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PHYLOGENETIC SYSTEMATICS, SCALING RELATIONSHIPS, AND THE EVOLUTION OF GLIDING PERFORMANCE IN FLYING LIZARDS (GENUS *DRACO*)

Approved by
Dissertation Committee:

David C. Cannatella, Supervisor

David M. Hillis, Supervisor

James J. Bull

Robert Dudley

Robert Dudley

Timothy B. Rowe

PHYLOGENETIC SYSTEMATICS, SCALING RELATIONSHIPS, AND THE EVOLUTION OF GLIDING PERFORMANCE IN FLYING LIZARDS (GENUS *DRACO*)

by

Jimmy Adair McGuire, B.S., M.S.

Dissertation

Presented to the Faculty of the Graduate School of
The University of Texas at Austin
in Partial Fulfillment
of the Requirements
for the Degree of

Doctor of Philosophy

The University of Texas at Austin
December, 1998

UMI Number: 9937095

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This dissertation is dedicated to Sharon Messenger,
for the support and encouragement that she has provided
throughout our graduate careers, and for selflessly dealing with all of
our real world problems during my long absences in the field

ACKNOWLEDGMENTS

There are many people who have made important contributions to my development as a scientist, as well as to the development and completion of this project. I am particularly grateful to Richard Etheridge and Lee Grismer, who provided my introduction to scientific research and are largely responsible for my escape from a career in finance. Richard and Lee remain two of my closest friends and colleagues.

My co-supervisors, David Cannatella and David Hillis, have each provided invaluable guidance and support in their own ways. Both have contributed tremendously to my understanding of phylogenetic systematics. David Cannatella has been my day to day advisor and, as such, has provided critical guidance in virtually all aspects of my dissertation research. David Hillis and Jim Bull generously funded much of my molecular lab work. I am also indebted to the remaining members of my committee, Jim Bull, Robert Dudley, and Tim Rowe. Through his excellent research design course, Jim Bull provided important guidance in the early development of this project. Robert Dudley deserves special praise because the project probably was intractable without his expertise in biomechanics and willingness to collaborate with a student who was not in his own lab. Robert and I wrote two large grants that funded most of the field work and together made two trips to Southeast Asia during which we conducted field gliding trials critical to the completion of the project.

I would like to thank the members of the Cannatella and Hillis labs for their support and guidance during the course of this project (Kelly Agnew, Chris Austin, Marty Badgett, Joe Bernardo, Matt Brauer, Rafe Brown, Dan Brumbaugh, Mike Charleston, Paul Chippindale, Keith Crandall, Wayne Crill, Cliff Cunningham, Laurie Dries, Anna Graybeal, Ken Halanych, John Huelsenbeck, Mark Holder, Kris Kichler, Travis La Duc, Barb Mable, Sharon Messenger, Steve Poe, Tod Reeder, Todd Schlenke, Kathrin Stanger–Hall, John Wiens, and Jennifer Yeh). Hillis–Bull lab technician extrordinaire Marty Badgett requires special praise for his willingness to patiently answer my numerous lab-related questions despite what must have been an overwhelming compulsion not to. Two undergraduate students, Michael Dillon and Peter Baik, spent many long hours processing scanned *Draco* images and gliding video footage. I am particularly grateful to Peter, who worked with me for several months, always impressing me with his precision and efficiency.

For assistance and companionship in the field, I would like to thank Chris Austin, Rafe Brown, Lito Bulalacao, Ron Crombie, Bettina Dudley, Robert Dudley, Lee Grismer, Brad Hollingsworth, Mohamed Izhan Bin Mohamed Ilhan, Ulrich Kuch, Humberto Wong, Vicente "the Terminator" Yngente, and Frank Yuwano.

I am grateful to Dr. Kiew Bong Heang of the Universiti Malaya, Francis Liew of Sabah Parks, Roger Sison of the Philippine National Museum, and Dr. Angel Alcala of Silliman University for facilitating the acquisition of collecting permits. Dr. Kiew recommended collecting localities and study sites on the Malay Peninsula that proved to be invaluable.

For funding my research, I am grateful to the University of Texas Department of Zoology, the Texas Memorial Museum, the National Geographic Society, the Explorer's Club, and the New England Herpetological Society. The California Academy of Sciences provided a Charles Stearns Fellowship that allowed me to travel to the academy to examine their *Draco* specimens.

