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A REVIEW OF THE SYSTEMATICS OF ANGEL SHARKS EMPHASIZING THE SPECIES OF THE EASTERN PACIFIC REGION WITH A MODIFIED SET OF MORPHOMETRICS FOR ORDER SQUATINIFORMES

A thesis submitted in partial satisfaction of the requirements for the degree Master of Arts in Biology

by

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ABSTRACT OF THE THESIS

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Professor Donald G, Buth, Chair

Members of the monofamilial chondrichthyan order Squatiniformes, commonly known as angel sharks, sand devils, ange de mer, and angelotes, are primarily benthic dwelling sharks found mainly in temperate and sub-tropical parts of the Atlantic and Pacific Oceans. Squatiniformes are very easily recognized from other shark-like fishes, but the individual species within the order are much more difficult to distinguish from each other. In the eastern North Pacific (ENP) region, three species descriptions were published from 1859 to 1913. Since the latter date, the systematics of the entire order of Squatiniformes has been in a state of flux, from having only one description recognized as valid to having all three being recognized as valid at different

points in history. Currently only two descriptions are considered valid *Squatina californica*, Ayers, 1859 and *Squatina armata* (Philippi, 1887). Herein, the presence of at least four phenotypic morphs in the ENP is confirmed and a revised dichotomous key for the Squatiniformes of the region is presented. Additionally, numerous mistakes in the classification and cataloging of museum specimens are noted and corrected.

The thesis of Dominic Alioto is approved.

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Table of Contents

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TAXONOMIC HISTORY

Squatiniformes are flat-bodied sharks superficially resembling batoids, which are found in benthic habitats, and eat smaller elasmobranchs, teleosts, and invertebrates. Their similarity with batoids seems to result from a process of convergent evolution more than close phylogenetic relationships (Castro-Aguirre et. al. 2006). The highly variable number of described species that are recognized worldwide reflects the relatively limited amount of knowledge about this group. The taxonomic classifications of angel sharks at and above the class level are not in dispute. Angel sharks are placed in the taxonomic domain Eucarya, kingdom Animalia, phylum Chordata and class Chondrichthyes. Within class Chondrichthyes, angel sharks have been placed in subclass Elasmobranchii, order Squatiniformes, de Buen 1926; suborder Squatinodea, Bigelow and Schroeder, 1948; family Squatinidae, Bonaparte, 1838; and genus *Squatina*, (Dumeril, 1806)

The taxonomic history of the Squatiniformes begins, like many organisms, with Linneaus (1758). According to Article 3 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) January 1, 1758 is the arbitrarily fixed date of the starting point of zoological nomenclature. Article 3.1 of the International Code of Zoological Nomenclature (henceforth referred to as the ICZN Code) establishes that only two works are recognized as having been published on this date, they are: 1) Clerck's *Aranei Svecici* and 2) Linnaeus's *Systema Naturae*, 10th Edition.

Article 3.1 of the ICZN Code further establishes that names listed in *Aranei Svecici* have precedence over names in the 10th Edition of *Systema Naturae*, and that names in *any other work* published in 1758 is deemed as published after the 10th Edition of *Systema Naturae* regardless of the date listed. Article 3.1 therefore establishes the 10th Edition of *Systema Naturae* as the first work containing a valid reference to any angel shark.

Article 3.2 of the ICZN Code states that no name or nomenclatural act published before 1 January 1758 enters zoological nomenclature. However, information including descriptions and illustrations from works published before that date may be used. Article 3.2 in particular is very relevant to the systematics of angel sharks because prior to the establishment and dissemination of the ICZN Code[1] these rules were not in place. Works published from 1758 to 1910 refer to the rule of priority in that the earlier a publication is disseminated the greater precedence its proposed zoological names have.

In the particular case of order Squatiniformes, many of the works published from 1758-1910 refer to the names proposed by Klein (1742), whose multi-volume publication contains, according to Garman (1913), supposed translations of names first given by Aristotle[2] from the originally published language of Greek into Latin. The genus name for angel sharks proposed in Klein's (1742) translation of Aristotle is regarded as having priority over Linneaus' (1758) names during the pre-ICZN Code era because Klein published before 1758. Interpreted through the citation of Garman, (1913) Aristotle lists a species with the Greek word "`Ρίυη". Klein's (1742) translation of Aristotle uses a Latin word: *Rhina*, as a translation of the original Greek term to denote a piscine genus. Schaeffer (1760) subsequently used the term *Rhina* to denote a

[1] The earliest specific International Commission on Zoological Nomenclature opinions and rulings relevant to Angel Shark systematics were published in 1910. The International Commission on Zoological Nomenclature itself was founded on 18 September 1895. However, it is difficult to pinpoint a unanimously accepted precise date for the establishment of the ICZN Code or the issuing of other published opinions and rulings prior to 1910. (International Commission on Zoological Nomenclature, 1910)

[2] No precise date for Aristotle's original publication is given in the citation or anywhere else in either Klein's translation (1742) or subsequent species account (1776). Garman (1913) cited Aristotle as: " `Ρίυη Aristotle, Hist. An., II, C. 11, V, C. 4, VI, C.10, IX, C. 25." No precise date for Aristotle's publication is given in the citation or anywhere else in Garman's account either. From this information it is assumed that Aristotle's Περὶ Τὰ Ζῷα Ἱστορίαι [English translation: History of Animals] publication date, 350 BC is the publication referred to. Garman's given citation indicated that Aristotle described a species of angel shark (currently recognized as *Squatina squatina* but in Garman's account listed as *Rhina squatina*) with the singular Greek word "`Ρίυη". Also given in Garman's account is a chronological listing of all subsequent descriptions for the species including both *Squalus squatina* (Linneaus, 1758) and *Rhina squatina* Klein 1776.

genus, but without inclusion of any species (thus making his publication irrelevant even before the ICZN Code era). Klein later formally described the same species listed in his earlier translation with the binominally formatted name *Rhina squatina* (Klein, 1776). Certain works published from 1742-1910 including Philippi (1887) and Garman (1913) subsequently referred to angel sharks as being placed in Klein's (Aristotle's) genus *Rhina*.

The use of the term "Rhina" to refer to angel sharks during this time period would later become particularly problematic when this same name was later formally used by Bloch and Schnieder (1801), likely unaware of the prior (subsequently invalid) use of *Rhina* by Klein (1742, 1776) and others, (including Schaeffer 1760, Walbaum, 1792 and Rafinesque, 1810a, 1810b)[3] to describe a completely different cartilaginous fish, a batoid, that was subsequently named *Rhamphobatis* (Gill, 1862) and currently recognized as referring to either of two valid genera: *Rhina* Bloch and Schnieder, 1801, and *Platyrhina* Müller and Henle, 1838. Bloch and Schnieder's (1801) description led to a great deal of confusion for the subsequent deposit of specimens in ichthyological collections. Bigelow and Schroeder (1948) identified the mix up that the genus name *Rhina* had become a homonym and noted in a footnote that Bloch and Schnieder's description was at the time properly referred to as *Rhamphobatis* (Gill, 1862). However, this did not stop the incorrect classifications. Angel sharks and batoids are difficult to distinguish to all but elasmobranch specialists. The author found several incorrectly classified specimens (including both batoids of genus *Rhina* erroneously classified as sharks of genus *Squatina* and sharks of genus *Squatina* classified as batoids of genus *Rhina*) in several ichthyological collections including the LA County Museum of Natural History, and the UCLA

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[3] Schaeffer did not list any species in his description of genus *Rhina*. The generic names proposed by Klein and republished by Walbaum (subsequently Rafinesque) are not to be taken into account according to Opinions 21 (International Commission on Zoological Nomenclature, 1910) and 89 (International Commission on Zoological Nomenclature, 1925) of the International Commission on Zoological Nomenclature.

Ichthyology Collection. Further frustrations are added especially in the case of batoids from genus *Rhina* misclassified as sharks of genus *Squatina* because the morphometrics taken from these batoid specimens (in particular those measurements associated with the pectoral fins) have mistakenly inflated the range of characters assigned to species of *Squatina*. This has led to difficulties identifying species-specific characters used to distinguish individual species and form proper dichotomous keys.

Linneaus published the first valid species description of any squatiniform shark with his description of *Squalus squatina* (1758). Linneaus did not designate a type specimen. At this time Linnean taxonomy had yet to expand to include the family level of classification. The first documented taxonomic use of the word "Squatina" in any manner takes genesis from Wottoni (1552) but, according to Article 3 of the International Code of Zoological Nomenclature (1999), Wottoni is not credited with the use of the name because his publication is dated prior to 1758. The use of *Squatina*, as a genus name, was first proposed by Valmont de Bomare (1764). Despite a post-1758 publication date, Valmont de Bomare's names are not to be taken into account according to Opinion 89 of the International Commission on Zoological Nomenclature (1925). Garman (1913) cites the next reference to the term "Squatina" (not the genus name *Squatina*) as coming from Duhamel and de LaMarre (1780[4]). Duhamel and de LaMarre's publication is invalid for use in denoting a genus because it gave only a species account (that was in synonymy with Linneaus, 1758) and not a genus description. Further Duhamel and de LaMarre did not use the established Linnean binominal format in describing their species nor did their description appear to even recognize the concept of a genus. Thus, their names are also not taken into account.

