

The Evolution of Iguanas

AN OVERVIEW OF RELATIONSHIPS AND A CHECKLIST OF SPECIES

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IN THIS CHAPTER, I provide an overview of the evolutionary diversity of iguanas to help synthesize the large volume of currently available knowledge and review the controversies that still exist. The family Iguanidae, as constituted by Frost and Etheridge (1989), was first formed as an informal taxonomic group of iguanian lizards referred to as "iguanines" (Savage, 1958; Etheridge, 1964). The current constitution of the family is based on the work of Etheridge (1964), who diagnosed the group by their unique caudal vertebrae. Since this early work, "iguanines" have been shown to be a natural group through characteristics of their skeletal morphology, behavior, digestive tract, and mitochondrial DNA (mtDNA) sequence (de Queiroz, 1987a; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Schulte et al., 1998). Although the evidence for this taxonomic constitution is strong, there is still debate over the recognition of the various iguanian groups as families or subfamilies (Frost and Etheridge, 1989, 1993; Lazell, 1992; Schwenk, 1994; Macey et al., 1997; Schulte et al., 1998; Frost et al., 2001). Until the philosophical and data conflicts are resolved, I prefer to adopt the taxonomy of Frost and Etheridge

(1989). No matter which taxonomic rank is eventually decided upon, iguanas represent a diverse monophyletic group.

Iguanid lizards are distributed over much of North and Central America; northern South America; and numerous islands, including the West Indies, the Galápagos, and the Fiji-Tonga Archipelago (Etheridge, 1982). The last checklist of the family was presented by Etheridge (1982), who recognized eight genera and thirty-one species. Today, eleven genera are recognized, containing forty-four species. The large increase in the number of species is attributable to the description of three extinct monotypic genera, the elevation of subspecies to species, and ongoing work within *Ctenosaura*. Our knowledge of iguanid diversity will likely increase as different philosophical approaches to species are applied and further insights into relationships revealed. Still, the increase in the number of taxa is somewhat astonishing, considering that these lizards are relatively large terrestrial vertebrates with conspicuous behaviors. The addition of known species over the past decade underscores the need for further taxonomic work throughout the family.

At the time Etheridge (1982) presented his overview of evolutionary diversity in iguanid lizards, almost nothing was known of their interrelationships. Furthermore, the studies up until that time were difficult to evaluate, with many lacking clear indications of how relationships were formulated (see historical reviews in Etheridge [1982] and de Queiroz [1987a]). The first modern phylogenetic analysis of the family was presented by de Queiroz (1987a). This study has served as the reference point for all subsequent analyses and made contemporary phylogenetic studies approachable. A number of phylogenetic analyses have been completed over the past decade and relationships between iguanid taxa are becoming clearer. However, there remain a number of competing hypotheses to consider.

EVOLUTIONARY RELATIONSHIPS

INTERGENERIC RELATIONSHIPS

The generic-level relationships presented by de Queiroz (1987a) were based on a morphological data set consisting of ninety-five characters evaluated across all of the recognized species known at that time. His preferred hypothesis (figure 2.1A) placed both *Dipsosaurus* and *Brachylophus* in a polytomy at the base of the tree with the remainder of the genera (i.e., *Amblyrhynchus*, *Conolophus*, *Ctenosaura*, *Sauromalus*, *Iguana*, and *Cyclura*) forming a monophyletic group designated as the Iguanini. *Amblyrhynchina* (*Amblyrhynchus* + *Conolophus*) and *Iguanina* (*Iguana* + *Cyclura*) were also recognized as suprageneric taxa.

Norell and de Queiroz (1991) incorporated the fossil taxa *Armandisaurus explorator*[†] Norell and de Queiroz 1991 and *Pumilia novackei*[†] Norell 1989 into a slightly modified data set. The results clarified the uncertain relationships at the base of the tree, placing *Dipsosaurus* + *Armandisaurus*[†] as the sister group to other iguanids, and *Brachylophus* as the sister taxon to the Iguanini (figure 2.1B). *Pumilia*[†] was confirmed to be a diminutive species closely related to *Iguana* (see also Norell, 1989). In both

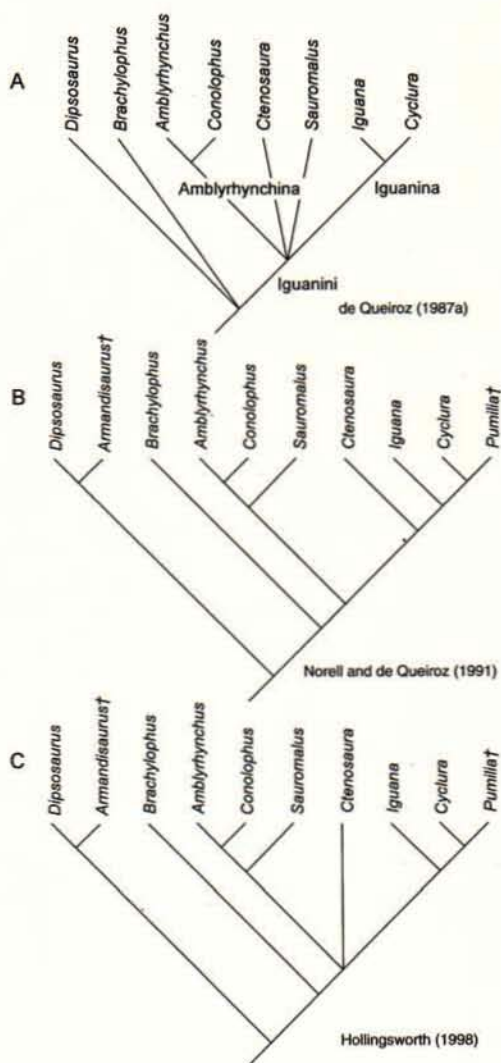


FIGURE 2.1. Generic-level relationships within Iguanidae. (A) de Queiroz (1987a); (B) Norell and de Queiroz (1991); (C) Hollingsworth (1998).

analyses, the placements of *Sauromalus* and *Ctenosaura* were considered dubious, although the most parsimonious tree of Norell and de Queiroz (1991) resulted in the relationships *Sauromalus* + *Amblyrhynchina* and *Ctenosaura* + *Iguanina*.

Later, Hollingsworth (1998) presented results from a phylogenetic analysis of Iguanini using 142 morphological characters, ninety-three of which originated from de Queiroz (1987a) and Norell and de Queiroz (1991). His results were similar to theirs, but generally with more sup-

port, the only difference being the unresolved position of *Ctenosaura* (figure 2.1C). All three morphological studies are highly congruent; the only apparent difference is the level of resolution achieved.

Three molecular-based studies addressing intergeneric relationships have been completed recently (Sites et al., 1996; Petren and Case, 1997; Rassmann, 1997). The results from the mitochondrial ribosomal DNA (rDNA) sequence data of Rassmann (1997) are in agreement with the outcome of the morphological analysis, although weakly supported. However, the results from the two studies using mtDNA sequence data from the protein coding ND4 (Sites et al., 1996) and cytochrome *b* (Petren and Case, 1997) genes are in some ways in conflict with the hypotheses produced from the morphological studies, although there are many points of agreement. These two studies produced strongly supported hypotheses placing *Cyclura* as the sister taxon to the remaining Iguanini and *Sauromalus* + *Iguana* as sister taxa. *Ctenosaura* was found to be allied to the Amblyrhynchina (figure 2.2A). Sites et al. (1996) also combined their sequence data with the existing morphological data and found no difference from the results based on the molecular data alone.

The dramatically different placements of *Cyclura* based on the morphological and protein-coding molecular data sets were analyzed further by Wiens and Hollingsworth (2000). In this study, the various data sets were standardized and reanalyzed. A comparison was made between the results analyzed using maximum parsimony and maximum likelihood methods. The molecular topologies based on the two protein-coding genes (ND4 and cytochrome *b*) and the morphological topology were significantly different. The *Cyclura* branch was 6.2 times longer than the average branch length when estimated by likelihood. When analyzed using parametric bootstrapping (see Huelsenbeck et al., 1996), the *Cyclura* branch was found to be susceptible to long-branch attraction, especially when analyzed with parsimony methods (Felsenstein,

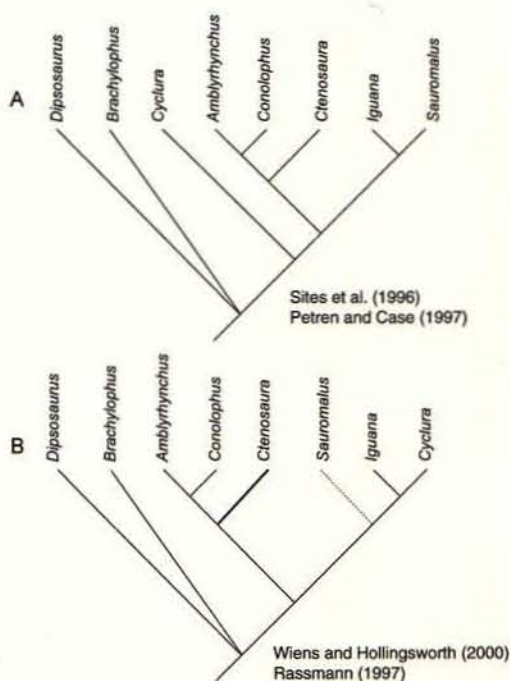


FIGURE 2.2. Generic-level relationships within Iguanidae. (A) Sites et al. (1996) and Petren and Case (1997), pruned to nominal genera; (B) Wiens and Hollingsworth (2000) preferred tree with *Sauromalus* in a tentative position (dashed line) and nearly identical to the 50% majority rule consensus tree of Rassmann (1997), with the exception of the unresolved basal node.

1978). Likewise, the *Sauromalus* branch in the morphological analysis was susceptible to the same problems. As a result, Wiens and Hollingsworth (2000) constructed a preferred hypothesis not represented by either the molecular or morphological studies (figure 2.2B; but see Malone et al., 2000; Malone and Davis, this volume). The Wiens and Hollingsworth (2000) tree is nearly identical to the hypothesis of Rassmann (1997).

Each of the extant genera in the family Iguanidae is well supported with numerous character state transformations (de Queiroz, 1987a). However, the recovery of their intergeneric relationships has been hampered by the disparate rates of transformations in the different data sets, as in the case for the *Cyclura* and *Sauromalus* branches. In addition, there is also relatively lower phylogenetic signal between taxa than there is in support of their individual

monophyly. The pattern of weak support for some parts of the topology while others are strongly supported has been associated with the process of rapid speciation at the base of the Iguanini (de Queiroz, 1987a; Sites et al., 1996; Rassmann, 1997; Hollingsworth, 1998). To recover the intergeneric relationships of iguana taxa further, researchers will have to sample a greater number of characters and further develop analytical methods that are not compromised by data with disparate rates of evolution.

INTERSPECIFIC RELATIONSHIPS WITHIN SAUROMALUS

Progress has also been achieved in recovering the interspecific relationships within the more species-rich genera. Petren and Case (1997) completed the first modern phylogenetic analysis within *Sauromalus* using mtDNA sequence data from the cytochrome *b* gene (figure 2.3A). Petren and Case (2002) repeated the analysis with six additional samples with similar results. The two large chuckwalla species, *S. varius* and *S. hispidus*, are hypothesized to be sister taxa deeply nested within the tree containing the remaining smaller-bodied species and populations. The arrangement of this topology infers that the ancestral body size was small and the evolution of a larger body occurred in the common ancestor of *S. varius* and *S. hispidus*. The internal nodes within the molecular tree are weakly supported by bootstrap values of 60% or less, with the exception of *S. varius* + *S. hispidus*, which is supported by a 99% bootstrap value. This topology supports the insular gigantic hypothesis of body size evolution first put forward by Case (1982). The hypothesis postulates that a large body is not selected against in an arid insular environment lacking large predators and containing an erratic food supply (Case, 1982; Petren and Case, 1997). Based on the results of the molecular analysis, the two large-bodied species evolved from a smaller ancestral form in response to insular selection pressures.

A morphological analysis of *Sauromalus* was completed by Hollingsworth (1998) using scalation, body proportions, color pattern, osteology,

and some soft anatomy. In contrast to the molecular tree, the morphological topology has the two large species, *S. varius* and *S. hispidus*, positioned sequentially at the base of the tree, with the smaller forms nested higher within the topology (figure 2.3B). The morphological tree is less resolved than the molecular topology, but has higher bootstrap values for the resolved basal nodes. The arrangement of this topology infers that the ancestral body size was large, and thus does not support the evolution of a large body size for two insular species, *S. varius* and *S. hispidus*. An alternative evolutionary hypothesis is that their large size is maintained by their insular environment, whereas smaller size was selected for in the ancestor of the remaining species, which likely lived on the adjacent continental areas (Grismer et al., 1995; Hollingsworth, 1998).

