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The Evolutionary Relationships of the Skunks to Each Other and the Rest of the Weasels; with a note on Behavioral Idiosyncrasies

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Striped skunks often are considered obnoxious pests in urban areas, and often are involved in the transfer of rabies. Therefore, skunks have a potential to affect human welfare. As a result, a significant amount of research has been conducted pertaining to behavior, ecology, and diseases associated with striped skunks. However, other members of this group of mammals have received less attention. Hooded, spotted, and hog-nosed skunk populations may be on the decline in this country and in Mexico, and little is known about the skunks of South America. Even less attention has been devoted to the systematic relationships of skunks. Skunks in general, are beneficial to our agricultural interests. They prey on harmful and damaging insects and rodents that plague crops. The objective of this paper is to generate more interest and an enhanced understanding of these much maligned carnivores.

I will discuss four aspects of my current research with respect to skunks. The first concerns the recognition and conservation of potentially endangered populations of hog-nosed skunks. The second pertains to the evolutionary relationships among the three genera of skunks, based on genetic data. The third aspect also is based on molecular data, and is a study of the relationship of the skunks to the rest of the Mustelidae (weasels). Finally, I will discuss some of the behavioral idiosyncrasies I have observed in my endeavors to obtain skunk specimens.

Methods Associated with Genetic Study

The first three topics of this research involve the in vitro amplification of various regions of nuclear deoxyribonucleic acid (DNA) and DNA found in organelles (mitochondria) associated with the cytoplasmic portion of the cell. DNA can be obtained from several sources. In the case of the hog-nosed skunks, I have extracted DNA from millimeter slivers of dried museum skins. DNA from many of the other carnivores was obtained from frozen organs (heart, liver, kidney, etc.) of road-killed animals, hunter \trapper killed animals, and frozen tissue collections stored at natural history museums. Amplification of the various gene regions is accomplished by the polymerase chain reaction (PCR).

PCR involves the enzymatic amplification of DNA in which specific segments of DNA can be amplified as much as a million fold in a matter of hours (Saiki, 1985). Oligonucleotide primers (length of about 20 base pairs of DNA) that flank the DNA segment to be amplified are annealed to complementary DNA strands. The primer extension products in one cycle serve as a template in the next cycle, thereby doubling the product every cycle. Amplification occurs through repeated cycles of heat denaturation of the DNA, annealing of the

primers and extension from this annealed primers with DNA polymerase, resulting in an exponential accumulation of target DNA (Saiki et al., 1988; Fig. 1).

The nucleotide sequence of the DNA then can be determined by using the dideoxy chain-termination method (Sanger et al., 1979; Fig.2). Primers are annealed to single stranded DNA and extended with a radioactive nucleotide. These initial extension reactions are divided into four reaction mixtures containing one of the four chain-terminating dideoxy nucleotides. When the extending DNA fragment incorporates a dideoxy nucleotide the reaction stops (Sanger et al., 1979). These reactions produce large numbers of various sized fragments, which can be separated on polyacrylamide gradient sequencing gels (1983).

Hog-nosed Skunks

Currently there are two recognized species of hog-nosed skunks in the United States. I presently am studying the biological and taxonomic status of these skunks. The western hog-nosed skunk (ten subspecies) ranges from the southwestern United States through most of Mexico into Central America, and borders the entire western edge of the distribution of the Gulf Coast hog-nosed skunk (two subspecies). This skunk occurs along this coastal plain of the Gulf of Mexico from Veracruz to the southern tip of Texas and has one of the smallest distributions of all skunks.

Population levels of hog-nosed skunks presumably are declining in number throughout a major portion of their historical range in the United States. The eastern Texas subspecies is considered extinct throughout its range in the Big Thicket region believed to be the most common skunk in the area at the turn of the century (Bailey, 1905). However, no new specimens of this subspecies have been collected in the Big Thicket of Texas since 1905. Occasional road-killed skunks have been reported, but not salvaged (Raun and Wilks, 1961). This subspecies, the subspecies occurring in Colorado, and the Gulf Coast hog-nosed skunk are being considered for threatened or endangered status.

My goal for this portion of the research is to identify uniquely evolving gene pools. Two independent data sets are being generated to accomplish this goal. The first involves a classical morphometric analysis of cranial measurements. I have measured over 800 skulls representing the hog-nosed skunks that occur from Colorado to Argentina. Preliminary results indicate that many of the currently recognized subspecies may not be valid. However, the Gulf-Coast hog-nosed skunk can bs distinguished from the western hog-nosed skunk based on the cranial measurements.