[4] Garman (1913) cites Duhamel and de LaMarre's publication as "*Traité"* with a publication date of 1782. However, Duhamel and de LaMarre's *Traité générale des pêches, et histoire des poissons: ou les animaux qui vivent dans l'eau.* lists an official publication date of 1780.

Dumeril (1806) was the next to mention *Squatina* as a genus name. In the *Zoologie Analytique: ou méthode naturelle de classificatio des animaux* (an encyclopedic attempt to classify all known animals at the time) Dumeril mentions the name *Squatina* in a genera level dichotomous key to cartilaginous fishes that includes some descriptive traits. However, it is important to note that despite this being the first supposedly valid use of *Squatina* as a genus name, no particular species are included in the description. Thus, Dumeril's use of the term "Squatina" is not recognized as the proper citation for the genus.

Risso (1810) published a second species description for angel sharks and used the name *Squatina vulgaris*. In contrast to Linneaus (1758) and Dumeril (1806), which were encyclopedic works that included cursory information on angel sharks as part of a catalog of larger taxa (all known organisms and all known animals respectively), Risso's publication is noteworthy as the first valid publication to focus on the description of a single species of angel shark as part of a list of known ichthyfauna in a specific region of the world. In his publication Risso also formally and correctly described the genus *Squatina* while attributing the genus name as coming from Dumeril's earlier work (without recognizing Dumeril's earlier omission of species) and assigns *Squatina vulgaris* as the type species in the genus. As a genus name, the term "Squatina" dates from Risso's 1810 revision of Dumeril or is properly cited with Dumeril's name in parentheses as: *Squatina* (Dumeril, 1806). Compagno (1984) would later further establish Risso's use of *Squatina* as not an original description. Compagno stated in his description of genus *Squatina* that it was "obvious" that Dumeril intended the use of genus *Squatina* to refer to *Squalus squatina* Linnaeus, 1758. Risso's action is therefore interpreted as a subsequent designation of a type species for *Squatina* Dumeril, 1806. Garman (1913) and Bigelow and Schroeder (1948) identified Risso's *Squatina vulgaris* as equivalent to *Squalus squatina*. Therefore Linneaus' original description of *Squalus squatina* was reclassified as *Squatina squatina* (Linneaus, 1758).

The next relevant event in angel shark systematics occurred when Lesueur (1818) published the second valid description of an angel shark with his *Squatina dumeril*. Lesueur compared his type specimen to the description for *Squatina squatina* given by Risso (1810) and based on this diagnosis, identified that his type represented a completely different species. Genus *Squatina* now contained two distinct species *S. dumeril* and *S. squatina* with *S. squatina* representing the type species in the genus.

Cuvier (1829)[5] added a third description for a species classified under genus *Squatina* with his description of *Squatina aculeata* found off the coast of northwest Africa and the Mediterranean Sea. Cuvier identified his species as distinct by comparison to the description given for *S. squatina*. Cuvier's species gave the first record of multiple angel shark species having an overlapping range and living in the same geographic locality as one another.

Bonaparte (1838) later redescribed the traits of genus *Squatina* under a new family named Squatinidae with *Squatina* being both the type genus in the family and the only member genus in the family. Bonaparte (1840) later added the fourth valid species description of angel sharks with his *Squatina oculata* distributed along the Atlantic coast of Western Africa and the Mediterranean Sea, and further emphasizing the notion that distinct angel shark species have overlapping ranges and live in the same geographic locality as one another-possibly living in sympatry. As Cuvier had done before him, Bonaparte identified his species as distinct by comparison to the description given for *S. squatina*. It is notable that both Cuvier and Bonaparte used a relatively minimal *number* of morphological character differences from *S. squatina* for the

[5] (Cuvier attributed his specimen from Dumeril's work. However, the species is validly cited as *Squatina aculeata*, Cuvier 1829)

diagnostic basis of their designation of *S. aculeata* and *S. oculata* respectively and instead relied on the use of very distinct differences in very few pronounced qualitative traits such as spines along the midline of the dorsal surface (*S. aculeata*) and strongly fringed nasal barbels (*S. oculata*) for their respective diagnoses. Perhaps for this reason both *S. aculeata* and *S. oculata* were regarded as junior synonyms of *S. squatina* at several points in taxonomic history. Still, Cuvier's and Bonaparte's diagnosis methods illustrated the precedent in angel shark systematic history of having even one drastic difference in a morphological trait constitute a basis for designation of a new species, even if the proposed new species occurs in the same geographic region as a previously described species.

Bleeker (1857) later added a description for a fifth species in the genus with his description of *Squatina japonica* found off the coasts of Japan in the western Pacific Ocean. At this time family Squatinidae encompassed a single genus, *Squatina*, which now contained five distinct species *S. aculeata, S. dumeril, S. japonica, S. oculata,* and *S. squatina* with *S. squatina* as the type species in the genus. *S. aculeata, S. oculata,* and *S. squatina* were found in the same geographic areas and possibly served as an example that sympatric distribution of species was a possibility for angel sharks.

THE EASTERN PACIFIC REGION

Ayers (1859) published the sixth valid description of a species in genus *Squatina* and the first formal description of a species occurring in the eastern Pacific Ocean. Ayers compared his single specimen (eventually recognized as the holotype) to *S. dumeril* that occurs in the western North Atlantic Ocean and that had been described earlier by Lesueur (1818). This is the first time that *S. squatina* was not used for comparison with a prospective new species. It is likely that Lesueur's description of *S. dumeril* was the most easily accessible formal description of a member of *Squatina* for Ayers to compare his type to because Linneaus' description was not as detailed. In the original description, Ayers recorded that *S. californica* differed from *S. dumeril* in the following five (5) areas:

1) Form of the orbits… a qualitative character that may be used in taxonomic keys.

2a) Both the Form of teeth… a qualitative character that may be used in taxonomic keys

2b) and Number of teeth… a merisitc trait that may be used in taxonomic keys.

3a) Both the Size of pectorals…a quantitative morphometric character that alone is not regarded as effective for use in taxonomic keys (without a reference measurement)

3b) and Form of pectorals…a qualitative character that may be used in taxonomic keys.

4) Form of the ventrals - qualitative character that may be used in taxonomic keys.

5) Form of the dorsals - qualitative character that may be used in taxonomic keys.

Ayers described the coloration patterns on his specimen as white on the ventral body surface, white on the "membranous fringe bordering the head" (this likely refers to the shark's "upper lip"), and colored grayish-ash with "more or less distinctly" whitish spots on the dorsal surface. Ayers made no note of the physical condition of his specimen when these observations were recorded, so it is not known if the coloration pattern described in his publication represents the species' natural appearance or resulted from desiccation after removal from the water, and/or resulted from staining due to chemical preservation. Ayers' description of *S. californica* is unique among the other species accounts in his paper in that the exact date the specimen was taken from San Francisco Bay is given. It is likely that Ayers' specimen was observed in a San Francisco fish market as many of the species described in Ayers' publication are noted as being seen frequently or rarely in San Francisco fish markets. However, no specific mention of its occurrence in fish markets is mentioned in the description. Ayers did not designate any paratype specimens in his description. His type specimen was deposited into the ichthyology collection of the California Academy of Sciences where it was subsequently lost due to the fire associated with the 1906 San Francisco earthquake.

Philippi (1887) was the next to describe another member of the genus occurring in the eastern South Pacific. This was the second description for an angel shark in the eastern Pacific Ocean. However, in many respects Philippi's description was the first of its kind in many relevant categories.

Philippi's description was never (as of 2012) formally translated into an English language version. This was in contrast to Ayers' (1859) and Lesueur's (1818) descriptions that were written in English while Linneaus' *Systema Nature* (1758) and Dumeril's *Zoologie Analytique: ou méthode naturelle de classificatio des animaux* (1806) were both translated to and published in an English version. It is also worth noting that Dr. Rodolfo Amando Philippi was not a native Chilean but rather an immigrant from Germany. In Chile, like much of the new world, Spanish is written in Castillian-Spanish, yet a linguistic analysis of Philippi's original publication shows it to be written in a different written form of the Spanish language with different terminology, quite in contrast to much of the Castillian-Spanish works of the region.

Unlike Ayers and Lesueur before him, Philippi did not assign his specimen to Dumeril's genus *Squatina* and instead assigned it to Klein's (Aristotle's) genus *Rhina* (Klein [Aristotle], 1742) with the complete name of *Rhina armata*. At the time of Philippi's publication, the ICZN Code had yet to be established and the general consensus regulation, which all individuals naming and describing species adhered to was that the earlier a publication date the greater priority given to the zoological names proposed within that publication. Philippi's initial classification would eventually be reassigned to Dumeril's genus *Squatina* by Bigelow and Schroeder (1948). However, the initial classification of Philippi's type to genus *Rhina* led to significant further taxonomic confusion for the identification and deposit of specimens collected from the Pacific coast of South America because Bloch and Schneider's (1801) published description of another genus, for batoids, also called *Rhina* was already in use. In the pre ICZN Code era, these two rather unique publication traits led to Philippi's description and its finer details "flying under the radar" from much of the subsequent systematic literature on angel sharks.