The differences between the molecular and morphological hypotheses have yet to be explained. Each topology suffers from poor support, and the disagreement between the trees appears to reflect conflicts between the data sets. The poor support is likely attributed to the undersampling of phylogenetically informative characters. Further analysis of morphological variation and continued DNA sequencing will eventually determine if the undersampling of characters is a source of error between the trees. However, if each tree is a preliminary insight into the structure of their respective trees, then other sources of error should be investigated to explain the conflict in the data. At this time, direct comparison between the two analyses is difficult because the taxonomic sampling in the molecular study is sparse for some geographic regions and different terminal lineages were designated in the morphological analysis (Hollingsworth, 1998).

INTERSPECIFIC RELATIONSHIPS WITHIN CTENOSAURA

As currently constituted, *Ctenosaura* contains seventeen species. Over the past two decades, five new species have been described (de Queiroz, 1987b; Köhler and Klemmer, 1994; Köhler, 1995;

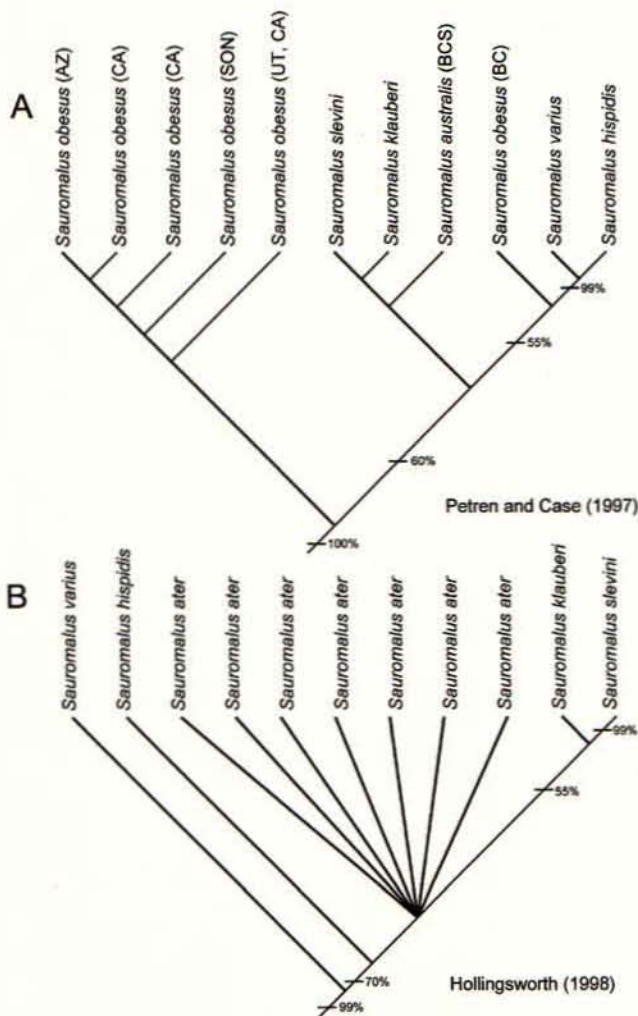


FIGURE 2.3. Interspecific relationships of *Sauromalus*. (A) Molecular topology after Petren and Case (1997), with *S. obesus* and *S. australis* terminal branches as originally presented (later synonymized with *S. ater* following Hollingsworth [1998], but see checklist remarks); (B) morphological topology modified from Hollingsworth (1998) with multiple terminal branches of *S. ater* representing the many isolated populations previously recognized under *S. ater*, *S. australis*, and *S. obesus*. Percentages are bootstrap values as reported in the different studies.

Buckley and Axtell, 1997; Köhler and Hasbun, 2001) and three subspecies of *C. hemilopha* elevated to species (Grismer, 1999a). None of the four most recent phylogenetic studies contain representatives of all the species. This is not likely a significant shortcoming in any of the analyses because each newly described species is clearly closely related to those included in the different studies. Three of the studies are based on morphological data (de Queiroz, 1987a,b; Hollingsworth, 1998), and one analyzes both morphological data and molecular randomly amplified polymorphic DNA (RAPD) markers (Köhler et al., 2000).

The two morphological analyses of de Queiroz (1987a,b) differ little, with the primary modifi-

cation between the two being the inclusion of *Ctenosaura oedirhina* (figure 2.4A). In these analyses, *C. hemilopha* was found to be closely related to the species formerly recognized as *Enyaliosaurus*, lending support to its recognition as a subgenus of *Ctenosaura* (de Queiroz, 1995). However, in Hollingsworth (1998; figure 2.4B) and Köhler et al. (2000; figure 2.4C), *C. hemilopha* was positioned, respectively, at the base of the tree or closely allied with *C. similis*, *C. acanthura*, and *C. pectinata*. Unfortunately, the topologies are not well supported at these basal nodes. It remains a possibility that *Enyaliosaurus* will be recognized as a genus again, as the sister taxon to *Ctenosaura*. Among the remaining relationships, there is a strong congruence between the

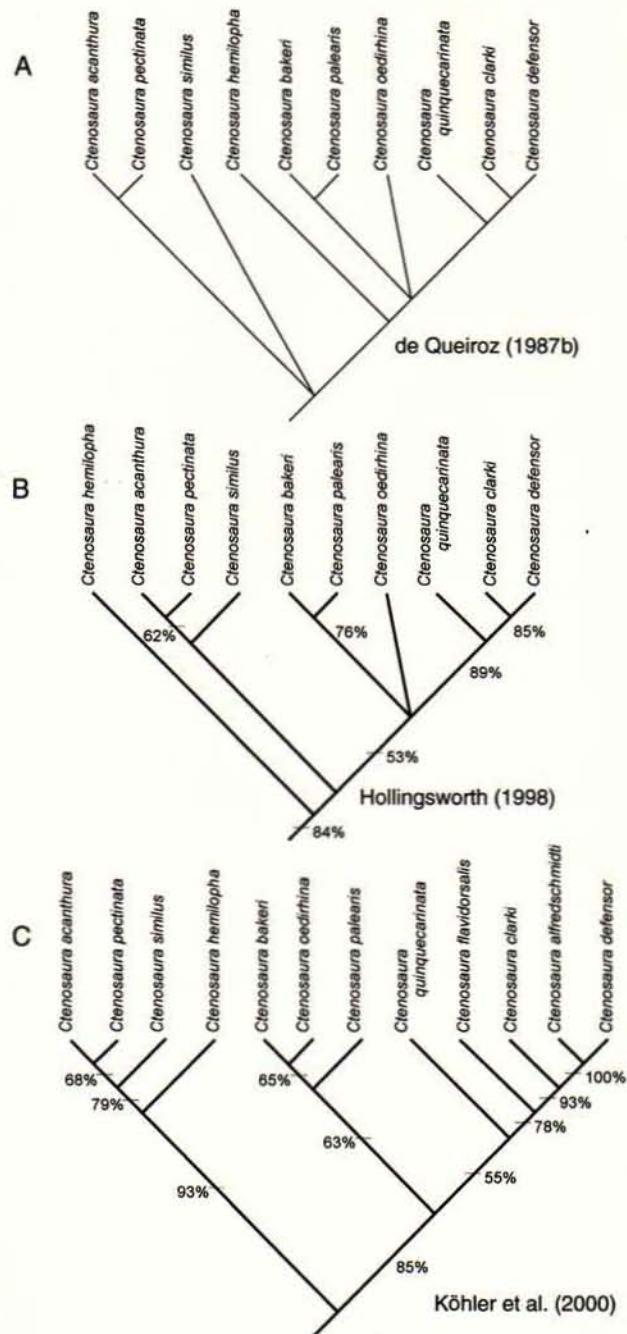


FIGURE 2.4. Interspecific relationships of *Ctenosaura*. (A) de Queiroz (1987b); (B) Hollingsworth (1998); (C) Köhler et al. (2000). Percentages are bootstrap values as reported in the different studies.

different studies in the remaining nodes of the tree.

INTERSPECIFIC RELATIONSHIPS WITHIN *CYCLURA*

A recent monographic revision of *Cyclura* is lacking, although two recent studies have proposed

phylogenetic relationships among its species (Hollingsworth, 1998; Malone et al., 2000). The morphological analysis of Hollingsworth (1998) proposed relationships at the species level (figure 2.5A), resulting in a topology that is not strongly supported. In comparison, Malone et al. (2000) used mtDNA sequence data from the

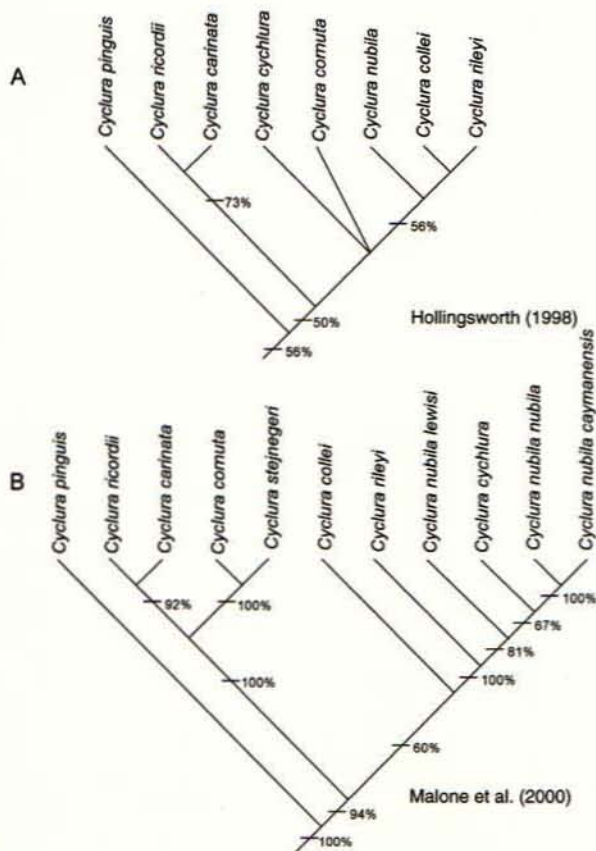


FIGURE 2.5. Interspecific relationships of *Cyclura*. (A) Hollingsworth (1998); (B) Malone et al. (2000), pruned to nominal species. Percentages are bootstrap values as reported in the different studies.

ND₄ gene and adjacent transfer RNAs (tRNA) and incorporated samples from all described species and subspecies. The more thorough analysis of Malone et al. (2000) resulted in a topology strongly supported at nearly every node (figure 2.5B). When the Malone et al. (2000) topology is pruned to include the species used in the morphological study, only two nodes are shared between the different analyses. These are the placement of *C. pinguis* as the sister taxon to the remaining species and the sister taxa relationship between *C. carinata* + *C. ricordii*. The difference between the two studies is likely attributable to the undersampling of phylogenetically informative characters in the morphological analysis. However, a combined analysis using both morphological and molecular data has yet to be completed. The need for a monographic revision is further emphasized by the placement of *C. nubila lewisi* as a distant relative to *C. n. nubila* and *C. n. caymanensis* (figure 2.5B). In the

future, the former is likely to be recognized as a separate species, given that the subspecies of *C. nubila* apparently do not form a monophyletic clade (see Malone et al., 2000; Malone and Davis, this volume).

CHECKLIST

The following checklist includes a listing of synonyms that chronicle the use of names for each species. This checklist is derived from the last comprehensive checklist for the family compiled by Etheridge (1982) and a more recent checklist of the Mexican species by de Queiroz (1995). It includes all taxa described subsequent to Etheridge (1982) and is intended to update both of these works. It also includes the numerous corrections identified by de Queiroz (1995) and makes further corrections when errors were found or new information became available. I have chosen to follow the general format of de

Queiroz (1995) for the inclusion of synonymous names. As such, this checklist does not represent a complete history of the use of names, but instead attempts to chronicle the different names formerly applied to each currently recognized species. To save space, I have chosen to abbreviate referenced works and exclude references to the collector of type specimens. Institutions were abbreviated following the standard acronyms recommended by Leviton et al. (1985). A general description of the distribution of each species is provided.

Finally, it is clear that more investigative work is needed to clarify the taxonomy of these lizards. In many instances, type specimens have not been located and the identification of type localities needs further research. Use of different criteria for the recognition of species and subspecies is a prevalent problem, and remarks are included to highlight current debates over their use. I consider subspecific taxa without a specific reference to a synonymy as valid names until further systematic work is completed.

AMBLYRHYNCHUS BELL

Amblyrhynchus Bell 1825, Zool. Jr., London 2:206. — Type species (by monotypy): *Amblyrhynchus cristatus* Bell 1825.