The next portion of this study involves the amplification and sequencing of DNA isolated from museum skins. Some of these specimens were collected in the late 1800's. In fact the only genetic material available for the eastern Texas subspecies are the 14 specimens collected in 1905. PCR and nucleotide sequencing will be used to examine genetic variation in museum specimens, thus providing an opportunity to evaluate genetic changes through ecological time and compare taxa that are either extinct or rare. Approximately 40 specimens housed in' the Texas Co-operative Wildlife Collections have been examined. I also have obtained skin samples from more than 300 specimens housed in museums around the

Polymerase Chain Reaction:

heat to separate strands

anneal oligonucleotide primers to single strand DNA

extend DNA from primers

continue 30-40 cycles to produce a million fold increase of target DNA

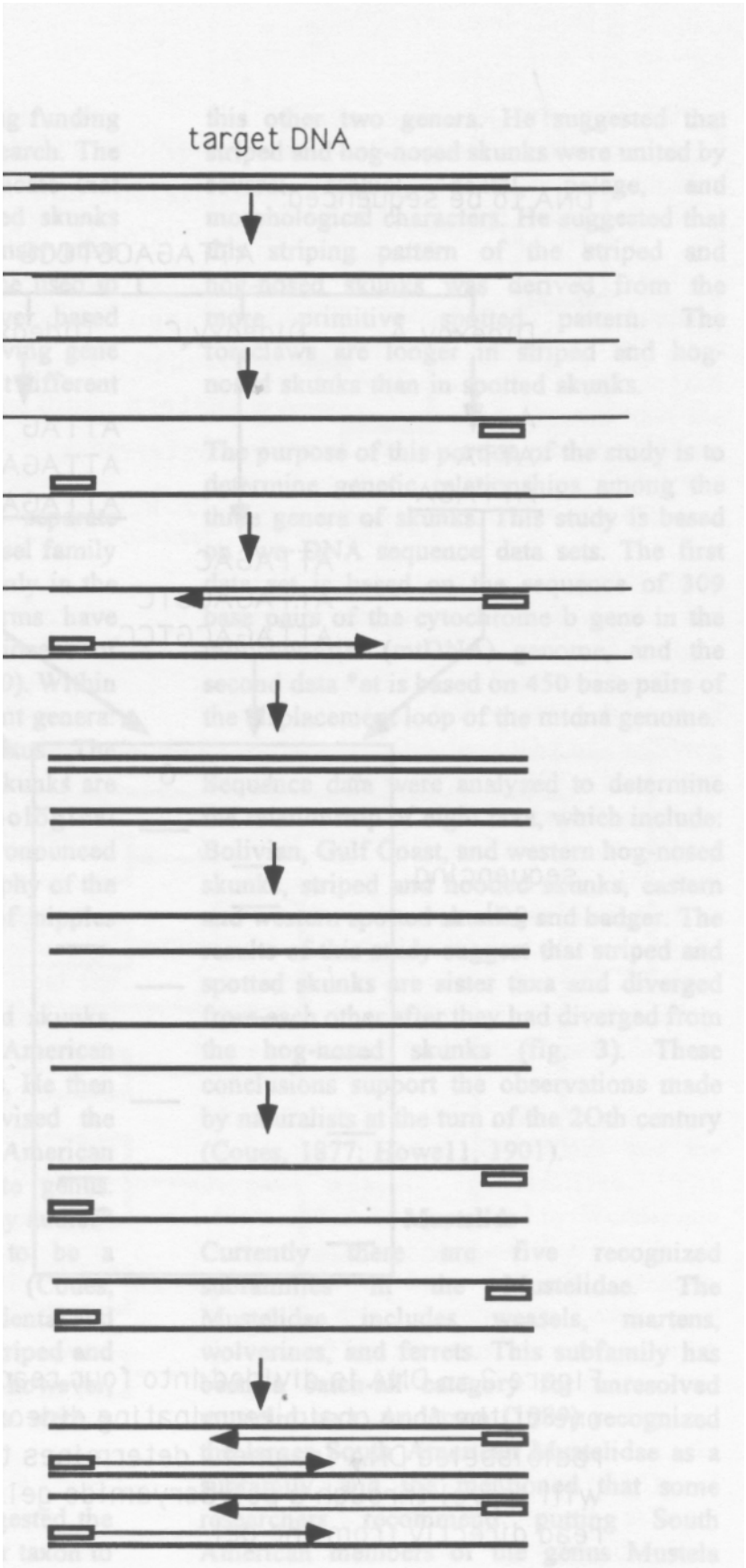

Figure 1 .– DNA

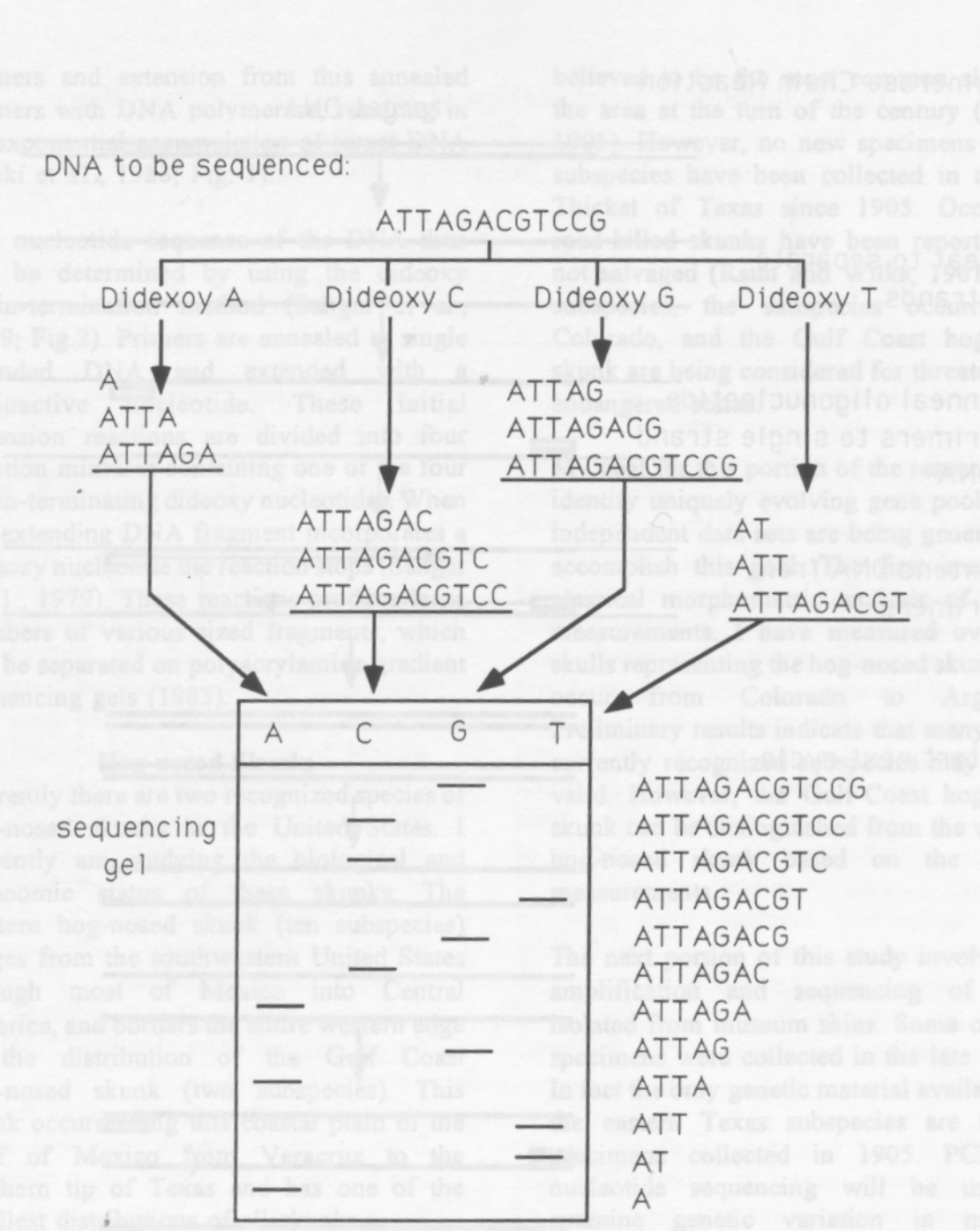

Figure 2.-- DNA is divided into four reactions, each containing one of the four chain-terminating dideoxy nucleotides. Size of the radiolabeled DNA fragment determines the distance the fragment will travel through a polyacryamide gel. The DNA sequence then is read directly from the gel.

country. At this time I am awaiting funding to continue this portion of my research. The preliminary results however, indicate that Gulf-Coast and western hog-nosed skunks are closely related. The more conservative (slower evolving) genes can not be used to distinguish the two forms. However, based on the more variable, faster evolving gene regions, the two forms do represent different genetic populations.

Mephitinae

Skunks are recognized as a separate subfamily, Mephitinae, of the weasel family Mustelidae. Today skunks occur only in the New World, although fossil forms have appeared in the Miocene and Pliocene of Europe (Kurten and Anderson, 1980). Within this subfamily there are three Recent genera: Mephitis, Spilogale, and Conepatus. The three genera of North American skunks are united by several morphological characteristics, which include a pronounced reduction of the baculum, hypertrophy of the scent glands, and development of nipples associated with these glands.