Philippi's description further differed from Ayers' in the comparison species used in the diagnosis section of his publication to distinguish the type specimen as representing a new unique species. Ayers' (1859) description is not cited in Philippi's paper, so it is unknown if Philippi was aware of the presence of *S. californica* in the northern portion of the Eastern Pacific before publishing his description. Coupled with the fact that Philippi attributed his specimen to *Rhina* instead of *Squatina* it is possible that Philippi may have believed he was describing the first angel shark from the eastern Pacific Ocean. Philippi compared his type,"brought" (Philippi 1887) from Iquique, Chile, to a description for a specimen noted in his paper as *Rhina squatina*, which denotes as Linneaus' *Squatina squatina* as reclassified into Dumeril's (1806) genus. However, Philippi described his comparison specimen as coming from the locality of Rio de Janeiro, Brazil where *Squatina squatina* does not occur. If Philippi's comparison specimen indeed came from off the coast of Rio de Janeiro, Brazil, it is likely that this specimen instead represented either one of the following four species of genus *Squatina* occurring in the area: *S. argentina* (Marini, 1930), *S. guggenheim* Marini, 1936, *S. punctata* Marini 1936, or *S. occulta*

Vooren and da Silva, 1991, all four of which were not described at the time. Additionally, all four of these western South Atlantic species were confirmed to be sympatric with at least one of the other three species over a part of their range (Vooren and da Silva, 1991). Distinguishing each of these four species from one another without using molecular methods remains difficult. The recognition of *S. occulta* Vooren and da Silva, 1991 as a distinct species was not formally published until 62 years after the first description of any species of angel shark in this part of the world, on that account it remains probable that further yet to be described angel shark species may remain unknown to science in the area. Therefore, in the absence of further analysis of Philippi's comparison specimen, it cannot be determined which species of angel shark it represented. It may be one of the four known species of angel sharks of the south Western Atlantic or perhaps even a still unknown species. Whatever species it was, there is sufficient evidence in the form of morphological notes from Philippi's publication to conclude that the specimen Philippi claimed was from the locality of Rio de Janeiro, Brazil, and used for his diagnosis of *S. armata* was clearly not Linneaus' *Squatina squatina*.

While presented in a different format from Ayers' description, Philippi's description for *S. armata* is by far more detailed and contains both descriptions of distinguishing features as well as morphometric and meristic notes. Philippi's description also includes an illustration plate. Philippi notes that his type specimen differs from the angel shark collected from the vicinity of Rio de Janeiro Brazil, in the following seven (7) ways:

1a) Both Form of the pectoral fins… a qualitative character that may be used in taxonomic keys.

1b) and Size of the pectoral fins… a quantitative morphometric character that alone is not regarded as effective for use in taxonomic keys (without a reference measurement).

2) Width of the head... a quantitative morphometric character that alone is not regarded as effective for use in taxonomic keys (without a reference measurement). However, Philippi's description provided a reference measurement for both his type and the specimen used for diagnosis.

3a) Both Shape of the spiracles… a qualitative character that may be used in taxonomic keys

3b) and Size of the spiracles… a quantitative morphometric character that alone is not regarded as effective for use in taxonomic keys (without a reference measurement).

4) Form of the total body… a qualitative character that may be used (but is generally not used because it contains too great a range of values) in taxonomic keys.

5) Length of the pectoral-pelvic space… a quantitative morphometric character that alone is not regarded as effective for use in taxonomic keys (without a reference measurement).

6) Form of the tail… a qualitative character that may be used in taxonomic keys.

7) Presence of enlarged "denticles" on the pectoral fins… a dichotomous qualitative character that may be used in taxonomic keys.

From using only the information found in the original published descriptions of Ayers and Philippi it can already be deduced that *S. californica* and *S. armata* differ from each other in the following two (2) ways:

1) Form of the anterior margin of the pectoral fins …*S. armata* having a sinuate or "S" shape to them while *S. californica* possessed a more linear to concavely crescent shape.

2) Presence of enlarged "denticles" on the mid-dorsal surface and on the pectoral fins… *S. armata* having these enlarged "denticles" present on the mid-dorsal surface and on the pectoral fins while *S. californica* did not possess either.

The use of the latter character regarding the presence or absence of enlarged dermal denticles on a specific region of a sample angel shark specimen's body may initially appear to be a good candidate for use in dichotomous keys. However, there have yet been no validating studies addressing whether or not the presence of such dermal denticles reflect ontogenetic differences between the two specimens. Without a validating study eliminating this scenario using an increased sample size representing both species, the distinction of *S. californica* and *S. armata* using this character remains moderately effective. Thus, when restricted to only the information provided by the original descriptions, the form of the anterior margin of the pectoral fins is the best character to use to distinguish the two species.

In accordance with the precedent methods used previously to diagnose new species of angel sharks including *S. aculeata, S. dumeril*, *S. japonica*, and *S. oculata,* the sole use of the information from these two descriptions is sufficient to diagnose *S. californica* and *S. armata* as two distinct species. Family Squatinidae now included one single genus, *Squatina*, and seven species within the single genus: *S. aculeata, S. armata*, *S. californica, S. dumeril*, *S. japonica*, *S. oculata and S. squatina*, with *S. squatina* representing the type species for genus *Squatina*. *S. armata* and *S. californica* were the only members of the genus found in the eastern Pacific region.

Garman's (1913) encyclopedic work *The Plagiostoma (Sharks, Skates, and Rays)* was the next to describe a new species of *Squatina* found in the Eastern Pacific. In contrast to Linneaus and Dumeril who produced works intended to classify all known organisms and animals respectively, Garman's encyclopedic work dealt exclusively with known elasmobranchs and was the first comprehensive account of worldwide elasmobranch ichthyofauna known at the time. In the section of his publication describing the angel sharks, Garman included a description for one new species. Like Philippi did earlier, Garman assigned the angel sharks in his account to Klein's (Aristotle's) genus *Rhina* (Klein [Aristotle], 1742). Garman apparently even designated his own family, Rhinidae, (Garman cited no previous works in his description of family Rhinidae, so this invalid family is attributed to him) in which to place Klein's (Aristotle's) genus *Rhina*.

Garman described his type for a new angel shark species from the South Eastern Pacific as *Rhina philippi*, which would later become recognized as *Squatina philippi* (Garman, 1913) by Bigelow and Schroeder (1948). His specimen is listed as being collected from "Mexillones." It is assumed that this word is a misspelling of Mejillones, Antofagasta, Chile, a small port town found south of Iquique, Chile, the locality from where the type of *S. armata* was "brought" (Philippi 1887). Garman's account included a description of all angel sharks known at the time and also for the first time, a complete, albeit brief, dichotomous key for the entire group, including Garman's newly described *S. philippi*. Garman's notes included the first osteological character analyses for Eastern Pacific angel sharks. From analyses of the skull structure of his specimens, Garman wrote that two of the eastern Pacific angel sharks, *S. californica* and *S. philippi*, can be distinguished from all the other species in the genus, in that they are the only two species in the genus that do not have their postorbital process uniting with the skull at the front of the foramen-thus completing the foramen. Rather, in *S. californica* and *S. philippi*, there is no such union and the foramen remains open toward the orbit. This is the first formally documented morphological character exclusive to eastern Pacific angel sharks. It is not known if Garman had access to any specimens of *S. armata* to also include in this analysis to verify whether all three known eastern Pacific species posses this character state.

Garman's publication is notable in that it used the word "cirrus" (a collective zoological term for any slender tendril or hairlike filament, such as the appendage of a barnacle, the barbel of a fish, or the intromittent organ of an earthworm) to refer to a morphological character that was historically referred to as "barbel" (a term specifically referring only to a fleshy filament growing from the mouth or snout of a fish) or more specifically "nasal barbel" in prior angel shark taxonomic literature. This inconsistency in naming morphological characters made some of Garman's recorded observations less apparent for use in comparison to earlier published works and highlighted the need for consistency in the precise terminology used to identify morphological traits.

Garman was also the first to hint that the use of certain morphological characters to distinguish species may be ineffective due to high levels of individual variation of these characters within one species. Garman mentioned the use of the three characters of point of origin of the first dorsal fin in relation to the extremities of the ventral fins, the condition of the fringes of the nasal valves, and the presence of tubercles on the back, as examples of characters possessing such an unsuitable degree of intraspecific individual variation. Garman stated that these characters were not used in his account to distinguish species, in favor of the characters of form of the subcaudal fin, the angle formed by the meeting of a line along the outer edge of the pectoral fin with another across the hind margin of the same pectoral fin, the shape of the fold along the side of the head, and the completeness of the foramina for the process of the pterygoquadrates in the top of the skull (Garman 1913). This established Garman as the first to highlight the need to eliminate characters possessing a high degree of individual variation when distinguishing angel shark species. However, Garman provided few validating details as to why certain characters were not favored and others were supposedly safe for use. Garman further provided no hints as to whether or not such noted individual variation was a result of possible ontogenetic differences or even due to sexual dimorphism. The stated ineffective characters of nasal valve (nostril's) fringe's condition and presence of tubercles on the back in particular are two characters that are especially vulnerable to environmental damage both prior to and post collection. Although Garman identified a potential source of error coming from the use of characters with a high degree of individual variation, there had yet to exist a proper protocol in angel shark taxonomic literature to adequately address the issue. Garman's preferred use of a character described by the angle formed by the meeting of a line along the outer edge of the pectoral fin with another across the hind margin of the same pectoral fin was a particularly convoluted one that led to further complications. Prior descriptions, including Ayers (1859) and Philippi (1887) had directly measured the precise shape formed by the perimeter of the pectoral fin margins across the entirety of the fin. In contrast, Garman's character was measured with the use of two-straight edges contacting the extreme edges of the fins without necessarily noting the precise shape of the margin of the pectoral fin between the two extremes in consistency with the prior literature. This made comparing Garman's observed characters to Ayers' (1859) and Philippi's (1887) descriptions difficult and highlighted another problem, the need for a standardized set of morphometric characters for angel sharks and a precise accompanying description for how to measure each of those characters.