Iguana (*A. [mblyrhynchus]*) – Gray 1831, in Cuvier, Anim. Kingd., London 9:37.

Amblyrhincus (*part.*) – Duméril and Bibron 1837, Erpét. Gén., Paris 4:193 (invalid emendation).

Hypsilophus (*Amblyrhynchus*) – Fitzinger 1843, Syst. Rept., Wien 1:55.

Oreocephalus Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 189. — Type species (by monotypy): *Amblyrhynchus cristatus* Bell 1825.

***Amblyrhynchus cristatus* Bell**

Amblyrhynchus cristatus Bell 1825, Zool. Jr., London 2:206. — Holotype: OUM 6176 (Etheridge, 1982). — Type locality: "Mexico." — Corrected type locality: Narborough (Fernandina) (Eibl-Eibesfeldt, 1956).

Iguana (*A. [mblyrhynchus]*) *Cristatus* – Gray 1831, in Cuvier, Anim. Kingd., London 9:37.

Iguana (*A. [mblyrhynchus]*) *Ater* Gray 1831 (syn. fide Gray, 1845), in Cuvier, Anim. Kingd., London 9:37. — Type: not located (Etheridge, 1982). — Type locality: "Galápagos."

Amblyrhincus cristatus Duméril and Bibron 1837, Erpét. Gén., Paris 4:195.

Amblyrhincus ater Duméril and Bibron 1837, Erpét. Gén., Paris 4:196.

Hypsilophus (*Amblyrhynchus*) *cristatus* – Fitzinger 1843, Syst. Rept., Wien 1:55.

Hypsilophus (*Amblyrhynchus*) *ater* – Fitzinger 1843, Syst. Rept., Wien 1:55.

Oreocephalus cristatus – Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 189.

Amblyrhynchus nanus Garman 1892, Bull. Essex Inst., Salem, 24:8. — Holotype: BMNH 99.5.4 = BMNH RR 1946.8.30.20 (Etheridge, 1982). — Type locality: "Tower Island."

Amblyrhynchus cristatus cristatus Eibl-Eibesfeldt 1956, Senckenberg. Biol., Frankfurt a. M., 37:88; pl. 9, fig. 1, 2a–b, fig. 1a, 2.

Amblyrhynchus cristatus venustissimus Eibl-Eibesfeldt 1956, Senckenberg. Biol., Frankfurt a. M., 37:90; fig. 3a–b. — Holotype: SMF 49851. — Type locality: "Nordküste der Insel Hood (Española)."

Amblyrhynchus cristatus hassi Eibl-Eibesfeldt 1962, Senckenberg. Biol., Frankfurt a. M., 43(3):181; pl. 15 (fig. 4); fig. 2e, 3b. — Holotype: SMF 57407. — Type locality: "Indefatigable Südküste, westliche Akademiebuch . . . Indefatigable (Santa Cruz), Galápagos-Inseln."

Amblyrhynchus cristatus albermarlensis Eibl-Eibesfeldt 1962, Senckenberg. Biol., Frankfurt a. M., 43(3):184; pl. 14 (fig. 2); fig. 2f. — Holotype: Eibl-Eibesfeldt private coll. (Etheridge 1982). — Type locality: "Insel Albemarle (Isabella)."

Amblyrhynchus cristatus mertensi Eibl-Eibesfeldt 1962, Senckenberg. Biol., Frankfurt a. M., 43(3):185; fig. 2c-d, 3d-e. — Holotype: SMF 57430. — Type locality: "etwa 3 km südwestlich der Wrack-Bucht der Insel Chatham (S. Cristobal) . . . Chatman (Chatham [S. Cristobal]), Galápagos-Inseln."

Amblyrhynchus cristatus sielmanni Eibl-Eibesfeldt 1962, Senckenberg. Biol., Frankfurt a. M., 43(3):188; fig. 2h, 3f. — Holotype: SMF 57417. — Type locality: "Westküste der Insel Abingdon."

Amblyrhynchus cristatus nanus Eibl-Eibesfeldt 1962, Senckenberg. Biol., Frankfurt a. M., 43(3):189; pl. 15, (fig. 6); fig. 2b, 3g.

REMARKS

Few authors have adopted the use of the subspecies described by Eibl-Eibesfeldt, yet no formal synonymy has been proposed. Rassmann et al. (1997a) showed the close genetic relationship between various insular populations and discussed the plasticity of the morphological characters used to distinguish subspecies. They found that some of the subspecies are genetically indistinguishable from one another, a finding supported by the earlier immunological work (see Higgins and Rand, 1974, 1975; Higgins et al., 1974; Higgins, 1977; Wyles and Sarich, 1983). Until a formal synonymy is established, the seven subspecies are currently valid names.

DISTRIBUTION

Galápagos Archipelago: Fernandina (= Narborough), Isabela (= Albemarle), Santa Cruz (= Indefatigable), San Cristóbal (= Chatham), Santiago (= James), Genovesa (= Tower), Pinta (= Abingdon), Española (= Hood), and Gardner Islands. Also reported on the islands of Floreana (= Charles), Pinzón (= Duncan), Wenman, and Culpepper (Heller, 1903).

ARMANDISAURUS[†] NORELL AND DE QUEIROZ

Armandisaurus[†] Norell and de Queiroz 1991, Amer. Mus. Novitates, New York, 2997:2;

fig. 1-5. — Type species (by monotypy): *Armandisaurus explorator*[†] Norell and de Queiroz 1991.

Armandisaurus explorator[†] Norell and de Queiroz 1991, Amer. Mus. Novitates, New York, 2997:2; fig. 1-5. — Holotype: AMNH-FAM 8799. — Type locality: "White Operation Ridge, Sante Fe County, New Mexico, USA."

GEOLOGIC AGE

The type locality is in the Tesuque Formation, Skull Ridge Member, and is estimated to be between 11.6 and 16.5 million years old (Norell and de Queiroz, 1991).

DISTRIBUTION

This species is only known from the holotype specimen, collected from White Operation Ridge, Sante Fe County, New Mexico, U.S.A. (Norell and de Queiroz, 1991).

BRACHYLOPHUS CUVIER

Iguana (*part.*) Brongniart 1800, Bull. Soc. Philom., Paris 2:90.

Agama (*part.*) — Daudin 1802, Hist. Nat. Rept., Paris 3:352.

Brachylophus Cuvier 1829, in Guérin-Méville, Icon. Règ. Anim., Paris 1:9; pl. 9, fig. 1. — Type species (by monotypy): *Iguana fasciata* Brongniart 1800.

Iguana (*Brachylophus*) — Gray 1831, in Cuvier, Anim. Kingd., London 9:37.

Hypsilophus (*Brachylophus*) — Fitzinger 1843, Syst. Rept., Wien 1:55.

Chloroscates Günther 1862, Proc. Zool. Soc. Lond., 189. — Type species (by monotypy): *Chloroscates fasciatus* Günther 1862 (*non* Brongniart, 1800).

Brachylophus fasciatus (Brongniart)

Iguana fasciata Brongniart 1800, Bull. Soc. Philom., Paris 2:90; pl. 6, fig. 1. — Type: none designated. — Type locality: none given. —

Comments on type locality: probably Tongatapu in the Tonga Islands (Gibbons, 1981).

Agama fasciata – Daudin 1802, Hist. Nat. Rept., Paris 3:352.

Brachylophus fasciatus – Cuvier 1829, in Guérin-Ménil, Icon. Règ. Anim., Paris 1:9; pl. 9, fig. 1, 1a–c.

Iguana (Brachylophus) Fasciatus – Gray 1831, in Cuvier, Anim. Kingd., London 9:37.

Hypsilophus fasciatus – Fitzinger 1843, Syst. Rept., Wien 1:55.

Chloroscraetes fasciatus Günther 1862, Proc. Zool. Soc. London, 189; pl. 25. — Syntypes: BMNH 55.8.12.1–2 = BMNH RR 1946.8.3.83–84 (Etheridge, 1982). — Type locality: "Feegee Islands."

Brachylophus brevicephalus Avery and Tanner 1970 (syn. fide Gibbons, 1981), Great Basin Nat., Provo, 30 3:167. — Holotype: BYU 32662. — Type locality: "Nukalofa, Tongatabu Island, Friendly Islands."

DISTRIBUTION

Fiji Island Group, including the islands of Aiwa, Avea, Balavu, Beqa, Dravuni, Fulaga, Gau, Kabara, Kandavu Ono, Lakeba, Moturiki, Nggamea, Oneata, Ovalau, Taveuni, Vanua, Vanua Levu, Vanua Vatu, Vatu Vara, Vatuvele, Viti Levu, and Wakaya (Etheridge, 1982). Etheridge (1982) noted that specimens from Cikobia, Koro, Naviti, and Yasawa were likely this species as well. Tonga Island Group, from Tongatapu, Ha'apai, Vava'u, and 'Eua (Gibbons and Watkins, 1982; Zug, 1991). Also on Iles Wallis, northeast of Fiji (Etheridge, 1982). Recently introduced in the Tonga Island Group on Vanuatu (Bauer, 1988; Zug, 1991) and in the New Hebrides on Efate Island (Etheridge, 1982).

Brachylophus vitiensis Gibbons

Brachylophus vitiensis Gibbons 1981, J. Herpet., 15(3):257; pl. 1, 11a, c–d; fig. 2, 4a, 5a. — Holotype: MCZ 157192. — Type locality: "Yaduatapa island (16°50' S; 178°20' E), Fiji."

DISTRIBUTION

Fiji Island Group, found on the island of Yadua Taba and the northern islands of the Yasawa group (Zug, 1991). Zug (1991) noted that specimens from the northern coast of Viti and Vanua Levu represent this species as well.

CONOLOPHUS FITZINGER

Amb. [lyrhynchus] (part.) Gray 1831, Zool. Misc., London 1831:6. — Type species (by monotypy): *Amb. [lyrhynchus] subcristatus* Gray 1831.

Amblyrhincus (part.) Duméril and Bibron 1837, (syn. fide Gray, 1845), Erpét. Gén., Paris 4:197. — Type species: *Amblyrhincus Demarllii* Duméril and Bibron 1837.

Hypsilophus (Conolophus) – Fitzinger 1843, Syst. Rept., Wien 1:55.

Trachycephalus Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 188. — Type (by monotypy): *Amblyrhynchus subcristatus* Gray 1831.

Conolophus pallidus Heller

Conolophus subcristatus (part.) Garman 1892, Bull. Essex Inst. 24:5.

Conolophus pallidus Heller 1903, Proc. Wash. Acad. Sci., Washington, D.C. 5:87. — Holotype: CAS-SU 4749. — Type locality: "Barrington Island, Galápagos Archipelago."

DISTRIBUTION

Galápagos Archipelago, found only on the island of Santa Fé (= Barrington) (Heller, 1903).

Conolophus subcristatus (Gray)

Amb. [lyrhynchus] subcristatus Gray 1831, Zool. Misc., London 1831:6. — Type: not located (Etheridge, 1982). — Type locality: "Galápagos?"

Amblyrhincus Demarllii Duméril and Bibron 1837, (syn. fide Gray, 1845), Erpét. Gén., Paris 4:197. — Type: not located (Etheridge, 1982). — Type locality: not given.

Hypsilophus (Conolophus) Demarllii – Fitzinger 1843, Syst. Rept., Wien 1:55.

Trachycephalus subcristatus – Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 188.

Conolophus subcristatus – Steindachner 1876, Festschr. Zool.-Bot. Ges., Wien p. 322; pl. 4–7.

Conolophus subcristatus pictus Rothschild and Hartert 1899 (syn. fide Van Denburgh and Slevin, 1913) Novit. Zool., London 6:102. — Syntypes: BMNH 99.5.6.41–44. — Type locality: “Narborough.”

DISTRIBUTION

Galápagos Archipelago, including the islands of Santiago (= James), Santa Cruz (= Indefatigable), Isabela (= Albemarle), Fernandina (= Narborough), Baltra (= South Seymour), and Rábida (= Jervis) (Heller, 1903; Etheridge, 1982; Steadman and Zousmer, 1988).

CTENOSAURA WIEGMANN

Lacerta (part.) – Shaw 1802, Gen. Zool., London 3(1):216. — Type species: *Lacerta Acanthura* Shaw 1802.

Uromastix (part.) – Merrem 1820, Tent. Syst. Amphib., Marburg p. 56.

Cyclura (part.) – Harlan 1825 (syn. fide Gray, 1845), J. Acad. Nat. Sci. Philadelphia 4:250. — Type species: *Cyclura teres* Harlan 1825.

