"W; ***Gastrocopta riograndensis***, Sacramento Canyon Falls, Otero Co., New Mexico, 32°42'51"N, 105°45'15"W; ***Gastrocopta rogersensis***, Beams Cabin, Jones Co., Iowa, 42°8'32"N, 91°20'44"W; ***Pupilla muscorum*** , Crawford Quarry, Linn Co., Iowa, 41°59'12"N, 91°44'24W; ***Pupisoma dioscoricola***, Wadboo Creek, Berkeley Co., South Carolina, 33°11'50"N, 79°56'46"W; ***Pupoides hordaceus***, Duran, Torrance Co., New Mexico, 34°26'56"N, 105°25'6"W; ***Sterkia eyriesi rhoadsi***, Kyk-over-All, Kartabo, British Guiana, CM 62.19700 (color has faded in long-term storage); ***Vertigo alabamensis*****,** Lanier Quarry, Pender Co., North Carolina, 34°37'49"N, 77°40'27"W; ***Vertigo arizonensis,*** Devils Den Canyon, Eddy Co., New Mexico, 32°1'59"N, 104°48'17"W; ***Vertigo arthuri***, Devils Lake Wayside, Manitoba, 52°24'13"N, 98°54'43" W; ***Vertigo malleata***, Holly Shelter Game Lands, Pender Co., North Carolina, 34°31'57"N, 77°44'41"W (paratype); ***Vertigo meramecensis***, North Bear Creek, Winneshiek Co., Iowa, 43°26'52"N, 91°37'19"W; ***Vertigo milium***, Berlin Fen, Green Lake Co., Wisconsin, 43°57'47"N, 88°45'20"W; ***Vertigo modesta***, South Fork Koyukuk River, Alaska, 67°1'11"N, 150°17'19"W; ***Vertigo nylanderi***, Sturgeon Gill Road, Manitoba, 53°28'23"N, 99°9'55"W; ***Vertigo oscariana***, Wadboo Creek, Berkeley Co., South Carolina, 33°11'50"N, 79°56'46"W; ***Vertigo oughtoni***, West Twin Lake Fen, Churchill, Manitoba, 58°37'46"N, 93°50'35"W; ***Vertigo teskeyae***, Huffs Island Park, Lincoln Co., Arkansas.

Ozarks (up to eight species per site), and *Vertigo* in the upper Midwest (up to six) and the Alaskan interior (up to eight). In spite of this, there is little evidence for interbreeding based on either DNA sequence or conchological data.

Some pupillid species have unique habitat requirements and ecological patterns. *Vertigo alabamensis* and *V. malleata*, for instance, are limited to base poor pine savanna, bay forest, and bog habitats along the eastern seaboard. These sites are so highly acidic that it is rare to find unpitted living shells, with these being dissolved completely within a few months. Because *V. alabamensis* juveniles only hatch during the spring, it is thus only possible to find adult shells during late spring and early summer. Shells from this cohort will completely vanish by late summer. Another interesting species is *Vertigo meramecensis*, which is limited to mesic limestone and dolomite cliffs from the Ozarks to southeastern Minnesota. When aestivating, its mucus trail dries to form a resistant cord that attaches the snail to its vertical habitat, in essence a self-made belay-line. If dislodged, the snail is able to crawl back up this cord and onto the cliff face.

Field Collection Techniques

The best way to collect pupillid land snails is by the field sieving of leaf litter. This procedure consists of throwing handfuls of litter onto a shallow sieve of 2mm mesh nesting loosely inside a sieve of 0.6mm mesh, accompanied by vigorous shaking, tapping, or other agitation (Figure 5). Both coarse (>2mm) and fine (0.6mm - 2mm) fractions should be observed in the field (with magnification as necessary) to estimate the location of favored microsites, species richness and abundance. Appropriate microsites are then targeted for additional sampling, with approximately 50-500ml of fine material (0.6-2.0 mm) being collected per site, with a goal of capturing at least 200 individual shells. Sievings are removed from the field, dried at room temperature, and then passed through a 0.6mm sieve, with fractions being hand picked against a neutral background using low magnification as necessary. Though use of this method, it is relatively easy to accumulate large numbers of pupillid individuals from many sites.

A Sampling of North American Pupillids

The final plate (Figure 6) provides a glimpse of the continental diversity in this group. This image includes examples of most known genera from North America, with multiple species being represented for *Gastrocopta* and *Vertigo*. Except for the images of *Sterkia* and *Bothriopupa* individuals, which are century-old collections from the Carnegie Museum, the remainder represents recent collections made by either myself or Brian Coles.

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From the Red Sea

Moti Kovalis

An endemic and rare *Spondylus* from the Red Sea is the beautiful *S. pickeringae* Lamprell, 1998. This *Spondylus* is quite variable and typically varies from forms with numerous dense short spines to forms with massive long spines. The rarest form is the albino shell. The two specimens shown here are from the north part of the Gulf of Aqaba, from 40-45 meters deep. The usual color form for the *S. pickeringae* is white ribs ending with large white spines. Between the major ribs are tiny brown spines giving the upper and lower valves their recognizable appearance. In the albino form these tiny spines are white. Both specimens are otherwise typical for this species. They measure 120mm for top image and 130mm for the bottom image.

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