Howell (1901) revised the striped skunks, stated that until 1838 all North American skunks were considered one genus. He then mentions that Liechtenstein revised the genus and separated the North American hog-nosed skunks into a separate genus. Until Howell's (1901) revision, many author* considered the spotted skunks to be a subgenus of the striped skunk* (Cones, 1877). Coues (1877) listed several dental and cranial characters that united the striped and spotted skunks. Howell (1901) however, suggested that the spotted skunks were a separate genus.

More recently, Holms (1988) suggested the

spotted skunk was a primitive sister taxon to this other two genera. He suggested that striped and hog-nosed skunks were united by several cranial, dental, pelage, and morphological characters. He suggested that this striping **pattern** of the striped and hog-nosed skunks was derived from the more primitive spotted pattern. The foreclaws are longer in striped and hognosed skunks than in spotted skunks.

The purpose of this portion of the study is to determine genetic relationships among the three genera of skunks. This study is based on two DNA sequence data sets. The first data set is based on the sequence of 309 base pairs of the cytochrome b gene in the mitochondrial (mtDNA) genome, and the second data *et is based on 450 base pairs of the displacement loop of the mtdna genome.

Sequence data were analyzed to determine the relationship of eight taxa, which include: Bolivian, Gulf Coast, and western hog-nosed skunks, striped and hooded skunks, eastern and western spotted skunks, and badger. The results of this study suggest that striped and spotted skunks are sister taxa and diverged from each other after they had diverged from the hog-nosed skunks (fig. 3). These conclusions support the observations made by naturalists at the turn of the 20th century (Cones, 1877; Howell, 1901).

Musteli ds

Currently there are five recognized subfamilies in the Mustelidae. The Mustelidae includes weasels, martens, wolverines, and ferrets. This subfamily has been a catch-all category for unresolved mustelid taxa. Anderson (1989) recognized the larger South American Mustelidae as a subfamily, and she mentioned that some

researchers recommend putting South

American members of the genus Mustela

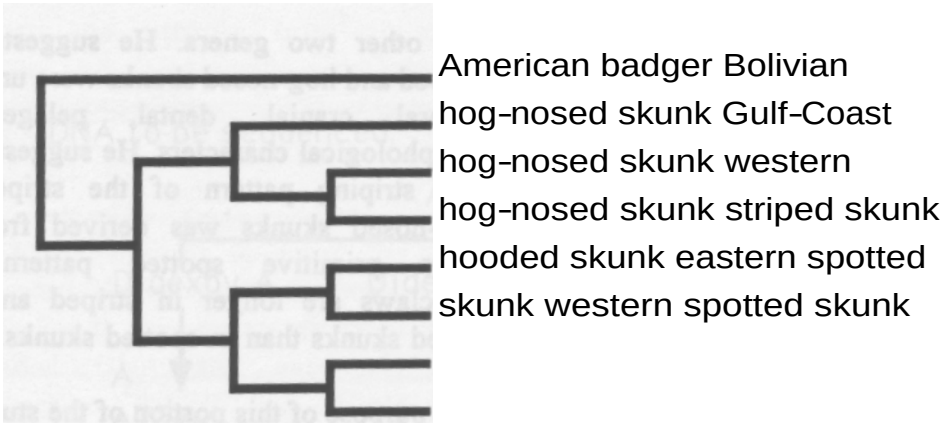

Figure 3.-- Phylogeny of the Mephitinae, based on 760 by of the mtDNA genome (Dragoo et al., in prep.).