Using information noted in both Garman's key to angel shark species and the diagnostic notes from the brief description section for *S. philippi*, Garman distinguished it from *S. squatina*, and also most importantly from *S. californica*, and *S. armata*. Garman's publication identified that *S. philippi* was distinct from *S. armata* using the following three (3) qualitative characters:

1) Form of the subcaudal fin… *S. philippi* possessing an obliquely truncate shaped subcaudal fin, while *S. armata* possessed a pointed subcaudal fin.

2) Form of the margins of the pectoral fins… *S. philippi* possessing pectoral fin margins forming a right (90 degree) angle, while *S. armata* possessed pectoral fin margins forming an obtuse (larger than 90 degree) angle.

3) Tubercles on the back… *S. philippi* did not possess a row of tubercles along the median line of the back whereas *S. armata* did possess a row of tubercles along the median line of the back. (Garman noted this character difference only in the species descriptions and not in his key to species.)

Garman's publication also identified that *S. philippi* was distinct from *S. californica* using the following three (3) qualitative characters:

1) Form of the subcaudal fin… *S. philippi* possessing an obliquely truncate shaped subcaudal fin, while *S. californica* possessed a rounded subcaudal fin.

2) Form of the margins of the pectoral fins… *S. philippi* possessing pectoral fin margins forming a right (90 degree) angle, while *S. californica* possessed pectoral fin margins forming an obtuse (larger than 90 degree) angle.

3) Form of the supracaudal fin… *S. philippi* possessing a very broadly shaped supracaudal fin, while *S. californica* possessed a "substantially less" broad supracaudal fin.

Garman's actual description for *S. philippi* was more brief than either Ayers' (1859) or Philippi's (1887) earlier descriptions, but still consisted of sufficient morphometric and meristics (for the teeth) notes to distinguish the species. Garman recorded that the type specimen for *S. philippi* bore no row of tubercles along the median line of the back. It possessed rows consisting of 20 individual teeth on both the upper and lower jaw. The cirri (barbels) were not lobed, the outer border of the pectoral fins was nearly linear to just slightly convex, and the posterior border of the pectoral fins was nearly linear and just slighty concave.

Garman recognized Ayers' description of *S. californica* in his list of valid species. In his key to species, Garman identified a third character that can be added to the list of character differences used to distinguish *S. californica* from *S. armata*, which is the:

3) Form of the subcaudal fin… *S. armata* possessing a pointed subcaudal fin, while *S. californica* possessed a rounded subcaudal fin.

Though Garman also recognized Philippi's description of *S. armata* in his list of species he stated that, "Little to serve to establish this species can be drawn from either description or figure as published; for the time it must be considered doubtful." It is difficult to comprehend how Garman arrived at such a conclusion as Philippi's publication clearly stated and identified several morphological characters that distinguish it from the "supposed *S. squatina* specimen" from the Rio de Janeiro area of the western Atlantic Ocean used for comparison. Garman was also very careful to distinguish Philippi's *S. armata* from Ayers' *S. californica* in his key for the entire genus by stating that only *S. californica* has a rounded subcaudal fin tip whereas *S. armata* has a very pointed subcaudal fin tip. Garman's description of *S. armata* included coarse notes on the form of the spiracles, the form of the pectoral fins, and the form of the ventral fins. Garman acknowledges that in the preceding three respects *S. armata* "agrees with neither" of the known species of the eastern Pacific (Garman 1913). It must be noted that although these characters, which Garman mentioned, are sufficient to distinguish *S. armata* from other Eastern Pacific species, these characters are only those that are visibly apparent from Philippi's illustration plate (Philippi 1887). Additional distinguishing characters, including the length of the pectoral-pelvic space and shape of the spiracles, which would only be known from reading Philippi's description, are not listed. Garman also appears to attempt to quote Philippi's own remarks word for word when acknowledging certain features of the type by stating that "The type was taken at Iquique, Chile; it bore a median row of tubercles on the back." This is nearly precisely what Philippi's own words (more specifically it is an imprecise literal English translation of the original Spanish words) stated in the original paper making it likely Garman never examined Philippi's actual type specimen for himself. Recognizing that Garman intended to document every known cartilaginous fish in the world at the time, it is plausible that he could not review Philippi's publication in sufficient detail and merely had the document translated for him. It is further plausible that either such a translation was ineffective (Philippi's publication contains both uncommon Spanish terms and some misspelled words) or Garman simply overlooked its details.

Almost a century after family Squatinidae was described by Bonaparte, de Buen (1926) formally described the order Squatiniformes. Like Philippi's publication, de Buen's work was originally published in Spanish, not initially translated into an published English version, and would not be immediately recognized and consistently cited for its contribution to the taxonomy of angel sharks in subsequent literature for some time. Nevertheless, de Buen's work represented the final step in the valid establishment of the major higher taxonomic classifications for angel sharks. The order Squatiniformes only contained one family, Squatinidae. The family Squatinidae only contained one genus, *Squatina*. At the time order Squatiniformes was established, there were three (3) species of genus *Squatina* found in the Eastern Pacific, *S. californica*, *S. armata*, and *S. philippi*.

Garman's work was later reproduced in even greater detail by Bigelow and Schroeder (1948) as part of their comprehensive taxonomic account of all fishes known at the time from the western North Atlantic region. Bigelow and Schroeder did not list de Buen's (1926) order Squatiniformes in their work and instead denoted the highest classification for angel sharks with the term suborder Squatinodea. Bigelow and Schroeder did not cite any other earlier publications when describing the characteristics of suborder Squatinodea, so it is assumed that Bigelow and Schroeder were the first to formally describe it. Bigelow and Schroeder documented for the first time in angel shark taxonomic history the precise catalogued specimen numbers for all the specimens that they used to obtain data for the construction of the key to the species in the genus *Squatina*. However, unlike Garman, Bigelow and Schroeder championed the use of nasal valve (nostril) fringe condition as well as nasal barbel form as morphological characters to distinguish species in their key. Analysis of Bigelow and Schroeder's brief section dealing with the genus *Squatina* as a whole, prior to the in depth description given for *S. dumeril* and *S. argentina*, the only two species of *Squatina* found in the western North Atlantic region, indicates that it is highly probable that Bigelow and Schroeder's treatment of genus *Squatina* (Dumeril, 1806) largely follows Garman's (1913) account of genus *Rhina* (Klein (Aristolte), 1742).

Like Garman before, Bigelow and Schroeder stated in regard to Philippi's *S. armata* that the original account for the species was not sufficiently detailed to establish it as a unique species in nearly a precise word-for-word reiteration of Garman's rather puzzling statement. Bigelow and Schroeder noted that the data they used for their description of *S. armata* did not come from any collected specimen identified as *S. armata* but rather came from a specimen believed to be the type of *S.philippi* (Garman 1913), which was conveniently cataloged in the fish collection at the Harvard Museum of Comparative Zoology ichthyology collection and available for examination. Bigelow and Schroeder stated that because the original account for *S. armata* did not provide enough details to locate the species in their new key, they used characters from a specimen with the Harvard Museum of Comparative Zoology catalog number of: No. 531, which they believed was the type of *S. philippi* (Garman 1913). However, Bigelow and Schroeder listed this cataloged specimen as coming from the locality of "Mejillones Island, Peru." This is not in accordance with Garman's (1913) original locality data of "Mexillones" (assumed as a misspelling of Mejillones, Antofagasta, Chile), for the type of *S. philippi*. It is highly probable that Bigelow and Schroeder simply interpreted Garman's locality data incorrectly as no island (or even location) known in either English, Spanish, or other language as "Mejillones" occurs in Peru, save for the name of a small street in the inland city of Cajamarca, Peru. It should therefore be noted that the specimen from which Bigelow and Schroeder took their detailed morphological notes came from a locality south of the locality for the type of *S. armata*, instead of a locality north of it as Bigelow and Schroeder erroneously stated.