I thank the following curatorial staff and their institutions for the loan of specimens invaluable to this study: Darrel Frost (AMNH), Barry Clarke and E. N. Arnold (BMNH), Jens Vindum, Bob Drewes, and Alan Leviton (CAS), Ellen Censky and John Wiens (CM), Robert S. Kennedy and John Ferner (CMNH), Robert Inger, Alan Resetar, and Harold Voris (FMNH), Frank Burbrink and Doug Rossman (LSU), John Cadle and Jose Rosado (MCZ), Richard Etheridge (SDSU), Ron Crombie and Kevin de Queiroz (USNM), and Ric Howe (WAM).

Tissue samples for *Draco* and outgroup species were provided by Rafe Brown, Ric Howe, Bob Macey, and Bob Murphy. The samples for Lesser Sunda flying lizards provided by Ric Howe and colleagues were particularly valuable in that they provided the only samples representing the Lesser Sunda *Draco* clade.

PHYLOGENETIC SYSTEMATICS, SCALING RELATIONSHIPS, AND THE EVOLUTION OF GLIDING PERFORMANCE IN FLYING LIZARDS (GENUS *DRACO*)

Publication No.____________

Jimmy Adair McGuire, Ph.D.
The University of Texas at Austin, 1998

Supervisors: David C. Cannatella and David M. Hillis

Flying lizards (genus *Draco*) occur throughout the rain forests of southeast Asia. *Draco* are unique in their ability to glide long distances using wing-like patagial membranes supported by elongated thoracic ribs as an airfoil. The purpose of this study was to formulate and test predictions regarding the role that *Draco* size evolution has had on the evolution of gliding performance. Flying lizards exhibit substantial size variation, which has important consequences for gliding performance.

In Chapter 1, I performed a taxonomic revision of the Philippine *Draco* assemblage. This assemblage has had a chaotic taxonomic history and I concluded that the most recent taxonomy substantially underestimated species

diversity. Based on this study, I recognized 10 evolutionary species in the Philippines.

In Chapter 2, I performed phylogenetic analyses of *Draco* relationships based on mitochondrial DNA sequence data. The data set is composed of 1121 base pairs of the ND2 protein-coding gene for 51 species/populations. The data were analyzed under both parsimony and maximum likelihood optimality criteria. Although the parsimony and maximum–likelihood estimates are not entirely congruent, nonparametric bootstrap analysis under the parsimony criterion identifies many well–supported clades, all of which are also recovered in the maximum–likelihood analyses.

In Chapter 3, I analyzed area/mass scaling relationships in 29 species of *Draco* and explored the implications that size variation has for the evolution of gliding performance. Regression analyses were conducted using independent contrasts calculated in the context of the molecular phylogenetic estimate of *Draco* relationships. The results indicate that isometry cannot be rejected for *Draco*, whereas functional equivalence is strongly rejected. Given this result, I hypothesized that larger species are relatively poor gliders when compared with smaller species and that evolution of large size requires a cost in decreased gliding performance.

In Chapter 4, I presented gliding performance data obtained for 11 species of *Draco* spanning the entire size distribution of the genus. To obtain the data, I conducted field gliding trials in Malaysia. These data confirm that larger species of *Draco* are relatively poor gliders when compared with smaller species.

TABLE OF CONTENTS

CHAPTER 1. A TAXONOMIC REVISION OF THE FLYING LIZARDS OF THE PHILIPPINE ISLANDS (CHAMELEONIDAE: AGAMINAE: *DRACO*), WITH A DESCRIPTION OF A NEW SPECIES

CHAPTER 2. PHYLOGENETIC SYSTEMATICS OF SOUTHEAST ASIAN FLYING LIZARDS (GENUS *DRACO*) BASED ON MITOCHONDRIAL DNA SEQUENCE DATA

CHAPTER 3. BODY SIZE EVOLUTION IN SOUTHEAST ASIAN FLYING LIZARDS (GENUS *DRACO*): IMPLICATIONS FOR THE EVOLUTION OF GLIDING PERFORMANCE

CHAPTER 4. THE EFFECTS OF BODY SIZE EVOLUTION ON GLIDING PERFORMANCE IN FLYING LIZARDS (GENUS *DRACO*)