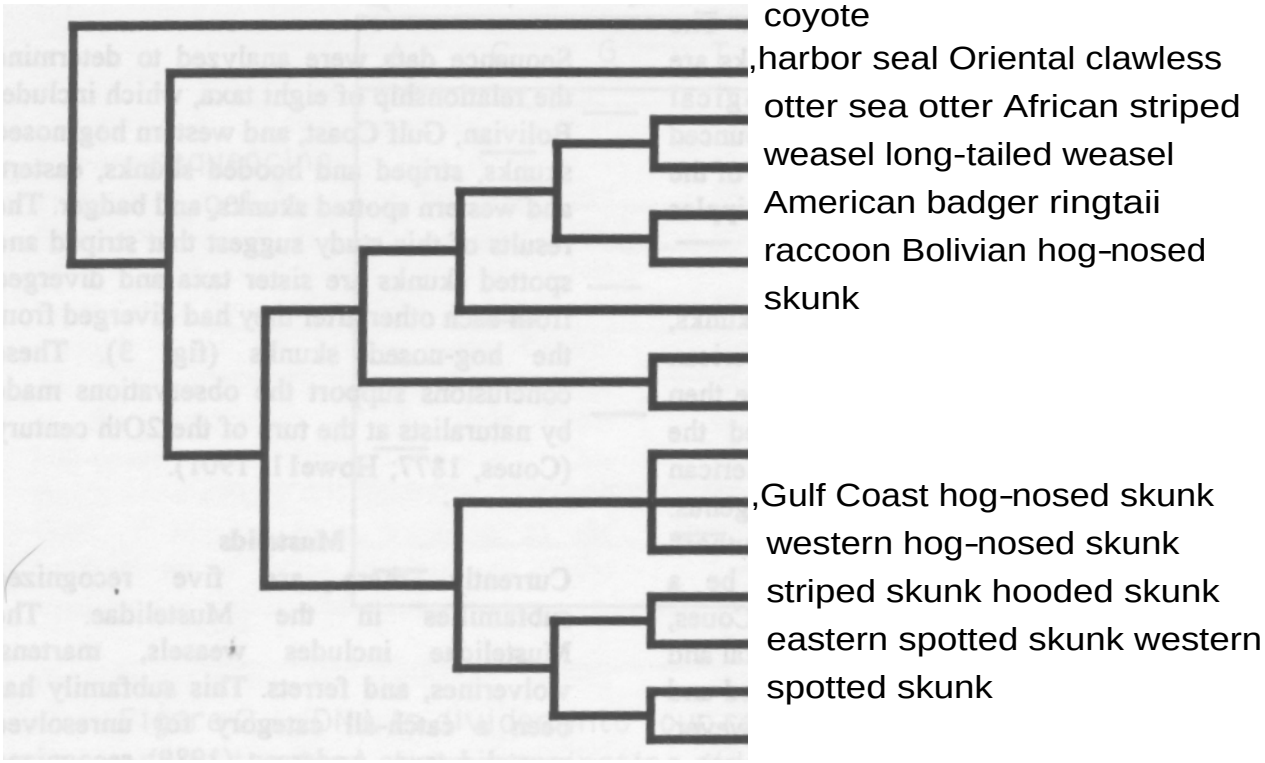

Figure 4.-- Relationship of the skunks to the other arctoid carnivores, based on 309 by of the cytochrome b gene.

into their own genus or even their own subfamily.

The Melinae includes the badgers. Radinsky (1973) suggested that this subfamily may have several origins, based on middle ear anatomy, dentition, and brain morphology. Petter (1871) split the badgers into four tribes with one tribe representing the American badger. Also, he indicated that the stink badger may have affinities with the skunks. Wozencraft (1989) suggested that the American badger was not a true Melinae, but he was unsure where to place it.

The third subfamily, Mellivorinae, includes the single species of honey badger. However, Anderson (1989) also includes the wolverine in this subfamily, but Wozencraft (1989) and Holms (1988) consider the honey badger to be a Mustelinae.

The fourth subfamily is the Lutrinae, which includes the river otters and sea otters. Again, Radinsky (1973) suggested that this subfamily too may have several origins with the sea otter being quite distinct from the other otters. Wozencraft (1989) concluded that sea otters were probably the first taxon to diverge in this subfamily.

Finally, the **fifth** subfamily is the Mephitinae; the skunks. Radinsky (1973) suggested, based on brain morphology, anatomy of the middle ear, and dentition, that the stink badger may actually be a skunk and not a true badger. Also, O'Brien et al. (1989) used protein electrophoresis to determine the relationship of black-footed ferrets to other weasels in the genus. They suggested an ancient split between skunks, including the zorilla, and the weasels. However, the zorilla has classically been placed in the same subfamily as the weasels.

The African zorilla is very similar in appearance to the North American spotted skunks, and many of the earlier naturalists often confused the two genera (Nowak, 1990).

Coues (1877), Pocock (1921), and Simpson (1945) regarded the badgers as the sister taxon to the skunks, based on morphological characters. Simpson also suggests that the badgers and skunks may not be distinct subfamilies. Radinsky (1973) suggested that the stink badger may actually be a skunk.

Hunt (1974) examined the auditory bulla of carnivores and resolved that skunks and otters shared a similar bulla. This bulla type also was shared by sea lions and bears. He also suggested that bones within the ears of skunks are the least developed of any living carnivore. Wozencraft (1989) used 100 characters dealing with cranial morphology, dentition, and soft anatomy to produce a phylogeny of the Carnivora. His data revealed that the otters were sister taxa to the skunks with the other mustelids being the next branch in the clade. Also, he indicated that raccoons and their allies and the earless seals were sister taxa to the Mustelidae.