Bigelow and Schroeder believed *S. philippi* (Garman 1913) was a junior synonym of *S. armata*. Bigelow and Schroeder used the same argument for suggesting (albeit coming short of stating) that *Squatina tergocellata* McCulloch, 1914 was a junior synonym of *Squatina australis* Regan, 1906, and subsequent specimen analysis (Compagno 1984) maintained the distinction of these two species. However, no subsequent publication (through 2012) ever verified the conclusion that *S. philippi* refers to the same species as *S. armata*. Therefore, *S. philippi* was subsequently regarded as a junior synonym of *S. armata*, which was considered the valid name for the species despite having the morphological characters Bigelow and Schroeder used to describe *S. armata* come from a specimen that previously served as the type for a distinct species. Bigelow and Schroeder's statements are therefore properly interpreted as identifying a fourth character that can be added to the list of character differences used to distinguish *S. californica* from *S. philippi*, (not *S. armata*), which is the:

4) Form of the inner nasal barbel… *S. philippi* possessing a narrow and tapering inner nasal barbel, whereas *S. californica* possessed broadly spatulate inner nasal barbel.

Squatina armata was later itself placed in the synonymy of *S. californica* by Kato et al. (1967), but was later tentatively acknowledged as a possible separately recognized species again by Compagno (1984). Compagno (1984) published the first truly comprehensive worldwide catalogue of all known sharks, which at last presented the first standardized set of morphometric characters used for sharks. This was particularly important because it was the first solution offered to address the prior issue of variation in the precise terms used to describe the very same morphometric characters. For example Garman (1913) had used the word "cirrus" to refer to the same morphological structure called a "barbel" by Bigelow and Schroeder (1948). Philippi (1887) used the word "*fistulas*" to refer to the spiracles, but the English translation of this word means "hollow tube/opening to a cavity." This led to the word "*fistulas*" being interpreted as referring to the ventral body cavity opening. Compagno's morphometric characters listed precisely what area of a shark's body they were referring to and gave an abbreviated title that standardized the term for each character.

Compagno's characters were not without certain weaknesses. The characters were designed primarily for the more fusiform shaped orders of sharks including Lamniformes, Squaliformes, and Carcharhiniformes. Many of these characters were not specific to the unique body form exhibited by Squatiniformes and did not include characters corresponding to many of the morphological traits previously used to distinguish angel shark species from each other. Differences among the squatiniform species traditionally used the nasal barbel shape, interorbital and interspiracle distances, ocellus patterns, number of dermal folds about the mouth, and the presence of midback thorns as phenotypic characters for distinguishing species. Compagno did not describe any morphometric instructions for these specific characters with the initial publication. Years later Compagno (2001) published an updated version of the earlier catalog that included more detailed instructions and procedures for approximately 103 total elasmobranch morphometric characters (of which three: the sixth gill slit height, seventh gill slit height, and subocular pocket depth were immediately not applicable to angel sharks) accompanying an updated treatment for only the orders Orectolobiformes, Heterodontiformes and Lamniformes. While this update still did not translate how the characters should be applied to the unique morphology of Squatiniformes, Compagno's updated catalog (2001) has been considered the prototype standard in elasmobranch taxonomy and systematics to this day.

Unfortunately, Bigelow and Schroeder's (1948) treatment of angel sharks was used as a template for Compagno's section on Squatiniformes in the original (1984) catalogue and this further perpetuated the strengths and weaknesses of the earlier publication. Compagno (1984) seemed to acknowledge that the angel sharks were poorly known and that there was a strong possibility that Bigelow and Schroeder's treatment contained errors and stated a disclaimer that his section dealing with angel sharks largely follows Bigelow and Schroeder (1948) and that Compagno's treatment of the entire order is "provisional in the extreme" (Compagno 1984). Compagno identified angel sharks with the most broad taxonomic classification of Squatiniformes, de Buen 1926, but did not attribute the order to de Buen. Compagno's publication was also the first to indicate that the specimens of *S. californica* found in the Gulf of California region demonstrated peculiar morphometric traits unlike that of specimens found elsewhere. The angel sharks occurring in the Gulf of California were noted to be abundant in very deep water down to 183 meters, whereas those occurring in the Pacific Ocean were only abundant up to around a 46 meter depth. In particular, Compagno cited a 1982 personal communication from S. P. Appelgate (which is not included in Compagno's bibliography section) that indicated that the angel sharks found in the Gulf of California region might represent a separate species from *S. californica*.

Villavicencio-Garayzar et al. (1997) found differences in both the average total length and length at first maturity between angel sharks from the Gulf of California and those occurring along the Pacific coast of the Baja California Peninsula using morphometric analysis. These findings further reinforced Compagno's (1984) documentation that the possibility of at the least two distinct populations or possibly two species are represented by the angel sharks occurring in these areas.

Gaida (1997) published the first molecular population structure study of eastern Pacific angel sharks. Gaida used allozyme markers to demonstrate that the population of angel sharks occurring in the area of the Southern California Bight and the Channel Islands was not one genetically homogenous population and was instead composed of several genetically isolated sub-populations. Prior radio-tracking experiments conducted by Standora and Nelson (1977) suggested that although angel sharks moved significant distances around the perimeter of Santa Catalina Island they always did so while staying in the shallow depths and did not leave the vicinity of the island. Gaida used data from seven polymorphic loci that encoded for enzyme systems in the sharks, and found that the angel shark populations present in the northern Channel Island region were significantly different than the angel shark populations present in the southern Channel Island region. The total geographic distance between the two regions compared in the study was about 75 km (Gaida 1997). Gaida reported that these results were the first instance of significant allele-frequency differences over such a small geographical distance published for an elasmobranch species, and hypothesized that the angel sharks behavioral traits of lying motionless of the sea bottom waiting for suitable prey to wander by in combination with the very deep sea floor topography (500 meter depth) between the two sample areas may have led to the structuring observed. Gaida also deposited voucher specimens from his study in the UCLA Ichthyology Research Collection and indicated them with the catalog number of UCLA W90-1.

Grijalva-Chon et al. (2002) later used restriction fragment length polymorphism of the mitochondrial DNA control region to demonstrate that there existed genetic homogeneity between two sample populations occurring within the Gulf of California. Their two sites within the Gulf of California were from in the Isla Tiburon region in the northeastern portion of the Gulf and from the Isla San Jose region in the southwestern portion approximately 1,500 kilometers apart from each other. This distance is nearly twenty orders of magnitude farther than the sample sites used in Gaida's (1997) study. Grijalva-Chon et al. used three restriction enzymes that, after digesting the mitochondrial DNA control region, yielded polymorphic loci that encoded for a total of three haplotypes in the angel sharks, with 94% of the total sharks sampled possessing the most common haplotype and one single individual from each of the two sites possessing the sole example of the other two haplotypes. Therefore, Grijalva-Chon et al. reasoned that the two populations sampled were not significantly different and that there existed genetic homogeneity across the range for the mitochondrial DNA control region.

However, other geological literature including Larson et al. (1968), Holt et al. (2000), and Sandoval-Castillo et al. (2004) noted that the land forming the Baja California peninsula has been in its present condition that completely isolates the waters of the Gulf of California from the Pacific Ocean for only the past 10,000 years. This is fairly recently in geologic time when compared to other the formation of other geological features of the eastern Pacific coastline. The degree of genetic homogeneity observed in this region may reflect the limited initial genetic diversity available from founding populations of angel sharks because the Gulf of California has been relatively recently separated from those occurring in the Pacific Ocean. It is not known if Grijalva-Chon et al. deposited voucher specimens from their study.

Ebert (2003) noted in his catalog of California cartilaginous fishes that the angel sharks occurring in the Gulf of California, though considered synonymous with the populations occurring in the Pacific Ocean, were so distinct that they may constitute two distinct species. Ebert cited both populations as being assigned to the name *S. californica*, Ayers, 1859, yet remarked that the systematics of eastern Pacific angel sharks were still poorly understood. Ebert specifically stated that in the Gulf of California angel sharks mature at a much smaller size, about 780 mm total length for males and 850 mm total length for females, than those angel sharks found at the same latitudes along the Pacific coast of the Baja California peninsula. Here they did not reach maturity until reaching about 900 mm (Natanson and Cailliet 1986) to 1000 mm total length for males and 1000 mm to 1200 mm total length in females (Ebert 2003). These observations were in support of previously published morphometric notes (Villavicencio-Garayzar et al. 1997) and hinted at the occurrence of an "island dwarfism" pattern in these angel sharks, possibly due to founder effect. Ebert's account indicated the strong possibility that the population of *S. californica* occurring in the Gulf of California may have undergone a form of allopatric speciation from the populations occurring in the Pacific Ocean.

Sandoval-Castillo et al. (2004) used restriction fragment length polymorphism of the mitochondrial DNA control region to demonstrate that Gulf of California populations of *Rhinobatos productus*, commonly known as the shovelnose guitarfish, were cryptically isolated from the populations in the Pacific Ocean. Their methods yielded nine haplotypes that were unique to the samples from the Gulf of California and eight haplotypes that were unique to the samples from the Pacific Coast. Not one haplotype was shared by both of the sample areas indicating a deep phylogeographic break between the haplotype distributions of this region. *R. productus* fills a similar ecological niche and has many similar behavioral and life history traits with angel sharks. As had been previously documented in angel sharks, Sandoval-Castillo et al. noted that prior to their study morphometric analysis of *R. productus* revealed a significant degree of character differences between samples from the populations occurring in the Gulf of California and those occurring in the Pacific Ocean. Sandoval-Castillo et al. postulated that their results showed a pattern of genetic structure and levels of divergence consistent with the geological history of the region. Their data for the first time revealed the existence of a high degree of intraspecific variation revealed using molecular methods. The observations added to the growing support for the notion that the Gulf of California populations of angel sharks were distinct from those in the Pacific Ocean.