Ctenosaura Wiegmann 1828, Isis von Oken, Leipzig 21:371. — Type (subsequent designation by Fitzinger, 1843): *Ctenosaura cycluroides* Wiegmann 1828 = *Lacerta acanthura* Shaw 1802.

Enyaliosaurus Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London p. 192. — Type (by monotypy): *Cyclura quinquecarinata* Gray 1842.

Cachryx Cope 1866, Proc. Acad. Nat. Sci. Philadelphia 18:124. — Type species (by monotypy): *Cachryx defensor* Cope 1866.

Ctenosaura acanthura (Shaw)

Lacerta Acanthura Shaw 1802, Gen. Zool., London 3(1):216. — Holotype: BMNH XXII.20.a = BMNH RR 1946.8.30.19 (Etheridge, 1982). — Type locality: not given. — Designated type localities: California (Boulenger, 1885), in error (Smith and Taylor, 1950); Mexico (Bailey, 1928); Tampico, Tamaulipas, Mexico (Bailey,

1928), inappropriate restriction (de Queiroz, 1995).

Uromastix acanthura – Merrem 1820, Tent. Syst. Amphib., Marburg 56.

Cyclura teres Harlan 1825 (syn. fide Gray, 1845), J. Acad. Nat. Sci. Philadelphia 4:250. — Holotype: ANSP, number not given; lost (Smith and Taylor, 1950; Malnate, 1971). — Type locality: “Tampico.”

Cyclura acanthura – Gray 1827, Phil. Mag., ser. 2 2:57.

Ct. [*enosaura*] *cycluroides* Wiegmann 1828 (syn. fide Gray, 1845), Isis von Oken, Leipzig 21:371. — Syntypes: ZMB 576–578 (Bailey, 1928); ZMB 577 = MCZ 22453 (Bailey, 1928). — Type locality: Mexico, by implication (de Queiroz, 1995). — Designated type localities: Mexico (Bailey, 1928); Veracruz (Smith and Taylor, 1950), without justification (de Queiroz, 1995); Tampico (Etheridge, 1982), in error (de Queiroz, 1995).

Iguana (*Ctenosaura*) *Cycluroides* – Gray 1831, in Cuvier, Anim. Kingd., London 9:37.

Iguana (*Ctenosaura*) *Acanthura* – Gray 1831, in Cuvier, Anim. Kingd., London 9:38.

Cyclura Shawii Gray 1831 (replacement name for *Lacerta acanthura* Shaw 1802), in Cuvier, Anim. Kingd., London 9:38.

Iguana (*Ctenosaura*) *Armata* Gray 1831 (syn. fide Gray, 1845) in Cuvier, Anim. Kingd., London 9:38. — Type: Mus. [of Mr.] Bell [number not given] (de Queiroz, 1995); lost (Smith and Taylor, 1950). — Type locality: not given. — Designated type locality: Tampico, Tamaulipas (Smith and Taylor, 1950), without justification (de Queiroz, 1995).

Iguana (*Ctenosaura*) *Lanceolata* Gray 1831 (syn. fide Gray, 1845) in Griffith (ed.) Cuvier's Anim. Kingd., London 9:38. — Type: Mus. [of Mr.] Bell [number not given] (de Queiroz, 1995); lost (Smith and Taylor, 1950). — Type locality: not given. — Designated type locality: Tampico, Tamaulipas (Smith and Taylor, 1950), without justification (de Queiroz, 1995).

Iguana (Ctenosaura) Bellii Gray 1831 (syn. fide Bailey, 1928) in Cuvier, Anim. Kingd., London 9:38. — Type: Mus. [of Mr.] Bell [number not given] (de Queiroz, 1995); lost (Smith and Taylor, 1950). — Type locality: not given. — Designated type locality: Tampico, Tamaulipas (Smith and Taylor, 1950), without justification (de Queiroz, 1995).

Iguana (Cyclura) Teres — Gray 1831 in Cuvier, Anim. Kingd., London 9:39.

C. [yclura] articulata Wiegmann 1834 (syn. fide Gray, 1845) Herp. Mex., Saur. Spec., Berlin, 1:42. — Type: unknown (Smith and Taylor, 1950). — Type locality: "Mexico."

C. [yclura] denticulata Wiegmann 1834 (replacement name for *Ctenosaura cycluroides*; Wiegmann, 1828) Herp. Mex., Saur. Spec., Berlin 1:42; pl. 3.

Cyclura (Ctenosaura) denticulata — Fitzinger 1843, Syst. Rept., Wien 1:56.

Cyclura (Ctenosaura) semicrista — Fitzinger 1843 1834 (replacement name for *Cyclura denticulata* Wiegmann 1834, Syst. Rept., Wien 1:56).

Cyclura (Ctenosaura) articulata — Fitzinger 1843, Syst. Rept., Wien 1:56.

Cyclura (Ctenosaura) Shawii — Fitzinger 1843, Syst. Rept., Wien 1:56.

Cyclura (Ctenosaura) Bellii — Fitzinger 1843, Syst. Rept., Wien 1:56.

Ctenosaura acanthura — Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 191.

Cyclura (Ctenosaura) acanthura — Cope 1870, Proc. Am. Philos. Soc., Philadelphia (1869) 11:161.

Ctenosaura teres — Bocourt 1874, in Duméril, Bocourt and Mocquard, Miss. Sci. Mex., Paris 3:142.

Ctenosaura multispinis (part. de Queiroz, 1995) Cope 1886 (syn. fide Bailey, 1928), Proc. Am. Philos. Soc., Philadelphia 23:267. — Holotype: Sumichrast collection No. 201; = USNM 72737 (Smith and Taylor, 1950; Cochran, 1961). —

Type locality: "Dondomingo, in the State Oaxaca." — Corrected type locality: Dondomingo (Smith and Taylor, 1950).

DISTRIBUTION

The lowlands of eastern Mexico, from Llera and Tepehuaje de Arriba in Tamaulipas southward to the Isthmus of Tehuantepec in southeastern Veracruz and eastern Oaxaca (Bailey, 1928; Etheridge, 1982; de Queiroz, 1995; Köhler and Streit, 1996).

Ctenosaura alfredschmidti Köhler

Ctenosaura alfredschmidti Köhler 1995, Salamandra, Rheinbach 31(1):5; fig. 4–8, 10. — Holotype: SMF 69019. — Type locality: "70 km östl. von Escarcega auf der Straße nach Chetumal, Campeche, Mexico."

DISTRIBUTION

Known only from the type locality on the Yucatán peninsula, in the Mexican state of Campeche (Köhler, 1995).

Ctenosaura bakeri Stejneger

Ctenosaura bakeri Stejneger 1901, Proc. U.S. Natl. Mus., Washington, D.C. 23:467. — Holotype: USNM 26317. — Type locality: "Utila Island, Honduras."

Enyaliosaurus bakeri — Cochran 1961, Bull. U.S. Natl. Mus., Washington, D.C. 220:105.

DISTRIBUTION

Isla de Utila, Departamento de Islas de la Bahía, Honduras (de Queiroz, 1990a; Köhler, 1998).

Ctenosaura clarki Bailey

Enyaliosaurus quinquecarinatus (part.) — Dugès 1897, La Nature, ser. 2 2:523; pl. 34.

Ctenosaura clarki Bailey 1928, Proc. U.S. Natl. Mus., Washington, D.C. 73(12):44; pl. 27. — Holotype: MCZ 22454. — Type locality: "Ovopeo, Michoacan, Mexico." — Corrected type locality: "Oropeo . . . at an elevation of about 1000 feet in the lower Tepalcatepec Valley about 8 miles south of La Huacana" (Duellman and Duellman, 1959).

Enyaliosaurus clarki – Smith and Taylor 1950, Bull. U.S. Natl. Mus., Washington, D.C. 199:76.

Ctenosaura (Enyaliosaurus) clarki – de Queiroz 1995, Publicaciones Especiales del Museo de Zoología, Mexico City 9:13.

DISTRIBUTION

Western Mexico, in the Balsas-Tepalcatepec Basin in Michoacán, between 200 and 510 meters in elevation (Duellman and Duellman, 1959; Duellman, 1961; Etheridge, 1982; Gicca, 1982; de Queiroz, 1995).

Ctenosaura conspicuosa Dickerson

Ctenosaura conspicuosa Dickerson 1919, Bull. Am. Mus. Nat. Hist., New York 41(10):461. — Holotype: AMNH 5027; = USNM 64440 (Bailey, 1928; Cochran, 1961; de Queiroz, 1995). — Type locality: "San Esteban Island, Gulf of California, Mexico."

Ctenosaura hemilopha conspicuosa Lowe and Norris 1955, Herpetologica 11:89.

REMARKS

Recently, *Ctenosaura conspicuosa* was elevated from its subspecific inclusion within *C. hemilopha* (Grismer, 1999a,b). Lowe and Norris (1955:90) relegated this taxon to a subspecies, choosing to recognize *C. hemilopha* as "a polytypic species with four subspecies," but commenting that *C. h. conspicuosa* was the most distinctive among them. Lowe and Norris (1955) found it distinctive in both color and pattern. Following the evolutionary species concept and recognizing its distinctiveness, Grismer (1999a,b) elevated it to species rank.

DISTRIBUTION

Isla San Esteban, Sonora, Mexico (Lowe and Norris, 1955; Smith, 1972; de Queiroz, 1995; Grismer, 1999a,b). Introduced onto Isla Cholludo, Sonora, Mexico (Grismer, 1999a,b).

Ctenosaura defensor (Cope)

Cachryx defensor Cope 1866, Proc. Acad. Nat. Sci. Philadelphia 18:124. — Syntypes: USNM 12282 [3 specimens]; Exped. Coll. 585 (de Queiroz, 1995). — Type locality: not given;

Yucatán, by implication (de Queiroz, 1995) — Restricted type locality: Chichén Itzá, Yucatán, Mexico (Bailey, 1928); inappropriate restriction (de Queiroz, 1995).

Ctenosaura erythromeles Boulenger 1886 (syn. fide Duellman, 1965), Proc. Zool. Soc. London 1886:241; pl. 23. — Holotype: BMNH 86.8.9.1 = BMNH RR 1946.8.30.18 (Etheridge, 1982). — Type locality: "not known." — Designated type locality: Mexico (Bailey, 1928); Balchacaj, Campeche (Smith and Taylor, 1950); latter inappropriate restriction (de Queiroz, 1995).

Cachryx erythromeles – Cope 1887, Bull. U.S. Natl. Mus., Washington, D.C. 32:43.

Ctenosaura defensor – Günther 1890, Biol. Cent. Amer., Rept. and Batr. p. 58.

Ctenosaura (Cachryx) annectens Werner 1911 (syn. fide Bailey, 1928), Jahrb. Hamb. Wiss. Anst. 27(2):25. — Holotype: ZMH 3420; destroyed (Etheridge, 1982). — Type locality: not given. — Designated type locality: Mexico (Bailey, 1928).

Enyaliosaurus erythromeles – Smith and Taylor 1950, Bull. U.S. Natl. Mus., Washington, D.C. 199:77.

Enyaliosaurus defensor – Smith and Taylor 1950, Bull. U.S. Natl. Mus., Washington, D.C. 199:77.

Ctenosaura (Enyaliosaurus) defensor – de Queiroz 1995, Publicaciones Especiales del Museo de Zoología, Mexico City 9:13.

DISTRIBUTION

Southern Mexico on the Yucatán Peninsula, from Balchacaj, Campeche to Telchac, Yucatán (Duellman, 1965; Lee, 1980; Etheridge, 1982; Köhler, 1996).

Ctenosaura flavidorsalis Köhler and Klemmer

Enyaliosaurus quinquecarinata (part.) Meyer and Wilson 1973, Contrib. Sci. Nat. Hist. Mus. Los Angeles Co. 244:25.

Ctenosaura flavidorsalis Köhler and Klemmer 1994, Salamandra, Rheinbach, 30(3):197; fig. 2–8. — Holotype: SMF 75845. — Type

locality: "1 km südl. La Paz (750 m ü. N.N.; 14°16', 87°40'; Dpto. La Paz, Honduras)."

DISTRIBUTION

Eastern Guatemala, from the Departamento de Jutiapa, through northern El Salvador, from Departamentos de Santa Ana, Cabañas, San Vicente, Morazán, and La Unión, and southern Honduras, from the Departamentos de Intibucá and La Paz (Hasbun et al., 2001).

Ctenosaura hemilopha Cope

Iguana (Cyclura) acanthura (non Shaw 1802) Blainville 1835 (homonym of *Lacerta acanthura* Shaw), Nouv. Ann. Mus. Hist. Nat., Paris 4:288; pl. 24; fig. 1. — Lectotype: MNHN 2245 (Brygoo, 1989; de Queiroz, 1995). — Type locality: "Californie."