Molecular data, however, indicate a different relationship between the skunks and the other "weasel" subfamilies. The chromosomal data presented by Wurster and Benirschke (1968) indicate that skunks are quite different from the other weasels. Molecular data presented by Ledoux and Kenyon (1974), who studied serum proteins, suggest that the weasels, badgers, and otters shared a common ancestor long after the lineage leading to the modern skunks diverged. Amason and Widegren (1986) used DNA hybridization to determine the ancestry of seals and sea lions. However, they also

found skunk DNA to be more divergent than other mustelid DNA than either raccoon or seal DNA. Wayne et al. (1989) also used DNA hybridization to produce a phylogeny of carnivore relationships. They suggested that the skunks diverged from the other mustelids at about the same time (40 million years ago) as the raccoons, bears, and seals.

Mustelids have been a difficult group to classify. They exhibit similar adaptations in regard to diet, behavior, and locomotion. According to Anderson (1989) the fossil record is incomplete, and many of the early workers named new taxa without sufficient comparative material. This resulted in the placement of many taxa into the incorrect subfamilies or families.

The earliest fossils appear in the late Eocene and are rare due to the body size and preferred habitat of these early mustelids (Kurten and Anderson, 1980). In the Eocene four modern families of carnivores were present: cats, dogs, civets, and the weasels. Weasel-like forms also appeared in the late Oligocene. According to Martin (1989) during this time period there was a major radiation of the ground-dwelling rodents as the savannas expanded. With this rodent radiation there was also a radiation of semi-fossorial weasel-like carnivores. However, many of these turned out to be unrelated to true mustelids. By the Oligocene, bears, raccoons, dogs, and weasel could be distinguished by characters of the braincase. Many Oligocene and early Miocene taxa had been identified as weasels, but after careful examination it was concluded that these taxa were actually related to raccoons (Baskin, 1982).

The early radiation of the modern families of the Camivora was rapid in the Eocene and resulted in many similar traits in many of the early families. The early weasel-like forms did not appear to give rise to this modem mustelids. Modern mustelid subfAmilies first appeared in this Miocene, and included extinct genera of martens, weasels, otters, badgers, and skunks (Kurten and Anderson, 1980).

It is generally assumed that the mustelids are a part of this arctoid carnivore radiation (references cited above). I have sequenced approximately 309 base pairs of the cytochrome b gene in the mtDNA genome from a number of arctoid carnivore taxa that represent cats, dogs, raccoons, seals, and weasels. The weasel taxa involved represent four of the five recognized subfamilies. The results of a preliminary analysis showed that the coyote was this first taxon to branch off the phylogram. The next taxon to branch off was the harbor seal. However, it has been suggested that the seals may have diverged after the skunks and before the modern mustelids (Wayne et al., 1989; Amason and Widegren, 1986). Therefore, I have kept the harbor seal within the ingroup.

The results of my analysis are presented in figure 4. This phylogenetic tree was composed of 16 taxa: coyote, seal, Oriental clawless otter, sea otter, zorilla, long-tailed weasel, badger, ringtail, raccoon, and the seven skunk species listed above. The zorilla was grouped with the long-tailed weasel and not the skunks as suggested by O'Brien et al. (1989). The raccoon and ringtail split the two clades of mustelids; one containing the skunks, and the other containing the rest of the weasels.

The hypothesis I am testing now (which is the focus of my Ph.D. research) is the msnophyly (related to a common ancestor)

of the weasel family. I will be examining five gene regions from the mitochondrial and this nuclear genome. These genes represent variable to highly conserved genetic material. They include protein coding regions (introns) and non-coding regions (exons and ribosomal DNA). These genes are associated with growth regulation, energy metabolism, and RNA production. I am just starting this research, but the preliminary results indicate that skunks may not be in the weasel family.

Can Skunks Spray *While* Being Held *By the Tail?*

One cannot truly be considered a Mephitologist if he or she has not experienced the southern end of a north bound skunk. Two questions frequently asked by non-mephitologists are: "Have you ever been sprayed?" and "Can skunks spray while being held by the tail?" I have trapped skunks and picked up dead skunks on the side of the road, but my primary technique of collection is to pursue and capture by hand all observed skunks. My answer to the first question is "Yes, about six or seven times ...per animal". My method of collecting skunks has allowed me to test the myth associated with the second question.

I have read the works of Merriam (1884), Dice (1921), and Seton (1929) relating to skunks. In my early years I would refer to these sources when I was asked the "tail" question. One day while I was reading Dr. James S. Findley's "The Natural History of New Mexican Mammals," I came across this passage: "It has been suggested that if one picks up a skunk by the tail one can avoid being sprayed, but few people have actually tested this recommendation". I was just the scientist to study this hypothesis.