Compagno et al. (2005) published an updated popular literature version of Compagno's earlier catalogue (1984) that once again fully regarded *S. armata* as a separate species. In this publication, *S. armata* was listed separately from the description for *S. californica* and was denoted with the common name of "Chilean Angel Shark." A rudimentary, yet distinctive, color illustration and description were also included. The illustration of Compagno et al. (2005) is strikingly similar to Philippi's (1887) original plate illustration and given a uniform grey color.

In a review and redescription of angel sharks occurring in the Western Pacific Ocean, Walsh and Ebert (2007) provided a new set of morphometric characters that included a total of 70 characters of which 54 were taken apparently unmodified from Compagno's (2001) most recently published set. Eight other of Compagno's characters (anterior nasal flap length [ANF], internarial space [INW], nostril width [NOW], dorsal caudal margin [CDM], lower postventral caudal margin [CPL], upper postventral caudal margin [CPU], preventral caudal margin [CPV], and subterminal caudal margin[CST]) were given a more detailed description specific to an angel shark's more distinctive snout and caudal fin regions, while the remaining eight characters listed appeared to be entirely new characters with new descriptions, although Walsh and Ebert's listed character of tail length [TAL] may refer to Compagno's (2001) character listed as vent-caudal fin length [VCL]. Seven of Walsh and Ebert's new proposed morphometric characters have sufficient descriptions to deduce what they refer to, but there are insufficient details attached to the proposed new character of dorsal fin space [DFS] to determine to what it refers. A detailed illustration of the snout and caudal fin region where the mix of redescribed and new characters are taken is also provided. Other than the introduction and precise denotation of the new characters on the snout region and five new characters on the caudal fin region, Walsh and Ebert followed Compagno's (2001) characters when making their analysis of western Pacific angel sharks.

In their description of three new species of angel sharks found in the western Pacific Ocean, Last and White (2008) subsequently provided a total of 50 morphometric characters. In contrast to Compagno's (2001) and Walsh and Ebert's (2007) earlier publications, Last and White attached a detailed statement of precisely what structures to measure with all 50 of their listed characters. 33 of these characters are present and referred to with the same three-letter designation as they appear in both Compagno's (2001) and Walsh and Ebert's (2007) publications. An additional eight characters were ones originally proposed by Compagno (2001), but that were omitted from Walsh and Ebert's (2007) publication. An additional five characters are completely new and proposed for the first time by Last and White (2008). The final four characters (width at pectoral origins [WP1], pectoral fin width [P1W], pelvic fin width [P2W], and preventral caudal-fin margin [CVM]) were also presented, as new in their designations and descriptions, yet their purpose appears to be to a substitution for some of Compagno's original characters. The new use of the pectoral fin width [P1W] is an efficient substitution for the two inefficient characters of pectoral fin height [P1H] and pectoral fin posterior margin [P1P], which do not translate well to an angel shark's body morphology. However, new designation of the preventral caudal-fin margin [CVM] character is an unnecessary redundant substitution for the Compagno's original character of pre-ventral caudal fin margin [CPV] as both characters precisely refer to the same structure. Last and White's designation of the new character of pelvic fin width [P2W] is an efficient substitution of Compagno's (2001) original characters of pelvic fin base [P2B], pelvic fin height [P2H], and pelvic fin posterior margin [P2P] which do not translate well to an angel shark's body morphology. However, the character of pelvic fin anterior margin [P2A], which Last and White also omitted should not be included in those substituted by Last and White's the new character of pelvic fin width [P2W], because this character translates well to an angel shark's body and provided it is described well can yield a useful metric for comparing and distinguishing individual species. Last and White also omitted the effective snout characters (upper lip arch height [UAH] and upper lip arch width [UAW]) proposed by Walsh and Ebert (2007) that should be used when measuring specimens. Last and White's most significant contribution to the development of angel shark morphometrics came in the form of their published illustration of an angel shark's body plan which provided instructions of precisely where on a specimen the 50 characters Last and White listed corresponded to.

Stelbrink et al. (2010) provided a nearly comprehensive global phylogeny for angel sharks based on two mitochondrial DNA markers (COI and 16S rRNA). Stelbrink et al. concluded that the genus *Squatina* was monophyletic and they used a molecular clock analysis of their data to determine if divergence times in emerged clades within genus *Squatina* corresponded with the estimated times of significant geological events. In the case of the eastern Pacific angel sharks, their study showed that the divergence time between their sequences from samples of *S. californica* and *S. dumeril* correspond with the estimate for the rise of the isthmus of Panama, which supposedly fractioned off the range of these two species. Stelbrink et al. obtained three samples of supposed *S. armata* listed as coming from the locality of Coquimbo, Chile from the eastern South Pacific, five samples of *S. californica* listed as coming from the locality of the California coast from the eastern North Pacific of which voucher specimen numbers are listed, and 29 samples of *S. californica* from the Gulf of California for their study. No voucher specimen numbers are listed for either the three samples of supposed *S. armata* or any of the 29 samples of *S. californica* from the Gulf of California. Stelbrink et al. avoided pooling their samples of *S. californica* and compared their data from those samples taken from the Gulf of California to the data from samples taken on the Pacific Ocean with the stated purpose of further investigating reports that the population of angel sharks in this region represent a new distinct species. It should be noted that Stelbrink et al. acknowledged that their data were obtained by being sent tissue samples in most cases. The publication supplementary materials explicitly stated that their five samples from the locality of the California coast came from collections with voucher numbers to match the tissues with the specimens from which they originated. However, the publication supplementary materials do not explicitly state whether or not Stelbrink et al. were sent tissue samples or whole specimens in the case of the three samples of supposed *S. armata* (tissue type is noted as “muscle/skin”) or any of the 29 samples of *S. californica* from the Gulf of California. There is no mention in their publication or supplementary materials as to how confirmation of the species identity of their three samples of supposed *S. armata* occurred. That

S. philippi occurs in the same region as *S. armata* leaves the possibility open that their samples may possibly have represented the former species.

The phylogeny of Stelbrink et al. (2010) established the sequences from their three samples of *S. armata* as basal to all North and South American angel shark species occurring in both the Pacific and Atlantic Oceans with *S. armata* being more similar to the sequences from samples of *S. guggenheim* Marini, 1936 than to sequences from samples of *S. californica*. Regarding the issue of differences in populations of *S. californica* from different areas of the species known range, Stelbrink et al. found four different mitochondrial haplotypes exclusive to the Gulf of California samples, which differed from the single mitochondrial haplotype exclusively found from the Pacific Ocean sample. Additionally, the Gulf of California population formed a sister group to the Pacific Ocean population of *S. californica* inferred from their concatenated sequences. However, their publication stopped short of naming the Gulf of California population a "good species" in the absence of their observed genetic differences also being supported by "morphological, anatomical or ecological traits, thus increasing the probability of reproductive isolation." (Stelbrink et al. 2010). These statements indicate that Stelbrink et al. used Mayr's Biological Species Concept (Mayr 1942) to define distinct species, which was not the species concept used to describe most species of angel sharks in the world, and is also impractical to test on angel sharks given their life history traits.

Vélez-Zuazo and Agnarsson (2011) provided another global phylogeny for 229 known species of sharks based on four mitochondrial DNA markers (COI, Cytb, NADH-2 and 16S rRNA) and one nuclear DNA marker (Rag-1) constructed using Bayesian phylogenetic analysis methods. Vélez-Zuazo and Agnarsson included in their sample all shark species listed in either Genbank or from the Barcoding of Life Project website as having a sequence from any of their five genes available. Vélez-Zuazo and Agnarsson did not list any Rag-1 sequence numbers for the samples of genus *Squatina* used in their study. Using Bayesian phylogenetic analysis methods, Vélez-Zuazo and Agnarsson confirmed the previous findings of Stelbrink et al. that the genus *Squatina* was monophyletic, and that the sequences from their samples of *S. armata* were the earliest diverging lineage amongst all other sequences from North and South American angel shark species occurring in both the Pacific and Atlantic Oceans.