Cyclura acanthura (part.) – Duméril and Bibron 1837, Erpét. Gén., Paris 4:222.

Cyclura (Ctenosaura) hemilopha Cope 1863, Proc. Acad. Nat. Sci. Philadelphia 15:105. — Syntypes: USNM 5295 [4 specimens]; Xantus collection No. 789; one recataloged as USNM 69489 (de Queiroz, 1995). — Type locality: "Cape St. Lucas"; "near Soria Ranch, Cape San Lucas, Baja California, Mexico" [USNM 5295] and "San Nicolás, between Cape San Lucas and La Paz, Baja California, Mexico" [USNM 69489] (Cochran, 1961; de Queiroz, 1995).

Ctenosaura hemilopha – Cope 1866, Proc. Acad. Nat. Sci. Philadelphia 18:312.

Ctenosaura acanthura (part.) – Bocourt 1874, in Duméril, Bocourt and Mocquard, Miss. Sci. Mex., Paris 3:138.

Ctenosaura interrupta Bocourt 1882 (syn. fide Boulenger, 1885), Le Naturaliste, Paris 2(6):47. — Syntypes: MNHN 2243, 2245, 2843; BMNH 85.II.2.1 = BMNH RR 1946.8.3.85 (Etheridge, 1982). — Type locality: "Californie." — Restricted type locality: "Cape San Lucas" (Smith and Taylor, 1950), without justification (de Queiroz, 1995).

Cyclura hemilopha – Yarrow 1882, Bull. U.S. Natl. Mus., Washington, D.C. 24:71.

Cyclura teres (part.) – Yarrow 1882, Bull. U.S. Natl. Mus., Washington, D.C. 24:71.

Ctenosaura insulana Dickerson 1919, Bull. Am. Mus. Nat. Hist., New York 41(10):462. — Holotype: AMNH 2694; = USNM 64439 (Bailey, 1928; Cochran, 1961; de Queiroz, 1995). — Type locality: "Cerralvo Island, Gulf of California, Mexico."

Ctenosaura hemilopha interrupta – Lowe and Norris 1955 (syn. fide Hardy and McDiarmid, 1969), Herpetologica 11:90.

Ctenosaura hemilopha insulana – Lowe and Norris 1955 (syn. fide Grismer, 1999a), Herpetologica 11:90.

Ctenosaura hemilopha hemilopha – Smith 1972 (syn. fide Grismer, 1999a), Great Basin Nat., Provo 32(2):104.

DISTRIBUTION

Baja California Sur, Mexico, from the vicinity of Loreto southward through the Cape Region, and Isla Cerralvo (de Queiroz, 1995; Grismer, 1999a,b).

Ctenosaura macrolopha Smith

?*Ctenosaura multispinis* (part., see de Queiroz, 1995) Cope 1886, Proc. Am. Philos. Soc. Philadelphia 23:267.

Ctenosaura hemilopha hemilopha (part.) – Lowe and Norris 1955 (syn. fide Hardy and McDiarmid, 1969), Herpetologica 11:90.

Ctenosaura hemilopha macrolopha Smith 1972, Great Basin Nat., Provo 32(2):104. — Holotype: FMNH 108705. — Type locality: "La Posa, San Carlos Bay, 10 mi NW Guaymas, Sonora."

Ctenosaura macrolopha – Grismer 1999, Herpetologica 55(4):450.

REMARKS

Recently, this species was elevated from a subspecific rank from within *Ctenosaura hemilopha* by Grismer (1999a). It was found to be a separate evolutionary lineage and is diagnosable with morphological characters (see Grismer, 1999a: table 2).

DISTRIBUTION

Northwestern Mexico, from the vicinity of Hermosillo, Sonora, southward through the northern third of Sinaloa, and extreme western Chihuahua (Hardy and McDiarmid, 1969; Smith, 1972; de Queiroz, 1995).

Ctenosaura melanosterna Buckley and Axtell

Enyaliosaurus palearis (part.) Echternacht 1968, *Herpetologica* 24(2):151.

Ctenosaura palearis (part.) Etheridge 1982, in Burghardt and Rand (eds.), *Iguanas of the World*, New Jersey, p. 19.

Ctenosaura melanosterna Buckley and Axtell 1997, *Copeia*, 1997(1):139. — Holotype: KU 101441. — Type locality: "2 km south of Coyoles Central, Departamento of Yoro, Honduras."

DISTRIBUTION

North-central Honduras in the Río Aguan Valley, Departamento Yoro and Cayos Cochinos (= Hog Islands), 10–12 km due north of Nueva Armenia Yoro (Buckley and Axtell, 1997).

Ctenosaura nolascensis Smith

Ctenosaura hemilopha hemilopha (part.) — Lowe and Norris 1955, *Herpetologica* 11:90.

Ctenosaura hemilopha nolascensis — Smith 1972, *Great Basin Nat.*, Provo 32(2):107. — Holotype: UCM 26391. — Type locality: "Isla San Pedro Nolasco, Sonora."

Ctenosaura nolascensis — Grismer 1999, *Herpetologica* 55(4):450.

REMARKS

This species was elevated from a subspecific rank from within *Ctenosaura hemilopha* by Grismer (1999a,b), who applied the evolutionary species concept and found it diagnosable.

DISTRIBUTION

Isla San Pedro Nolasco, Sonora, Mexico (Smith, 1972, Grismer, 1999a,b).

Ctenosaura oaxacana Köhler and Hasbun

Ctenosaura quinquecarianata (part.) — Duellman 1966, *Copeia* 1966(4):700–719.

Ctenosaura (*Enyaliosaurus*) *quinquecarianata* (part.) — de Queiroz 1995, *Publicaciones Especiales del Museo de Zoología*, Mexico City 9:20.

Ctenosaura oaxacana Köhler and Hasbun 2001, *Senckenberg. Biol.*, Frankfurt 81(1/2):260. — Holotype: SMF 43259. — Type locality: "Tehuantepec, Estado de Oaxaca, Mexico."

DISTRIBUTION

Pacific versant of the Isthmus of Tehuantepec, Estado de Oaxaca, Mexico (Köhler and Hasbun, 2001).

Ctenosaura oedirhina de Queiroz

Ctenosaura bakeri (part.) Barbour 1928, *Proc. New England Zool. Club* 10:56.

Enyaliosaurus bakeri (part.) Cochran 1961, *Bull. U.S. Natl. Mus.*, Washington, D.C. 220:105.

Ctenosaura oedirhina de Queiroz 1987, *Copeia* 1987(4):892. — Holotype: UF 28532. — Type locality: "approx. 4.8 km (converted from 3 miles) west of Roatán on the path to Flowers Bay, Isla de Roatán, Departamento de las Islas de la Bahía, Honduras."

DISTRIBUTION

Isla de Roatán, and its satellite Isla de Santa Elena, Departamento de Islas de la Bahía, Honduras (de Queiroz, 1987b, 1990b).

Ctenosaura palearis Stejneger

Ctenosaura palearis Stejneger 1899, *Proc. U.S. Natl. Mus.*, Washington, D.C. 21:381. — Holotype: USNM 22703. — Type locality: "Gualan, Guatemala."

Enyaliosaurus palearis — Stuart 1963, *Misc. Publ. Mus. Zool. Univ. Mich.*, Ann Arbor 122:68.

DISTRIBUTION

Southeastern Guatemala in the Río Montgua Valley (Buckley and Axtell, 1997).

Ctenosaura pectinata (Wiegmann)

Cyclura pectinata Wiegmann 1834, *Herp. Mex.*, Berlin, 42; pl. 2. — Syntypes: ZMB 574–575 (Taylor, 1969; de Queiroz, 1995). — Type

locality: "Mexico" (de Queiroz, 1995). — Restricted type locality: Colima, Colima, Mexico (Bailey, 1928), inappropriate restriction (de Queiroz, 1995).

Cyclura (Cyclura) pectinata – Fitzinger 1843, Syst. Rep., Wien 1:56.

Ctenosaura pectinata – Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 191.

Ctenosaura acanthura (part.) Boulenger 1885, Cat. Liz. Brit. Mus. (Nat. Hist.), London 2:195.

Ctenosaura brevirostris Cope 1886 (syn. fide Smith, 1949), Proc. Am. Philos. Soc., Philadelphia [1885] 23:268. — Syntypes: USNM 24708–24709 (Cochran, 1961; de Queiroz, 1995). — Type locality: "Colima, in Western Mexico."

Ctenosaura teres brachylopha Cope 1886 (syn. fide Smith, 1935), Proc. Am. Philos. Soc., Philadelphia, [1885] 23:269. — Syntypes: USNM 7180–7183. — Type locality: "Mazatlan." — Restricted type locality: Mazatlan, Sinaloa, Mexico (Bailey, 1928).

Ctenosaura brachylopha – Bailey 1928, Proc. U.S. Natl. Mus., Washington, D.C. 73(12):22; pl. 6.

Ctenosaura parkeri Bailey 1928 (syn. fide Smith, 1949), Proc. U.S. Natl. Mus., Washington, D.C. 73(12):29; pl. 14, 15. — Holotype: USNM 18967. — Type locality: "Barranca Ibarra, Jalisco, Mexico."

DISTRIBUTION

Western Mexico from the vicinity of Pericos, Sinaloa (Hardy and McDiarmid, 1969) southward to the Isthmus of Tehuantepec in southeastern Oaxaca (Smith, 1949; Smith and Taylor, 1950; Köhler, 1996), including Isla Isabela and Islas de las Tres Marías, Nayarit (McDiarmid et al., 1976).

Ctenosaura quinquecarinata (Gray)

Cyclura quinquecarinata Gray 1842, Zool. Misc., London 1842:59. — Holotype: BMNH 41.3.5.61 = BMNH RR 1946.8.30.48 (Etheridge, 1982). — Type locality: "Demerara?"; in error

(de Queiroz 1995); "South America"; in error (BMNH Catalogue; de Queiroz, 1995). — Restricted type locality: "Tehuantepec, Oaxaca, Mexico" (Bailey, 1928), inappropriate restriction (de Queiroz, 1995); "to the southern portion of the distribution of *C. quinquecarinata* in Costa Rica and Nicaragua and consider Bailey's (1928) restriction of the type locality . . . to Oaxaca, Mexico as invalid" (Hasbun and Köhler, 2001).

Enyaliosaurus quinquecarinatus – Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 192.

Cyclura (Ctenosaura) quinquecarinata – Cope 1870, Proc. Am. Philos. Soc., Philadelphia [1869] 11:161.

Ctenosaura (Enyaliosaurus) quinquecarinata – Bocourt 1874, in Duméril, Bocourt and Mocquard, Miss. Sci. Mex., Paris 3:138.

Ctenosaura quinquecarinata – Sumichrast 1880, Bull. Soc. Zool. Fr. 5:175.

Ctenosaura (Enyaliosaurus) quinquecarinata (part.) – de Queiroz 1995, Publicaciones Especiales del Museo de Zoología, Mexico City 9:20.

DISTRIBUTION

From Nicaragua in Departamentos Boaca, Chontales, Jinotega, and Matagalpa, and from Costa Rica in Provincia de Guanacaste (Villa and Scott, 1967; de Queiroz, 1995; Hasbun and Köhler, 2001).

Ctenosaura similis (Gray)

Iguana (Ctenosaura) Similis Gray 1831, in Cuvier, Anim. Kingd., London 9:38. — Type: Mus. [of Mr.] Bell [number not given] (de Queiroz 1995); not located (Bailey 1928). — Type locality: not given. — Designated type locality: Tela, Honduras, Central America (Bailey, 1928), inappropriate restriction (de Queiroz, 1995).

Cyclura (Ctenosaura) similis – Wiegmann 1834, Herp. Mex., Berlin p. 42.

Ctenosaura completa Bocourt 1874 (syn. fide Bailey, 1928), in Duméril, Bocourt and

Mocquard, Miss. Sci. Mex., Paris 3:145. — Syntypes: MNHN 2252, 2256, 6499, 6500 (Guibe, 1954; Brygoo, 1989; de Queiroz, 1995). — Type locality: "Guatemala [and] . . . la Union." — Restricted type locality: La Unión [El Salvador] (Smith and Taylor, 1950), without justification (de Queiroz, 1995).

Ctenosaura acanthura (part.) — Boulenger 1885, Cat. Liz. Brit. Mus. (Nat. Hist.), London 2:195.

Ctenosaura similis — Bailey 1928, Proc. U.S. Natl. Mus., Washington, D.C. 73(12):32; pl. 16–20.

Ctenosaura similis similis — Barbour and Shreve 1934, Occas. Pap. Boston Soc. Nat. Hist. 8:197.