CHAPTER 1

A TAXONOMIC REVISION OF THE FLYING LIZARDS OF THE PHILIPPINE ISLANDS (CHAMELEONIDAE: AGAMINAE: *DRACO*), WITH A DESCRIPTION OF A NEW SPECIES

The flying lizards (genus *Draco*) of Southeast Asia are small to moderate–sized arboreal lizards that are remarkable in their ability to glide long distances using wing–like patagial membranes supported by elongate thoracic ribs. The taxonomy of the genus has had a chaotic history but benefited greatly from the recent revisions of Inger (1983) and Musters (1983). The taxonomies provided by both authors were rather conservative, and this approach was quite successful with the *Draco* assemblages of the greater Sunda shelf (i.e. the Malay Peninsula, Borneo, Sumatra, Java, Bali, and associated islands) where as many as six species can be found in sympatry at many localities (Inger, 1983; personal observation). Unfortunately, these conservative taxonomic views have obscured the presence of an entirely endemic and species–rich assemblage of *Draco* species in the Philippine archipelago. Taylor (1922) recognized 11 species of *Draco* in the Philippines, although he questioned the presence of *D. reticulatus* and *D. cornutus*, and came to no conclusions regarding the status of *D. guentheri*. Although Taylor had seen most of the Philippine species of *Draco* in life, later workers with little or no field experience with this fauna synonymized many of these taxa with *Draco volans* and *D. spilopterus*. Hennig (1936) synonymized *D. reticulatus*, *D. guentheri* (as *D. rizali*), and *D. cyanopterus* (as *D. everetti*) with *D. volans* (recognizing all as *D. volans reticulatus*) and synonymized *D. quadrasi* and *D. ornatus* with *D. spilopterus* (recognizing all as *D. spilopterus spilopterus*). Hennig (1936) also reduced *D. bimaculatus* to a subspecies of *D. lineatus* and *D. mindanensis* to a subspecies of *D. fimbriatus*. Thus, Hennig (1936) did not recognize any endemic species of *Draco* in the Philippines. Musters (1983) essentially followed the taxonomy of Hennig (1936), differing only in his recognition of *D. mindanensis* and *D. spilopterus* as full species. Inger (1983) recognized *D. bimaculatus* and *D. mindanensis* as full species, but synonymized all other Philippines taxa with *D. volans*. Alcala (1986), without commenting on the recent taxonomic revisions of Inger (1983) and Musters (1983), recognized most of Taylor's (1922) species including *D. volans*, *D. spilopterus*, *D. everetti*, *D. ornatus*, *D. quadrasi*, and *D. rizali*, but followed Hennig (1936) in treating *D. bimaculatus* as conspecific with *D. lineatus* and *D. mindanensis* as conspecific with *D. fimbriatus*. Ross and Lazell (1990) clarified several of the remaining taxonomic issues, recognizing *D. bimaculatus* and *D. mindanensis* as full species and providing improved diagnoses of *D. everetti* (=*D. cyanopterus*) and *D. ornatus*. Although Alcala (1986) and Ross and Lazell (1990) together resurrected several of the species recognized here, a number of taxonomic issues require further consideration. The purpose of this paper is to provide a revised taxonomy of the Philippine species of *Draco*, as well as diagnoses, keys, and a summary of the known distribution for each species. A currently undescribed species is described herein. Table 1.1 lists the names that have been applied to Philippine *Draco* populations and provides the current status for each.

MATERIALS AND METHODS

Scale counts were obtained from a total of 280 specimens, although several hundred additional specimens were examined with respect to color pattern (Appendix 1). Museum abbreviations follow Leviton et al. (1985). Scale counts, measurements, and color pattern characteristics retained in alcohol were made from preserved specimens, but many color pattern features are based on observations of live animals or photographs of live animals because the relevant colors are lost in preservative. With the exception of *Draco jareckii*, all of the species considered in this paper have been seen in life in the field by the authors. Scale terminology follows Smith (1946) and Lazell (1992) where appropriate. Numbers of "pleurodont teeth" refer only to those of the premaxilla and anterior maxilla, and not to freshly erupted posterior maxillary teeth which are also pleurodont.