The genus *Squatina* currently contains approximately 19 valid named species (Eschmeyer et al. 2005) with a localized distribution in temperate and sub-tropical zones of the world's oceans. Along the coasts of the Eastern Pacific Ocean there have been three published species descriptions given for angel sharks: *S. californica* Ayers 1859, which occurs from Alaska to Cabo San Lucas, *S. armata*, (Philippi 1887), which occurs from Ecuador to Chile, and *S. philippi* Garman, 1913 of which little is known but the type was collected off the coast of Mejillones, Antofagasta, Chile. The population of angel sharks occurring in the Gulf of California also meets the requisite criteria for designation as a distinct species when using the data already reported in published literature to compare them to other named angel sharks species occurring in any other region of the Eastern Pacific. This group is currently only known to occur in the Gulf of California region is tentatively recognized here as *Squatina* sp. pending formal designation of a proper name. These four names represent all current known angel sharks occurring in the eastern Pacific Ocean. It remains possible that more species remain unknown to science in this region, especially the very little known South Eastern Pacific. The relatively recent findings of new species in other more intensely studied areas including *S. mexicana*, Castro-Aguirre et al. 2006, *S. albipunctata*, Last and White, 2008, and *S. caillieti*, Walsh et al. 2011, suggest that this scenario is very likely. At present the precise range of all four angel sharks in the littoral zones of the eastern Pacific remains poorly defined. *S. philippi* is in all likelihood the most poorly defined as it has long been regarded as a junior synonym of *S. armata* and thus the species name may not form part of the known chondrichthyan fauna.

TAXONOMIC KEY TO EASTERN PACIFIC ANGEL SHARKS

Garman (1913) proposed a key, which represented the proper key for the limited number of known species of genus *Squatina* at the time, before many restrictions occurred in their geographic range. Compagno (1984) offered a provisional key for his elaborate identification of individual species in the genus *Squatina* based on the correspondence of Bigelow and Schroeder (1948), and while these two works were intended to be the standard utility used in the distinguishing of all known species of *Squatina* both keys collectively do not accomplish this objective due to the great homogeneous morphology that *Squatina* manifest and also due to the omission of several species erroneously placed in synonomy with one another. Here the following key is presented to properly identify all currently known *Squatina* occurring throughout the eastern Pacific Ocean.

1. Subcaudal fin not strongly pointed (not forming right angle); anterior margin of the pectoral fins not having a sinuate (“S” shape) to them …………………………………..……………..2.

- Subcaudal fin strongly pointed (forming a right angle); anterior margin of the pectoral fins having a sinuate (“S” shape) to them; ………………...……...….*Squatina armata* (Philippi 1887)

2. Inner nasal barbel broadly spatulate; outer nasal barbel possessing one small spatulate tipped frill toward center of snout; rounded subcaudal fin; pectoral fin margins forming an obtuse (larger than 90 degree) angle…………………………………………………………...………3

- Inner nasal barbel not strongly spatulate, but rather narrow and tapering; outer nasal barbel possessing one pointed tipped frill toward center of snout with frilled flap on the side oriented toward pectoral fins; obliquely truncate shaped subcaudal fin; margins of pectoral fins forming a right (90 degree) angle ……………….…………………...…..*Squatina phillipi* (Garman 1913)

3 Mature at 780 mm total length (males) and 850 mm total length (females), found in Gulf of California……………………….…………………………………………………..… *Squatina* sp.

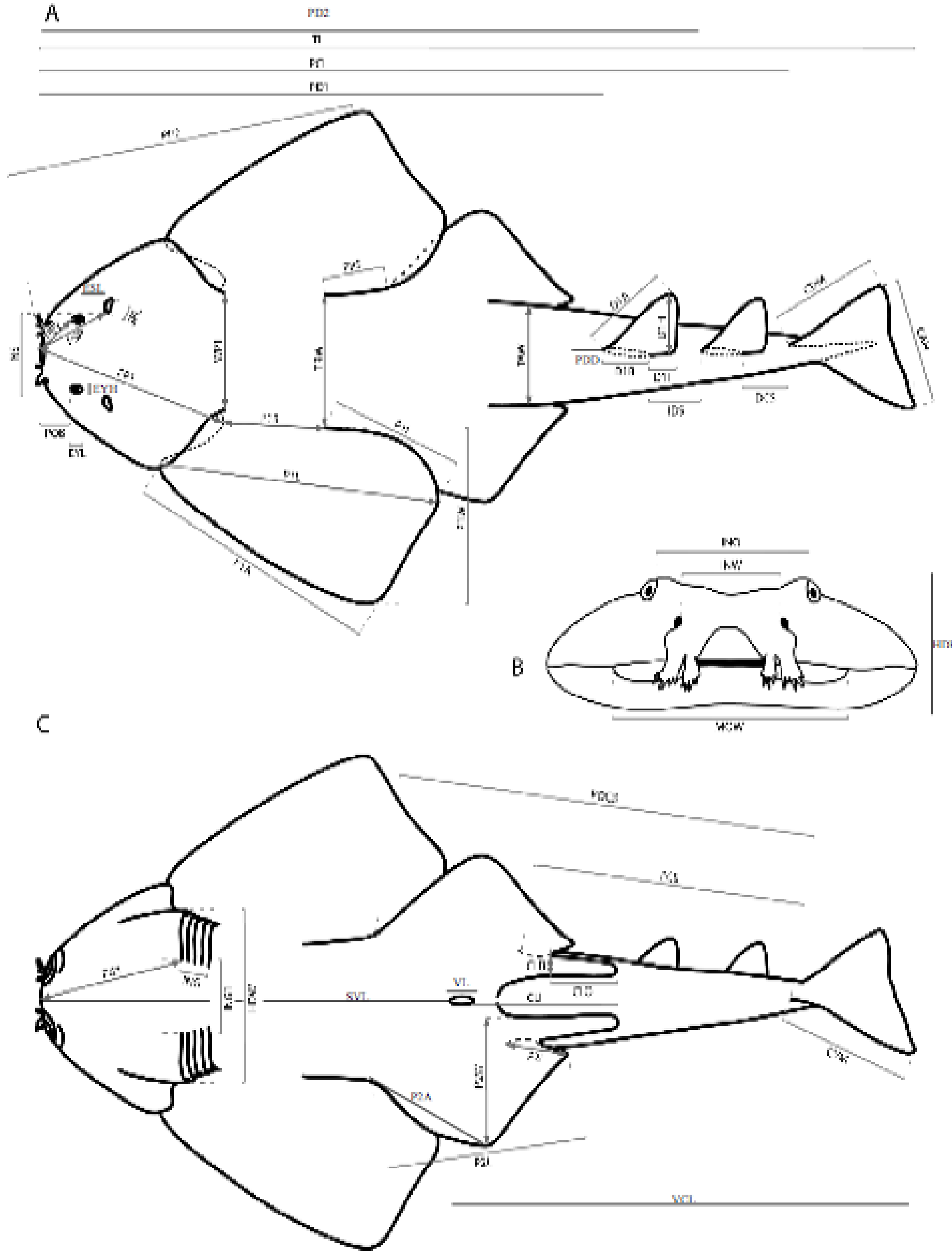
- Not yet mature at total length of 780 mm total length (males) and 850 mm total length (females), (but mature at 900 mm total length) found in north Eastern Pacific Ocean..………….
…..……..………..... ……………………….……………………….*Squatina californica* Ayers 1859.

MORPHOMETRIC CHARACTERS FOR SQUATINIFORMES

Morphometric numerical characters were selected to facilitate comparisons of all species of *Squatina.* Measurements are taken directly instead of exclusively horizontally. Actual measurements are to be taken to the nearest 0.1 mm. Methods generally followed the widely adopted scheme for elasmobranchs (Compagno, 1984, 2001), but are slightly modified for an angel shark's atypical body shape according to the more recently developed methods in previous *Squatina* systematics literature (Walsh and Ebert, 2007, Last and White, 2008). Of the three prior publications, only Last and White offered a description of the methodology for their 50 listed characters. However, in this work, all characters are now given a precise description of their methodology to ensure consistency in their application. One completely new laterally taken character:

1) PDD-Pelvic Dorsal Distance-(The distance from apex of free rear tip of pelvic fins and origin of first dorsal fin)

is added and highlighted (Figure 1.0). Some of the existing character descriptions are reclassified to avoid redundancies and allow for more intuitive matching the character's three letter abbreviation labels and descriptions (Table 1.0). Historically, all characters were presented as a proportion of total length (TL) to facilitate direct comparison. However, Cailliet et al. (1986) established that any character with a proportion greater than 90% or less than 10% is respectively too large or too small to be statistically informative. In teleost morphometrics, characters that yield proportions less than 10% are alternatively taken as a proportion of the operculum length character. Since angel sharks and other elasmobranches do not posses an operculum the most appropriate analogous character to use is the Pre-Branchial Length [PG1] character, which is taken ventrally and measures the direct distance from snout tip to inner edge of the first gill slit. Therefore in the case of characters that yield a proportion value smaller than 10%, the characters will also be recorded as a proportion of the Prebranchial length [PG1] character.



<u>FIGURE 1.0:</u> Diagram Representation of morphometric characters for use on genus *Squatina*.A, dorsal view; B, anterior head view; and C, ventral view. Illustration Adapted from Last and White (2008 figure 1 page 3).

<u>Table 1.0:</u> Detailed descriptions of morphometric character abbreviations for use on genus *Squatina*.