Ctenosaura similis multipunctata Barbour and Shreve 1934, Occas. Pap. Boston Soc. Nat. Hist. 8:197. — Holotype: MCZ 36830. — Type locality: "Old Providence Island."

DISTRIBUTION

From the Isthmus de Tehuantepec southward through Central America on both versants to Ciudad de Panamá and Colón, Panama (de Queiroz, 1995; Köhler, 1996), including the following islands: Cozumel, Mujeres, del Carmen, Mexico; Isla de Utila and Guanaja, Honduras; Maiz Grande, Nicaragua; and El Rey, Panamá, Povidencia, and San Andrés, Colombia (de Queiroz, 1995).

CYCLURA HARLAN

Iguana (part.) — Lacépède 1789, Hist. Nat. Quad. Ovip. et Serp., Paris 2:493.

Lacerta (part.) — Bonnaterre 1789, Tab. Encycl. Méth. Règ. Nat., Erpét., Paris p. 40.

Cyclura Harlan 1824, J. Acad. Nat. Sci. Philadelphia 4:250. — Type species (subsequent designation by Fitzinger, 1843): *Cyclura carinata* Harlan 1824.

Metapoceros Wagler 1830, Natur. Syst. Amphib., München 147. — Type (by monotypy): *Iguana cornuta* Bonnaterre 1789.

Iguana (*Cyclura*) — Gray 1831, in Cuvier, Anim. Kingd., London 9:39.

Aloponotus Duméril and Bibron 1837, Erpét. Gén., Paris 4:189. — Type species (by monotypy): *Aloponotus ricordi* Duméril and Bibron 1837.

Hypsilophus (*Alopontus*) — Fitzinger 1843, Syst. Rept., Wien 1:54.

Hypsilophus (*Metapoceros*) — Fitzinger 1843, Syst. Rept., Wien 1:54.

Cyclura (*Cyclura*) — Fitzinger 1843, Syst. Rept., Wien 1:54.

Cyclura carinata Harlan

Cyclura carinata Harlan 1824, J. Acad. Nat. Sci. Philadelphia, 4:250. — Type: not located (Etheridge, 1982). — Type locality: "Turk's Island."

Iguana (*Cyclura*) *Carinata* — Gray 1831, in Cuvier, Anim. Kingd., London 9:39.

Cyclura (*Cyclura*) *carinata* — Fitzinger 1843 (partim), Syst. Rept., Wien 1:48.

Cyclura carinata carinata — Barbour 1935, Zoologica, New York 19(3):118.

Cyclura carinata bartschi Cochran 1931, J. Wash. Acad. Sci., Washington, D.C. 21(3):39. — Holotype: USNM 81212. — Type locality: "Booby Cay, east of Mariguana Island, Bahamas."

REMARKS

A thorough taxonomic assessment is lacking and the most recent molecular study was unable to evaluate the phylogenetic position of *Cyclura carinata bartschi* due to the scarcity of samples. The two subspecies are currently valid names.

DISTRIBUTION

Bahamian Archipelago, Turks and Caicos Islands, including Salt, Joe Grant's, Major Hill, Dellis, Pine, Big Ambergris, Little Ambergris, East Bay, and Booby Cays (Gerber and Iverson, 2000; Buckner and Blair, 2000a).

Cyclura collei Gray

Cyclura Collei Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 190. — Holotype: BMNH 1936.12.3.108. — Type locality: "Jamaica."

Cyclura lophoma Gosse 1848 (syn. fide Grant, 1940), Proc. Zool. Soc. London 1848:99. — Holotype: BMNH 47.12.27.101. — Type locality: "Jamaica."

DISTRIBUTION

Jamaica, currently restricted to the Hellshire Hills (Vogel, 2000).

Cyclura cornuta (Bonnaterre)

Lacerta Cornuta Bonnaterre 1789, Tab. Encycl. Méth. Règ. Nat., Erpét., Paris 40; pl. 4, fig. 4. — Type: not located (Etheridge, 1982). — Type locality: "Sainte-Domingue . . . dans les mornes de l'Hôpital, entre l'Artibonite and les Gonaves."

Iguana cornuta – Lacépède 1789, Hist. Nat. Quad. Ovip. et Serp., Paris 2:493.

Metopoceros cornutus – Wagler 1830, Natur. Syst. Amphib., München p. 147.

Metapoceros cornutus – Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London 188 (invalid emendation).

Hypsilophus (Metapoceros) cornutus – Fitzinger 1843, Syst. Rept., Wien 1:54.

Cyclura cornuta (part.) – Cope 1886, Proc. Amer. Philos. Soc., Philadelphia 23:263.

Aloponotus cornutus – Perrier 1928, Traite Zool., Fasc. VIII:3095.

Cyclura cornuta cornuta – Barbour 1937, Bull. Mus. Comp. Zool., Cambridge 82(2):132.

Cyclura cyclura cornuta – Warner 1997, Iguana Times 6:59 (lapsus).

REMARKS

In prior taxonomic treatments of *Cyclura cornuta*, the species *C. stejnegeri* and *C. onchiopsis* were included as subspecies (see a review in Glor et al. [2000]). Recently, Powell (1999) and Glor et al. (2000) recognized the specific status of all three, although it is uncertain if this will be accepted by other researchers. Until further taxonomic treatments are completed, the specific and subspecific status of these three taxa will

likely be in debate. Here, I recognize their elevation to specific status because their character differentiation appears warranted (see Glor et al., 2000; R. Powell, 2000; Powell and Glor, 2000).

DISTRIBUTION

Hispaniola, including Isla Beata, Isla Saona, Ile de la Gonâve, Ile de la Petite Gonâve, Ile Grande Cayemite, and Ile de la Tortue (Glor et al., 2000; Ottenwalder, 2000a).

Cyclura cyclura (Cuvier)

Iguana cyclura Cuvier 1829, Règ. Anim., Ed. 2, Paris 2:45. — Holotype: MHNH 2367. — Type locality: "Carolina." — Corrected type locality: Andros Island, Bahama Islands (Schwartz and Thomas, 1975).

Cyclura baelopha Cope 1862 (syn. fide Schwartz and Thomas, 1975), Proc. Acad. Nat. Sci. Philadelphia (1861) 13:123. — Holotype: ANSP 8120. — Type locality: "Andros island, one of the Bahamas."

Cyclura inornata Barbour and Noble 1916, Bull. Mus. Comp. Zool., Cambridge 60(4):151; pl. 14. — Holotype: MCZ 11602. — Type locality: "U Cay in Allan's Harbor, near Highborn Cay, Bahamas."

Cyclura figginsi Barbour 1923, Proc. New England Zool. Club, Cambridge 8:108. — Holotype: MCZ 17745. — Type locality: "Bitter Guana Cay, near Great Guana Cay, Exuma Group, Bahama Islands."

Cyclura cyclura – Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:112.

Cyclura cyclura cyclura – Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:112.

Cyclura cyclura figginsi – Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:112.

Cyclura cyclura inornata – Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:112.

REMARKS

Since Schwartz and Thomas (1975), *Cyclura cyclura* has been recognized to contain three subspecific forms. Malone et al. (2000) described *C. c. cyclura* as being phylogenetically distinct from *C. c. figginsi* and *C. c. inornata*, but did not formally treat the first as a separate species. With regards to the latter two, Malone et al. (2000) believed the recovered polytomous relationships were not in agreement with their current constitution. Until these taxa are evaluated further, the subspecific names are currently valid.

DISTRIBUTION

Bahamian Archipelago, Great Bahama Bank on Andros Island, including North Andros, Mangrove Cay, and South Andros (Buckner and Blair, 2000b), central and southern Exumas including Guana, Bitter Guana, Gaulin, White Bay, Noddy, North Adderly, Leaf Cays (Knapp, 2000a), and northern Exumas, including Leaf and U Cays (Iverson, 2000).

Cyclura nubila Gray

Iguana (Cyclura) Nubila Gray 1831, in Cuvier, Anim. Kingd., London 9:39. — Holotype BMNH XXII.18.a = 1946.8.29.88 (Etheridge, 1982). — Type locality: "South America?" — Corrected type locality: Cuba (Schwartz and Thomas, 1975).

Cyclura Harlani (part.) Duméril and Bibron 1837 (syn. fide Schwartz and Thomas, 1975), Erpét. Gén., Paris 4:218. — Syntypes: MNHN A661, 2367; Lectotype: MNHN A661. — Type locality: "Caroline."

Cyclura MacLeayi Gray 1845 (syn. fide Schwartz and Thomas, 1975), Cat. Spec. Liz. Coll. Brit. Mus., London 190. — Holotype: BMNH XX.17.a = BMNH RR 1946.8.4.28 (Etheridge, 1982). — Type locality: "Cuba."

Cyclura macleayi — Barbour and Noble 1916, Bull. Mus. Comp. Zool., Cambridge 60(4):145; pl. 1, 2; pl. 13, fig. 5, 6.

Cyclura caymanensis Barbour and Noble 1916, Bull. Mus. Comp. Zool., Cambridge 60(4):148;

pl. 3. — Holotype: MCZ 10534. — Type locality: "Cayman Islands, probably Cayman Brac."

Cyclura macleayi caymanensis Grant 1940, Bull. Inst. Jamaica, Sci. Ser., Kingston 2:29.

Cyclura macleayi lewisi Grant 1940, Bull. Inst. Jamaica, Sci. Ser., Kingston 2:35; pl. 2; fig. 3, 4. — Holotype: BMNH 1939.2.3.68 = BMNH RR 1946.8.9.321 (Etheridge 1982). — Type locality: "Battle Hill, east end of Grand Cayman."

Cyclura nubila nubila Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:113.

Cyclura nubila caymanensis Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:113.

Cyclura nubila lewisi Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:113.

Cyclura nubila Schwartz and Carey 1977, Stud. Faun. Curaçao and Carib. Is., Utrecht 53(173):23.

REMARKS

Since Schwartz and Thomas (1975), *Cyclura nubila* has been recognized to contain three subspecific forms. In a molecular phylogenetic study, Malone et al. (2000) found that *C. n. nubila* and *C. n. caymanensis* were more closely related to *C. cyclura*, to the exclusion of *C. n. lewisi*. Malone et al. (2000) found *C. n. lewisi* to be phylogenetically distinct, and future studies may find there is further justification to elevate it to specific status (see Malone and Davis, this volume).

DISTRIBUTION + *Isla Mujeres*
Cuba, including as many as four thousand islets surrounding the mainland (Perera, 2000), Lesser Caymans, including Cayman Brac and Little Cayman (Gerber, 2000a), and Grand Cayman (Burton, 2000).

Cyclura onchiopsis† Cope

Metopoceros cornutus (part.) — Cope 1866, Proc. Acad. Nat. Sci. Philadelphia 18:124.

C. [yclura] nigerrima Cope 1885 (syn. fide Schwartz and Thomas, 1975), Am. Nat., Lancaster 19(10):1006. — Holotype: USNM 9974. — Type locality: "Navassa." (*Nomen nudum* fide Schwartz and Carey, 1977)

C. [yclura] onchiopsis Cope 1885, Am. Nat., Lancaster 19(10):1006. — Syntypes: USNM 9977, 12239, MCZ 4717. — Type locality: "from an unknown locality." — Designated type locality: Navassa Island (Cope, 1886).

Cyclura cornuta (part.) — Cope 1886, Proc. Amer. Philos. Soc., Philadelphia 23:263.

Cyclura cornuta nigerrima — Barbour 1937, Bull. Mus. Comp. Zool. Cambridge 82:132.

Cyclura cornuta onchiopsis — Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:112.

Cyclura cornuta onchiopsis — Blair 1993, California Herpetol. Soc. Spec. Publ., Davis, California 6:57 (*invalid emendation*).

Cyclura onchiopsis — Powell 1999, Carib. J. Sci., Puerto Rico 35:1–13.

REMARKS

Cyclura onchiopsis is believed to be extinct due to human exploitation, habitat alteration, and predation from exotics (Powell and Henderson, 1999; R. Powell, 2000). Recent studies have treated *C. onchiopsis* as a subspecies of *C. cornuta* (see Malone et al. [2000]), following the prevailing taxonomic arrangement, and did not comment on the recommendations of Powell (1999) and Powell and Henderson (1999).

DISTRIBUTION

Navassa Island, off the west coast of Hispaniola (R. Powell, 1999, 2000).

Cyclura pinguis Barbour

Cyclura pinguis Barbour 1917, Proc. Biol. Soc. Wash., Washington, D.C. 30:100. — Holotype: MCZ 12082. — Type locality: "Anegada, British Virgin Islands."

DISTRIBUTION

Puerto Rican Bank, Anegada Island (Carey, 1975; Etheridge, 1982).