During my first assays of this technique I acquired a driver, Dr. Kent M. Reed, at the time, a graduate student in the Biology Department at Texas A & M. When we observed a skunk, he was to stop the truck and shins a spot-light on the animal while I gave chase. The first animal we saw was a striped skunk foraging in the mowed grass just off the shoulder. I was out of the truck and headed for the skunk. As soon as Kent stopped the vehicle and put the light on, I achieved top velocity. Skunks do not rely on a speedy flight to escape a predator so you would think they would be easy to run down. However, due to a low center of gravity, they are able to make some remarkable cuts. Besides, while I was chasing this animal in circles, my driver had a difficult time keeping light on the subject as he was rolling over with laughter.

The skunk held its tail high and sprayed as I moved closer. The tail became my target. When I caught up to the animal I reached out and grabbed the tip of the tail and lifted the animal off the ground. The skunk stopped spraying. I carried him (when working with this end of the animal, it is easy to determine the sex of the individual) back to the truck and tried to maneuver him into a live trap. As I let his feet touch the ground, he crawled forward while I maintained my grip on his tail. He sprayed again; there was a thick yellow stain on my jeans.

This second animal that night, also foraging in the mowed grass, was a hog-nosed skunk. We were better organized this time. I leapt from this truck as the skunk made a bee-line for the fence. I had the angle and was able to prevent his escape. The skunk stopped, threw its tail up and while facing me, stomped its front feet on the ground (a

common threat behavior exhibited by skunks). I stopped and this skunk reversed direction and headed for the road. He was mine before we reached pavement. This animal never sprayed after I caught him.

Another hog-nosed skunk I collected was in a public area, and I was unprepared. It was about three o'clock in the afternoon when to noticed a black and white bail of fur rummaging around under a prickly pear cactus. Hp instincts set me in motion before I had time to think. I had reached through the cactus pads and grabbed the animal. I held the tail down against this ground as the animal struggled to crawl forward. I pulled the skunk out and let her hang there. Then I started thinking. I realized I had no place to put this *skunk and in* order to get back to my vehicle I had to pass by several people. I figured I could wrap her up in my jacket if I had a better grip. I let her feet down so I could pin her head and grab the scruff of her neck. As soon as her front feet hit the ground she sprayed. It was beginning to look like the old adage was true.

However, on one occasion while staying at a research facility in southern Texas, I was out before sundown with a few Range Science students. They were interested *in* photographing wildlife. I was riding in the back of a pick-up truck and wearing nothing but a pair of cut-off jeans and tennis shoes (black with white stripes). We happened to observe a striped skunk. Again my reflexes kicked in and I was in hot pursuit. The skunk was ambling away from me until I was within 25 yards of him. His tail went up and he bolted. Running near-naked through south Texas brush on a hot summer afternoon; pores open, dripping sweat; mesquite and prickly pear thorns ripping flesh; adrenalin and testosterone surging; while all about me was the Amber mist of anal secretions, burning and tingling bare skin, is the second most stimulating experience I have enjoyed.

Needless to say I caught the animal. As I was walking back to the truck, with the skunk in my hand at arms length from my side, he fired a stream that caught my right eye. My eye swelled shut as tears were flowing. Imagine my surprise! I held the animal in front of me so I could see it with my good eye. The sphincter around the anal orifice was puckering and I observed two pink nipple* being exposed (a note of caution for those who try this at home: never let your jaw drop in utter Amazement while holding a skunk by the tail at arms length in front of you). He fired again; hit me point blank in the face. My lens protected my eyes this time, but I was unable to see through the thick yellow ooze covering my glasses.

None of the "wildlife photographers" snapped a single picture. They threatened to make me walk back to the bunk house, but decided in the end to take me with them. The five of them piled in the cab of the truck and left me in the back, skunk still in hand. They would not let me back in the bunk house, so I decided to cruise the roads of southern Texas for more skunks.

Another incident in eastern Texas I was on a mammalogy class field trip with another Mephitologist, Dr. Robert F. Patton. He earned his Ph.D. from Texas A&M, working with four species of skunks in Trans-Pecos Texas. The first night we took a crew of seven in an open-top jeep to spot-light various mammals. Early in the evening we observed a skunk. I was in the field with one of my heroes, and again the adrenalin and testosterone were pumping through my

veins. My reflexes kicked in end I was in high gear before someone in the jeep yelled "SKUNK!" The skunk was about 75 yards out when I started pursuit. By the time I reached him I was out of breath; he decided to flee. I maneuvered him through the underbrush as best I could in order to keep him from escaping. By then the jeep arrived and one of my students and Patton's youngest son had joined the chase. They tried to steer the animal toward me, but whenever it approached them they would retreat. Meanwhile the skunk was spraying copious clouds left and right, enveloping everybody and everything. I was staggering like a drunkard; the skunk was barely moving at a trot. I was afraid of loosing face with my hero, my major professor, and my mammalogy class. I recalled a lesson from an old football coach: "Never pick up a fumble; dive on it." The first thing I noticed was pressure on the first digit of my left hand as the skunk's incisors and canines clasped onto my finger (when ail else fails, skunks will bite). The hairy tail tickled my nose as it flipped across my face. Then Harvey puckered up and kissed me right on the mouth. I've found that when you've kissed the back end of a skunk it is socially acceptable to refer to them by their first name (Actually, when you've kissed the back end of a skunk, you're not socially acceptable!).