Code	Morphometric Character	Methodology	Taken	Proportion of PG1 also taken	Prior Use	Modified from Previous Use
TL	Total Length	Direct distance between snout tip and apex of lower caudal-fin lobe	Dorsally	-	C, W&E, L&W	-
PCL	Pre-Caudal Length	Direct distance from snout tip to origin of upper caudal lobe	Dorsally	-	C, W&E, L&W	-
PD1	Pre-Dorsal Length	Direct distance from snout tip to first dorsal-fin origin	Dorsally	-	C, W&E, L&W	-
PD2	Pre-Second Dorsal Length	Direct distance from snout tip to second dorsal-fin origin	Dorsally	-	C, W&E	-
PP1	Pre-Pectoral Length	Direct distance from snout tip to pectoral-fin origin (under cutaneous fold of head)	Dorsally	-	C, W&E, L&W	-
PP2	Pre-Pelvic Length	Direct distance from snout tip to pelvic-fin origin (use finger to find origin)	Dorsally	-	C, W&E, L&W	-
PSP	Pre-Spiracular Length	Direct distance from snout tip to inner margin of spiracle	Dorsally	X	C, W&E, L&W	-
PEY	Pre-Eye Length	Direct distance from snout tip to anterior margin of orbit	Dorsally	X	L&W	-
POR	Pre-Orbital Length	Horizontal distance from snout tip to anterior margins of eyes	Dorsally	X	C, W&E, L&W	Called 'POR' in W&E
EYL	Eye Length	Length of eye	Dorsally	X	C, W&E, L&W	-
EYW	Eye Width	Width of eye	Dorsally	X	C, W&E	Called 'EYH' in C and W&E
ESL	Eye Spiracle Length	Horizontal distance from posterior margins of eye to anterior margins of spiracle	Dorsally	X	C, W&E	
SPL	Spiracle Length	Maximum diameter of spiracle opening	Dorsally	X	C, W&E, L&W	-
IDS	Inter-Dorsal Space	Distance between first dorsal-fin insertion and second dorsal-fin origin	Dorsally	X	C, W&E, L&W	-
DCS	Dorsal–Caudal Space	Distance between second dorsal-fin insertion and upper caudal-fin origin	Dorsally	X	C, W&E, L&W	-
PPS	Pectoral–Pelvic Space	Direct distance from pectoral-fin insertion to pelvic-fin origin	Dorsally	X	C, W&E, L&W	-
WP1	Width at Pectoral Origins	Width between dorsally visible pectoral-fin origins	Dorsally	-	L&W	Description
TRW	Trunk Width	Width of body at pectoral-fin insertions	Dorsally	-	C, W&E, L&W	-
TAW	Tail Width	Width of body at pelvic-fin insertions	Dorsally	X	C, L&W	-
P1L	Pectoral-Fin Length	Distance from apex of anterior lobe to apex of free rear tip	Dorsally	-	C, W&E, L&W	-
P1A	Pectoral-Fin Anterior Margin	Distance from apex of anterior lobe to apex of fin	Dorsally	-	C, W&E, L&W	-
P1B	Pectoral-Fin Base Length	Distance from pectoral-fin origin (under cutaneous fold of head) to pectoral-fin insertion	Dorsally	X	C, W&E, L&W	-
P1W	Pectoral-Fin Width	Distance from pectoral-fin inner margin to fin apex	Dorsally	-	L&W	-
P1I	Pectoral-Fin Inner Margin	Distance from pectoral-fin insertion to apex of free rear tip	Dorsally	-	C, W&E, L&W	-
D1B	First Dorsal-Fin Base Length	Distance from first dorsal-fin origin to insertion of fin	Dorsally	X	C, W&E, L&W	-
D1A	First Dorsal-Fin Anterior Margin	Distance from first dorsal-fin origin to apex of fin	Dorsally	X	C, W&E, L&W	-
D1H	First Dorsal-Fin Height	Greatest vertical height from fin base to apex of fin	Dorsally	X	C, W&E, L&W	-
D1I	First Dorsal-Fin Inner Margin	Distance from first dorsal-fin insertion to apex of free rear tip	Dorsally	X	C, W&E, L&W	-
D2B	Second Dorsal-Fin Base Length	Distance from second dorsal-fin origin to insertion of fin	Dorsally	X	C, W&E, L&W	-
D2A	Second Dorsal-Fin Anterior Margin	Distance from second dorsal-fin origin to apex of fin	Dorsally	X	C, W&E, L&W	-
D2H	Second Dorsal-Fin Height	Greatest vertical height from fin base to apex of fin	Dorsally	X	C, W&E, L&W	-
D2I	Second Dorsal-Fin Inner Margin	Distance from second dorsal-fin insertion to apex of free rear tip	Dorsally	X	C, W&E, L&W	-
CDM	Caudal-Fin Dorsal Margin	Distance from upper caudal-fin origin to apex of dorsal caudal lobe	Dorsally	-	C, W&E, L&W	Character Name
CAH	Caudal-Fin Height	Distance between dorsal and ventral lobe apices	Dorsally	-	L&W	-
ISS	Inter-Spiracular space	Distance between inner margins of spiracles	Dorsally	X	L&W	Designation formerly 'ISP'
PDD	**Pelvic Dorsal Distance**	**Distance from apex of free rear tip of pelvic fins and origin of first dorsal fin**	**Dorsally**	**X**	-	-
PG1	Pre-Branchial Length	Direct distance from snout tip to inner edge of the first gill slit	Ventrally	-	C, W&E, L&W	-
HDW	Head Width	Width of head (not including cutaneous folds) at 1st gill slit	Ventrally	X	C, W&E, L&W	-
ING	Inter-Gill Length	Distance between inner margins of 1st and 5th gill slits	Ventrally	X	C, L&W	-
POCS	Pelvic (Origin)–Caudal Space	Direct distance from pelvic-fin origin to lower caudal-fin origin	Ventrally	-	L&W	-
PCS	Pelvic–Caudal Space	Direct distance from pelvic-fin insertion to lower caudal-fin origin	Ventrally	-	C, L&W	Listed as both 'PCA' and 'PCS' in L&W
P2L	Pelvic-Fin Length	Distance from pelvic-fin origin (use finger to find origin) to apex of free rear tip	Ventrally	-	C, W&E, L&W	-
P2W	Pelvic-Fin Width	Distance from pectoral-fin inner margin to fin apex	Ventrally	-	L&W	-
P2A	Pelvic-Fin Anterior Margin	Distance from pelvic fin origin to apex of fin	Ventrally	-	C, W&E	
P2I	Pelvic-Fin Inner Margin	Distance from pelvic-fin insertion to apex of free rear tip	Ventrally	X	C, W&E, L&W	-
CPV	Caudal-Fin Pre-Ventral Margin	Distance from lower caudal-fin origin to apex of ventral caudal lobe	Ventrally	-	C, W&E, L&W	Listed as 'CVM' in L&W
CIL	Clasper Inner Length	Distance from posterior end of cloaca to apex of clasper	Ventrally	X	C, L&W	Listed as 'CLI' in both C and L&W
COL	Clasper Outer Length	Distance between lateral junction of pelvic-fin inner margin to apex of clasper	Ventrally	X	C, L&W	Listed as 'CLO' in both C and L&W
CBW	Clasper Base Width	Width of clasper at pelvic-fin insertion	Ventrally	X	C, L&W	Listed as 'CLB' in both C and L&W
IGW	Inter-Gill Width	Distance between inner margins of 1st gill slits	Ventrally	X	L&W	Listed as 'ING1' in L&W
SVL	Snout Vent Length	Distance from snout tip to anterior edge of vent	Ventrally	-	C, W&E	
VCL	Vent Caudal Length	Distance from anterior edge of vent to apex of ventral caudal lobe	Ventrally	-	C, W&E	
VL	Vent Length	Distance from anterior edge of vent to posterior edge of vent	Ventrally	X	C, W&E	
TAH	Tail Height	Vertical height of body at pelvic-fin insertions	Anteriorly	X	C, L&W	-
INW	Inter-Narial Width	Shortest distance between exposed nostril apertures	Anteriorly	X	C, W&E, L&W	Character Name
MOW	Mouth Width	Distance between mouth corners	Anteriorly	-	C, W&E, L&W	-
IOS	Inter-Orbital Space	Distance between eyes (taken at mid-length of eye)	Anteriorly	-	C, W&E, L&W	Listed as 'INO' in C, W&E, and L&W
HDH	Head Height	Vertical height of head at 1st gill slit	Anteriorly	X	C, W&E, L&W	
NOW	Nostril Width	Direct distance from most dorsal edge of nostril to ventral ending of nasal flap (not including frilled extension)	Anteriorly	X	C, W&E	
ANF	Anterior Nasal Flap Length	Largest distance across edge of nasal flap (not including frilled extensions)	Anteriorly	X	C, W&E	New description from W&E and C
UAW	Upper Lip Arch Width	Distance between nasal flaps of lowest point of upper jaw	Anteriorly	X	W&E	
UAH	Upper Lip Arch Height	Vertical height of upper lip from mouth opening to nasal flap tissue line	Anteriorly	X	W&E	
CPU	Upper Post-Ventral Caudal Margin	Length of upper portion of post-ventral caudal margin	Laterally	X	C, W&E	
CST	Subterminal Caudal Margin	Length of subterminal caudal margin	Laterally	X	C, W&E	
CPL	Lower Post-Ventral Caudal Margin	Length of lower post-ventral caudal margin	Laterally	X	C, W&E	

Prior Use: C=(Compagno 2001), W&E=(Walsh and Ebert 2007), and L&W=(Last and White 2008).

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