Cyclura ricordii Duméril and Bibron

Aloponotus Ricordii Duméril and Bibron 1837, Erpét. Gén., Paris 4:190; pl. 38. — Holotype: MNNH 8304. — Type locality: "Sainte-Domingue."

Hypsilophus (Aloponotus) Ricordii — Fitzinger, Syst. Rept., Wien 1:54.

Cyclura ricordii — Cochran 1924, Proc. U.S. Natl. Mus., Washington, D.C. 66(6):5.

Cyclura ricordii — Schwartz and Carey 1977, Stud. Faun. Curaçao and Carib. Is., Utrecht 53(173):64.

DISTRIBUTION

Southwestern Dominican Republic, where it is restricted to Valle de Neiba and the Peninsula de Barahona, and includes Isla Cabritos located within the inland Lago Enriquillo (Ottenwalder, 2000b).

Cyclura rileyi Stejneger

Cyclura rileyi Stejneger 1903, Proc. Biol. Soc. Wash., Washington, D.C. 16:130. — Holotype: USNM 31969. — Type locality: "Watlings Island, Bahamas."

Cyclura nuchalis Barbour and Noble 1916, Bull. Mus. Comp. Zool., Cambridge 60(4):156; pl. 8, fig. 1, 2. — Holotype: ANSP 11985. — Type locality: "Fortune Island, Bahamas."

Cyclura cristata Schmidt 1920, Proc. Linn. Soc., New York 33:6. — Holotype: AMNH 7238. — Type locality: "White Cay, Bahama Islands"; corrected to White Cay, Exuma Cays, Bahamas (Schmidt, 1936).

Cyclura rileyi rileyi — Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:114.

Cyclura rileyi cristata — Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:114.

Cyclura rileyi nuchalis – Schwartz and Thomas 1975, Carnegie Mus. Nat. Hist. Spec. Publ., Pittsburgh 1:114.

REMARKS

Since Schwartz and Thomas (1975), *Cyclura rileyi* has been recognized to contain three subspecific forms. Until further taxonomic study, the subspecific names are currently valid.

DISTRIBUTION

Bahamian Archipelago, San Salvador, including Gaulin, Goulding, Green, Low, and Manhead Cays (Hayes et al., 1995; Hayes, 2000a), in the southern Exumas on White (= Sandy) Cay (Hayes, 2000b), and in the Aclins on Fish and North Cays (Hayes and Montanucci, 2000).

Cyclura stejnegeri Barbour and Noble

Metopoceros cornutus (part.) – Meerwarth 1901, Mitth. Naturg. Mus., Hamburg 18:26.

Cyclura cornuta (part.) – Stejneger 1904, Rep. U.S. Natl. Mus., Washington, D.C. 1902:670.

Cyclura stejnegeri Barbour and Noble 1916, Bull. Mus. Comp. Zool., Cambridge 60(4):163; pl. 12. — Holotype: USNM 29367. — Type locality: "Mona Island."

Cyclura cornuta stejnegeri – Barbour 1937, Bull. Mus. Comp. Zool. 82:132.

REMARKS

Cyclura stejnegeri has been treated as a subspecies of *C. cornuta* (see Malone et al., 2000), following the prevailing taxonomic arrangement prior to the recommendations of Powell (1999) and Powell and Glor (2000) to treat this taxon as a species.

DISTRIBUTION

Isla Mona, situated between Hispaniola and Puerto Rico (Powell and Glor, 2000; Wiewandt and Garcia, 2000).

DIPSOSAURUS HALLOWELL

Crotaphytus dorsalis (part.) Baird and Girard 1852, Proc. Acad. Nat. Sci. Philadelphia 6:126. — Type species (by monotypy): *Crotaphytus dorsalis* Baird and Girard 1852.

Dipso-saurus Hallowell 1854, Proc. Acad. Nat. Sci. Philadelphia 7:92. — Type species (by monotypy): *Crotaphytus dorsalis* Baird and Girard 1852.

Dipsosaurus catalinensis Van Denburgh

Dipsosaurus catalinensis – Van Denburgh 1922, Occas. Pap. Calif. Acad. Sci. 10(1):83. — Holotype: CAS 50505. — Type locality: "Santa Catalina Island, Gulf of California, Mexico."

Dipsosaurus dorsalis catalinensis – Soulé and Sloan 1966, Trans. San Diego Soc. Nat. Hist. 14(11):141.

REMARKS

Dipsosaurus catalinensis was relegated to subspecific status within *D. dorsalis* by Soulé and Sloan (1966) without comment. More recently, Grismer (1999a) provided justification to elevate it to specific rank.

DISTRIBUTION

Isla Santa Catalina, Baja California Sur, Mexico (Van Denburgh, 1922; Grismer, 1999a,b).

Dipsosaurus dorsalis (Baird and Girard)

Crotaphytus dorsalis Baird and Girard 1852, Proc. Acad. Nat. Sci. Philadelphia 6:126. — Holotype: USNM 2699 (Cochran, 1961). — Type locality: "Desert of Colorado, Cal." — Restricted type locality: Winterhaven (= Fort Yuma), Imperial County" (Smith and Taylor, 1950), without justification (de Queiroz, 1995).

Dipso-saurus dorsalis – Hallowell 1854, Proc. Acad. Nat. Sci. Philadelphia 7:92.

Dipsosaurus dorsalis – Baird 1859 in U.S. Dept. of Interior, United States and Mexican Boundary Survey, Washington, D.C. 2(2):8.

Dipsosaurus dorsalis dorsalis – Van Denburgh 1920, Proc. California Acad. Sci., fourth ser. 10(4):33.

Dipsosaurus dorsalis lucasensis – Van Denburgh 1920 (syn. fide Grismer, 1999a), Proc. California Acad. Sci., fourth ser. 10(4):33. — Holotype: CAS 46090. — Type locality: "San Jose del Cabo, Lower California, Mexico."

Dipsosaurus carmenensis Van Denburgh 1922, (syn. fide Soulé and Sloan, 1966), Occas. Pap. California Acad. Sci. 10(1):81. — Holotype: CAS 50504. — Type locality: "Near Puerto Bellandro, Carmen Island, Gulf of California, Mexico."

Dipso-saurus dorsalis sonoriensis Allen 1933, Occas. Pap. Mus. Zool. Univ. Michigan 259:4. — Type: UMMZ 72121. — Type locality: "Hermosillo, Sonora, Mexico."

REMARKS

Dipsosaurus dorsalis has contained as many as four subspecies. Grismer (1999a) elevated *D. catalinensis* (see above) and placed *D. d. lucasensis* in synonymy with the nominal species. Of the remaining subspecific names, *D. d. dorsalis* and *D. d. sonoriensis* remain valid.

DISTRIBUTION

Southwestern United States (in southern Nevada, southwestern Utah, southeastern California, and western Arizona), southward to northwestern Mexico (in western Sonora and northwestern Sinaloa), the peninsula of Baja California, and islands in the Gulf of California (including Ángel de La Guarda, Carmen, Cerralvo, Coronados, Espíritu Santo, Monserrate, Partida Sur, Santiago, San José, San Luis, and San Marcos), and the islands Magdalena and Santa Margarita in the Pacific Ocean (Etheridge, 1982; de Queiroz, 1995; Grismer, 1999a,b).

IGUANA LAURENTI

Iguana Laurenti, 1768. Spec. Med., Synop. Rept., Wien p. 47. — Type species (by tautonymy): *Lacerta iguana* Linnaeus 1758.

Prionodus Wagler 1828, Isis von Oken, Leipzig 21(8/9):860. — Type species (by monotypy): *Lacerta iguana* Linnaeus 1758.

Hypsilophus Wagler 1830, Natur. Syst. Amphib., München 147. — Type species (by monotypy): *Lacerta iguana* Linnaeus 1758.

Iguana (Iguana) – Gray 1831, in Cuvier edit. Griffith, Anim. Kingd., London 9:36.

Iguana (Hypsilophus) Wiegmann 1834, Herp. Mex., Saur. Spec., Berlin p. 44. — Type species: *Lacerta iguana* Linnaeus 1758.

Hypsilophus (Hypsilophus) – Fitzinger 1843, Syst. Rept., Wien 1:16.

Iguana delicatissima Laurenti

Iguana delicatissima Laurenti 1768, Spec. Med., Synop. Rept., Wien p. 48. — Holotype: Zool. Mus. Torino, not located (Etheridge, 1982). — Type locality: "Indiis." — Restricted type locality: Island of Terre de Bas, Les Iles de Saintes, Département de la Guadeloupe, French West Indies (Lazell, 1973).

Iguana nudicollis Merrem 1820 (referenced to ?*Iguana delicatissima* Laurenti, 1768), Tent. Syst. Amphib., Marburg p. 48.

Amblyrhynchus delicatissima – Wagler 1930, Natur. Syst. Amphib., München p. 148.

DISTRIBUTION

Lesser Antilles, from Anguilla, St. Martin, St. Eustatius, St. Barthélemy (including Ilet au Vent), Antigua, Guadeloupe (including Basse Terre, La Désirade, Iles de la Petite Terre, and Les Iles des Saintes), Dominica, and Martinique (including Ilet Chancel) (Day et al., 2000).

Iguana iguana (Linnaeus)

Lacerta iguana Linnaeus, Syst. Nat., Ed. 10, Stockholm 1:206. Syntypes: NHRM [one specimen, no number given]; ZMUU [one specimen, no number given] (Lönnberg, 1896; Anderson, 1900; Hoogmoed, 1973; de Queiroz, 1995). — Type locality: "Indiis." — Restricted type locality: "island of Terre de Haut, Les Iles des Saintes, Département de la Guadeloupe, French West Indies" (Lazell, 1973), inappropriate restriction (de Queiroz, 1995); "confluence of the Cottica River and Perica Creek, Surinam" (Hoogmoed, 1973).

?*Iguana minima* Laurenti 1768 (syn. fide Fitzinger, 1843), Spec. Med., Synop. Rept., Wien 48. — Holotype: Museo Illustrissimi Comitis Turriani [no number given]; not

located (Elter, 1981; Etheridge, 1982). — Type locality: not given.

Iguana tuberculata Laurenti 1768 (syn. fide Lönnberg, 1896), Spec. Med., Synop. Rept., Wien 49. — Holotype: Museo Illustrissimi Comitis Turriani [no number given]; not located (Elter, 1981; Etheridge, 1982). — Type locality: not given.

Iguana delicatissima (part.) — Latreille 1802, in Sonnini and Latreille, Hist. Nat. Rept., Paris 1:255.

Iguana coerulea (part.) Daudin 1802 (syn. fide Fitzinger, 1843), Hist. Nat. Rept., Paris 3:286. — Syntypes: MNHN [two specimens], lost (Brygoo, 1989; de Queiroz, 1995).

I. [iguana] vulgaris Link 1806 (replacement name for *Lacerta iguana* Linnaeus 1758, fide Peters and Donoso-Barros, 1970), Beschr. Natural.-Sammllung Univ. Rostock 2:58.

Iguana sapidissima Merrem 1820 (replacement name [in synonymy] for *Lacerta iguana* Linnaeus 1758), Tent. Syst. Amphib., Marburg 47.

Iguana squamosa Spix 1825 (syn. fide Gray, 1831), Spec. Nov. Lacert. Brazil, Monachii 1:5; pl. 5. — Lectotype: ZSM 537/0 (Hoogmoed and Gruber, 1983; de Queiroz, 1995). — Type locality: "Bahiae, Parae"; "Salvador and Belém" (Vanzolini, 1981).

Iguana viridis Spix 1825 (syn. fide Gray, 1831), Spec. Nov. Lacert. Brazil, Monachii 1:6; pl. 6. — Lectotype: ZSM 540/0 (Hoogmoed and Gruber, 1983; de Queiroz, 1995). — Type locality: "Rio St. Francisci et Itapicuru."

Iguana coerulea Spix 1825 (non Daudin, 1802; syn. fide Fitzinger, 1843), Spec. Nov. Lacert. Brazil, Monachii 1:7; pl. 7. — Syntypes: ZSM 71/0 [two specimens]; destroyed (Etheridge, 1982; Hoogmoed and Gruber, 1983). — Type locality: "Rio St. Francisci."

Iguana emarginata Spix 1825 (syn. fide Gray, 1831), Spec. Nov. Lacert. Brazil, Monachii 1:7;

pl. 8. — Holotype: ZSM 535/0 (Hoogmoed and Gruber, 1983). — Type locality: "[Rio] St. Francisci."