The next night I had nothing to prove. The jeep moved in closer before I engaged in pursuit. Without breaking stride I grabbed the tail. The skunk only sprayed before I caught him. Neither of these animals sprayed after they had been collected and put in holding cages.

According to Dr. Richard Van Gelder (Natural History Magazine, 8/90), when skunks are "aware" of their predicament they can prepare. but if they are caught unaware they are unable to spray while suspended by the tail. His analysis is based on a single incident. The skunks I had collected were in the "red alert" stage. However, I also have collected them unaware as well. One animal was digging up a frog from under a light post when I grabbed its tail. It never sprayed. Another occasion, while baiting live traps in the San Carlos Mountains of Tamaulipas, Mexico, I had sardine oil on my hands and drippings on my boots from having just baited my last trap. I turned around and saw a skunk come down the bank of the stream. He was coming towards me. His tail was down. I just stood there in disbelief as he came to my feet end sniffed at my boots. He then proceeded about his business. I reached down without taking a step and grabbed his tail. I had to walk about a half a mile back to camp, and skunks tend to get heavier as you hold them at arms length for a period of time. Therefore, I switched hands. By now I had enough experience to point the animal away from me (though not as stimulating, it spares those with whom you share a camp site). Every time I changed hands, the skunk sprayed.

The data I have obtained over the past few years suggest that whether or not skunks can spray while being held by the tail depends on the individual animal. My data do not support the hypothesis that suspended skunks are limited by physical constraints, but rather are controlled by psychological and behavior idiosyncracies. Merriam (1884) said that, "A skunk generally waits 'till he is hurt before discharging his battery... I have never known one to eject a single drop of the precious fluid except when hard pressed and very much excited - and it takes considerable to

excite an adult skunk". Cuyler (1924) stated, "the skunk is usually loathe to waste its musk, and therefore does not discharge it promiscuously". It has been my experience that skunks will spray under the slightest provocation, or not at all. The skunks that sprayed while being held were ail high-strung and nervous and tended to spray frequently in holding cages, whereas the skunks that did not spray were more laid-back and docile; some would even allow me to handle them as long as I moved cautiously. I have run the dull side of a scalpel along the nerves associated with the scent glands of freshly killed, skinned skunks and have caused the muscles to twitch and contract (albeit, without the strength to discharge).

Also, I have noticed that skunks have two methods of spraying and are able to control which method they will use. Often times when I am pursuing an animal through the brush, we are both zipping in and around obstacles. The skunk has no fixed target to expel its musk and thus emits the spray in a fine mist which forms a cloud that a predator (like myself) must run through. When the animal has been cornered or caught and has a target to focus upon, the spray is emitted in a stream as from a squirt gun; and skunks have a deadly aim!

Conclusion

At this time I have finished the majority of field work associated with my Ph.D. research, and I am tied down to the laboratory. I am examining three levels of systematic and evolutionary relationships regarding skunks. The relationships of this hog-nosed skunk populations will bs important to this U.S. Fish and Wildlife Service when this time comes to allocate resources for endangered species research and programs associated with recover these species. The study of the skunk gen relationships is nearly completed. This is first genetic data dealing with skunks. allows for an independent assessment relationship and hopefully will clear up t discrepancy associated with ti morphological data. The relationship of the skunks to the other carnivores also w stimulate further research with regard extinct weasel-like carnivores. Often timt the striped and spotted skunk are used in molecular study as incidental mustelid taxi The results of those studies often showed skunks to be evolving differently with regarding to the other weasels. No one has considered asking why, until now. Finally, when one thinks of wolverines, badgers, and least weasels, one imagines ferocious predators. However, this image does not come to mind when one thinks of skunks. Even the behavior of skunks is different than the rest of the weasels.

When I am chasing a skunk I have only two things on my mind one of which is the tail: I watch were it goes and what it does. As long as it stays up I know the animal is mine. However, if the tail goes down, I know I'm about to be impaled on mesquite or cactus, or flip over a barbed wire fence. A philosopher once said you can't really understand something until you love it. It is my intention to truly understand all I can pertaining to skunks.

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