Iguana lophyroides Spix 1825 (syn. fide Fitzinger, 1843), Spec. Nov. Lacert. Brazil, Monachii 1:8; pl. 9. — Lectotype: ZSM 546/0 A (Hoogmoed and Gruber, 1983; de Queiroz, 1995). — Type locality: "Rio de Janeiro, Bahiae"; "Rio de Janeiro and Salvador" (Vanzolini, 1981).

Iguana Iguana — Gray 1827, Phil. Mag., ser. 2 2:57.

Prionodus iguana — Wagler 1828, Isis von Oken, Leipzig 21: 860.

Iguana tuberculosa Bory de Saint-Vincent 1828 (replacement name for *Lacerta iguana* Linnaeus 1758), Résumé d'erpétologie, Paris p. 120; pl. 21.

Hypsilophus iguana — Wagler 1830, Natur. Syst. Amphib., München p. 147.

Iguana (Iguana) tuberculata — Gray 1831, in Cuvier, Anim. Kingd., London 9:36.

Iguana (Hypsilophus) rhinolophus Wiegmann 1834 (syn. fide Lazell, 1973), Herp. Mex., Saur. Spec., Berlin 44. — Syntypes: ZMB 571 [two specimens] (Etheridge, 1982); one recatalogued as ZMB 36300, ZMB 572 lost (de Queiroz, 1995). — Type locality: not given; Mexico by implication (de Queiroz, 1995). — Restricted type locality: Córdoba, Veracruz (Smith and Taylor, 1950), without justification (de Queiroz, 1995).

Iguana rhinolopha — Duméril and Bibron 1837, Erpét. Gén., Paris 4:207.

Hypsilophus (Hypsilophus) Rhinolophus — Fitzinger 1843, Syst. Rept., Wien 1:55.

Hypsilophus (Hypsilophus) tuberculatus — Fitzinger 1843, Syst. Rept., Wien 1:55.

Iguana rhinolophus — Gray 1845, Cat. Spec. Liz. Coll. Brit. Mus., London p. 186.

Metopoceros cornutus — Tyler 1850, Proc. Zool. Soc. London 1850:106; pl. 3.

?*Iguana Hernandezii* Jan 1857 (*nomen nudum* *vide* Smith and Taylor, 1950), *Indice Sistem. Rett. E. Anfib. Medesimo*, Milano p. 38.

Iguana tuberculata Var. *rhinolopha* – Boulenger 1885, *Cat. Liz. Brit. Mus.*, London 2:190.

Iguana iguana rhinolopha – Van Denburgh 1898, *Proc. Acad. Sci. Philadelphia* (1897) 49:461.

Iguana iguana iguana – Dunn 1934, *Copeia* 1934(1):1.

DISTRIBUTION

Northern Mexico, from Sinaloa and Veracruz, southward through Central America and into northeastern South America to the Tropic of Capricorn in Paraguay and southeastern Brazil (Etheridge, 1982; de Queiroz, 1995). The species occurs on numerous islands, including Cozumel, Utila, Roatán, de Guanaja, Corn, Providencia, San Andres, Aruba, Trinidad, Tobago, and various localities in the Lesser Antilles (Etheridge, 1982).

LAPITIGUANA† PREGILL AND WORTHY

Lapitiguana† Pregill and Worthy 2003, *Herpetologica* 59(1):60; figs. 2–3. — Type species (by monotypy): *Lapitiguana impensa*† Pregill and Worthy 2003.

Lapitiguana impensa† Pregill and Worthy

Lapitiguana impensa† Pregill and Worthy 2003, *Herpetologica* 59(1):60; figs. 2–3. — Holotype: MNZ 37015. Type locality: “Voli Voli Cave (Qara-ni-vokai Site) near Sigatoka, Viti Levu, Fiji, Southwest Pacific.”

GEOLOGIC AGE

The type locality is in the Late Quaternary. This now extinct species likely overlapped with the Lapita people approximately 3000 years ago (Pregill and Worthy, 2003).

DISTRIBUTION

Known only from Viti Levu, Fiji. Fossil remains have been recovered from the type locality on the southwest side of Viti Levu, in addition to Qara-

ni-oso near the village of Tau and Bukusia Cave near Raiwaqa Village (Pregill and Worthy, 2003).

PUMILIA† NORELL

Pumilia† Norell 1989, *Contr. Sci. Nat. Hist. Mus. Los Angeles Co.* 414:3; fig. 3. — Type species (by monotypy): *Pumilia novaceki*† Norell 1989.

Pumilia novaceki† Norell

Pumilia novaceki† Norell 1989, *Contr. Sci. Nat. Hist. Mus. Los Angeles Co.* 414:3; fig. 3. — Holotype: LACM 64115/13739. Type locality: “Vellacito Badlands of Anza Borrego Desert State Park, San Diego County, California” by implication.

GEOLOGIC AGE

The type locality is in the Late Neogene deposits of the Palm Springs Formation and is estimated to be between 2.0 and 3.4 million years old (Norell, 1989).

DISTRIBUTION

Known only from the type locality in Anza Borrego Desert State Park, San Diego County, California (Norell, 1989).

SAUROMALUS DUMÉRIL

Sauromalus Duméril 1856, *Arch. Mus. Hist. Nat., Paris* 8:535; pl. 23, fig. 3, 3a — Type species (by monotypy): *Sauromalus ater* Duméril 1856.

Euphryne Baird 1858, *Proc. Acad. Nat. Sci. Philadelphia* 10:253. — Type species (by monotypy): *Euphryne obesus* Baird 1859.

Sauromalus ater Duméril

Sauromalus ater Duméril 1856, *Arch. Mus. Hist. Nat., Paris* 8:535; pl. 23, fig. 3, 3a. — Holotype: MNHN 813. — Type locality: not given. — Designated type locality: “one of the following islands in the Gulf of California: Espíritu Santo, Isla Partida, San Marcos, San Diego, Santa Cruz, or San Francisco” (Shaw, 1945); “Espíritu Santo Island” (Smith and Taylor, 1950); “southern coastal Sonora” (Hollingsworth, 1998; but see Montanucci, 2000).

Euphyryne obesus Baird 1858, Proc. Acad. Nat. Sci. Philadelphia 10:253. — Type: USNM 4172. — Type locality: "Fort Yuma." (see Montanucci [2001] for further clarification).

Euphyryne obesa – Baird 1859, U.S. Mex. Bound. Surv., Washington, D.C. 2:6; pl. 27 (valid emendation).

Sauromalus interbrachialis Dickerson 1919 (syn. fide Schmidt, 1922), Bull. Am. Mus. Nat. Hist., New York 41:463. — Holotype: USNM 64443. — Type locality: "La Paz, Lower California, Mexico," in error (Schmidt, 1922).

Sauromalus townsendi Dickerson 1919, Bull. Am. Mus. Nat. Hist., New York 41:464. — Holotype: AMNH 5643. — Type locality: "Tiburon Island, Gulf of California, Mexico."

Sauromalus obesus – Schmidt 1922 (syn. fide Hollingsworth, 1998), Bull. Am. Mus. Nat. Hist., New York 46:618.

Sauromalus australis Shaw 1945 (syn. fide Hollingsworth, 1998), Trans. San Diego Soc. Nat. Hist. 10:286. — Holotype: SDSNH 30170. — Type locality: "San Francisquito Bay, Baja California, Mexico."

Sauromalus obesus townsendi – Shaw 1945 (syn. fide Hollingsworth, 1998), Trans. San Diego Soc. Nat. Hist. 10:290.

Sauromalus obesus tumidus Shaw 1945 (syn. fide Hollingsworth, 1998), Trans. San Diego Soc. Nat. Hist. 10:292. — Holotype: SDSNH 27323. — Type locality: "Telegraph Pass, Gila Mountains, Yuma County, Arizona."

Sauromalus obesus obesus – Shaw 1945 (syn. fide Hollingsworth, 1998), Trans. San Diego Soc. Nat. Hist. 10:295.

Sauromalus shawi Cliff 1958, Copeia, 4:259. — Holotype: CAS-SU 16120. — Type locality: "San Marcos Island."

Sauromalus obesus multiforminatus Tanner and Avery 1964 (syn. fide Hollingsworth, 1998), Herpetologica 20:38; fig. 1a, 1b. — Holotype: BYU 11376. — Type locality: "North Wash, 11 miles northwest of Hite, Garfield County, Utah."

Sauromalus ater ater – Soulé and Sloan 1966 (syn. fide Hollingsworth, 1998), Trans. San Diego Soc. Nat. Hist. 14:141.

Sauromalus ater shawi – Soulé and Sloan 1966 (syn. fide Hollingsworth, 1998), Trans. San Diego Soc. Nat. Hist. 14:141.

Sauromalus obesus australis – Case 1982 (syn. fide Hollingsworth, 1998), in Burghardt and Rand (eds.), Iguanas of the World, New Jersey, 185.

REMARKS

In the most recent taxonomic review of *Sauromalus*, Hollingsworth (1998) treated the names *Sauromalus ater*, *S. australis*, and *S. obesus* as synonyms, and following the principle of priority, the name *Sauromalus ater* was applied to a single, more broadly distributed species. A petition to the International Commission on Zoological Nomenclature (ICZN) is pending (Montanucci et al., 2001), requesting the ICZN use its plenary powers and place the name *Sauromalus ater* on the list of unavailable names. Rebuttal opinions are currently being submitted recommending the ICZN uphold the principle of priority and retain the name *S. ater*. Because of the disagreements over the use of *S. ater*, many authors chose to follow the taxonomy prior to Hollingsworth (1998) and recognize *S. obesus* (see Tracy, this volume).

DISTRIBUTION

Southwestern United States (in southern Nevada, southwestern Utah, southeastern California, and western Arizona), southward to northwestern Mexico (in western Sonora), the peninsula of Baja California, and the following islands in the Gulf of California: Willard, Tiburón, San Marcos, El Coyote, Danzante, San Cosme, Santa Cruz, San Diego, San José, San Francisco, Ballena, Gallo, Partida Sur, and Espíritu Santo (Shaw, 1945; Etheridge, 1982; de Queiroz, 1995; Hollingsworth, 1998; Grismer, 1999b).

Sauromalus hispidus Stejneger

Sauromalus ater Streets 1877 (*part.*), Bull. U. S. Natl. Mus., Washington, D.C. 7:36.

Sauromalus hispidus Stejneger 1891, Proc. Nat. Mus., Washington, D.C. 14:409. — Holotype: USNM 8563. — Type locality: "Angel de la Guardia Island, Gulf of California."

DISTRIBUTION

Found on the islands of Ángel de La Guarda, Granito, Mejía, Pond, San Lorenzo Norte, San Lorenzo Sur, and numerous islands in Bahía de Los Ángeles, including Cabeza de Caballo, La Ventana, Piojo, Flecha, Mitlán, and Smith, Gulf of California, Mexico (Shaw, 1945; Etheridge, 1982; de Queiroz, 1995; Hollingsworth, 1998; Grismer, 1999b).

Sauromalus klauberi Shaw

Sauromalus klauberi Shaw 1941, Trans. San Diego Soc. Nat. Hist. 9:285. — Holotype: SDSNH 6859. — Type locality: "Santa Catalina Island, Gulf of California, Mexico."

Sauromalus ater klauberi — Soulé and Sloan 1966 (syn. fide Hollingsworth, 1998), Trans. San Diego Soc. Nat. Hist. 14:141.

DISTRIBUTION

Isla Santa Catalina, Baja California Sur, Mexico (Shaw, 1941, 1945).

Sauromalus slevini Van Denburgh

Sauromalus slevini Van Denburgh 1922, Occ. Pap. Calif. Acad. Sci. 10(1):97. — Holotype:

CAS 50503. — Type locality: "South end of Monserrate Island, Gulf of California, Mexico."

Sauromalus ater slevini — Robinson 1974 (syn. fide Hollingsworth, 1998), Herpetologica 30(2):163.

DISTRIBUTION

Islas Carmen, Los Coronados, and Monserrate, Baja California Sur, Mexico (Shaw, 1945; Etheridge, 1982; de Queiroz, 1995; Hollingsworth, 1998; Grismer, 1999b).

Sauromalus varius Dickerson

Sauromalus varius Dickerson 1919, Bull. Am. Mus. Nat. Hist., New York 41:464. — Holotype: AMNH 5633. — Type locality: "San Esteban Island, Gulf of California, Mexico."

DISTRIBUTION

Islas San Esteban, Sonora and Roca Lobos, Baja California, Mexico (Hollingsworth et al., 1997; Hollingsworth, 1998).

ACKNOWLEDGMENTS

Early drafts of this chapter were read by Kevin de Queiroz and two anonymous reviewers. Both greatly enhanced the chapter and improved on a number of shortcomings. I am grateful for their help. Any errors, of course, are solely my responsibility.