The treatment of species in this study essentially conforms to the evolutionary species concept (Frost and Hillis, 1990) in that diagnosable allopatric lineages are recognized as full species. As discussed by Ross and Lazell (1990), several of the species synonymized with *Draco volans* by Hennig (1936), Inger (1983), and Musters (1983) occur in sympatry with no evidence of interbreeding or intergradation and as such are here treated as distinct species. Although scalation or osteology can be used to diagnose most of the species of Philippine *Draco*, all of the species can be readily differentiated on the basis of color pattern, particularly the coloration of the dewlap and patagia. Based on these criteria, the following species are recognized: *Draco bimaculatus*, *D. cyanopterus*, *D. guentheri*, *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. quadrasi*, *D. reticulatus*, and *D. spilopterus*. The taxonomic accounts of previously described species follow the description of the new species alluded to above.

Species Accounts

Draco palawanensis sp. nov.

Draco volans Mocquard, 1890:128.
Draco volans volans Hennig, 1936a:176.
Draco volans sumatranus Musters, 1983:87.

Holotype.—PNM 5770, an adult male, from Barangay Alfonzo 13, Quezon, Palawan Island, Palawan Province, Republic of the Philippines, less than 25 m elevation; collected on 12 June, 1994 by Rafe M. Brown.

Paratypes.—All specimens from Palawan Island, Palawan Province: CAS 28612, 28614 no additional locality data; CAS 28615 about 13 km SW of Iwahig, site 511, about 300 ft. elevation; CAS 28616 about 5 km S Iwahig, site 421b, 100 ft. elevation; CAS 28649 about 7 km WNW Iwahig, site 440, 1000 ft. elevation; CAS 157297–98, 96 km NE Puerto Princesa; CAS 157328 99 km NE Puerto Princesa, Tinitian River, 1–2 km upstream from mouth; CAS 157350 94.5–95.5 km NE Puerto Princesa, E side of coast road in coconut grove; Cincinnati Museum of Natural History (CMNH) 5636-42, PNM 5769–75 Barangay Alfonzo 13, Quezon; TNHC 56707–25 immediate vicinity of the National Museum, Quezon.

Diagnosis.—*Draco palawanensis* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) medium in size (maximum snout-vent length [SVL] of males = 82 mm [n=22], females = 84 mm [n=12]; (2) nostrils oriented laterally on the snout; (3) enlarged, thornlike superciliary scale absent; (4) dorsal scales variable in size, often keeled or rugose; (5) tympana unscaled; (6) six or rarely five ribs supporting patagium; (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle present; (9) in males, dorsal surface of patagium dull orange, with rectangular black blotches covering entire dorsal patagium; black blotches very small (1 mm in diameter) proximally, to large (5–9 mm in diameter) near patagial margin; (10) in females, dorsal surface of patagium dull yellow, with rectangular black blotches covering entire dorsal patagium; black blotches very small (1 mm in diameter) proximally, to large (5–9 mm in diameter) near patagial margin; (11) ventral patagium of males yellow over proximal one–third, dull orange over distal two–thirds, with several large black marginal blotches; (12) ventral patagium of females pale yellow over its entire surface, with several large black marginal blotches; (13) males with triangular, yellow–green dewlap; tissues underlying proximal portion of dewlap bright orange; (14) pale gray dorsal coloration with brown mottling in both sexes; (15) orbital region of males suffused with dark gray pigments.

Draco palawanensis can be distinguished from all other species of *Draco* by its unique patagial color pattern composed of a dull orange (males) or dull yellow (females) dorsal base color, overlain with rectangular black spots that increase in size from 1 mm in diameter proximally to large blotches 5–9 mm in diameter near the patagial margin. *Draco palawanensis* also can be distinguished from all other species of *Draco* on the basis of the unique morphology of its maxilla; the portion of the maxilla that forms the ventral edge of the lacrimal foramen forms a low wall where the lacrimal bone would lie. From *D. bimaculatus*, *D. palawanensis* can be further diagnosed on the basis of the number of ribs supporting the patagium (six versus five), its triangular greenish–yellow dewlap (versus rounded and off–white in males, black and white in females), by the absence (versus presence) of a large black spot at the corner of the mouth enclosing an enlarged white tubercle, and by its larger size (maximum SVL of 84 mm versus 71 mm). From *D. cyanopterus* and *D. reticulatus*, it can be further distinguished by the absence (versus presence) of an enlarged, thornlike superciliary scale, and by its greenish–yellow dewlap (versus reddish–brown with a yellow tip). From *D. jareckii*, *D. quadrasi*, and most populations of *D. spilopterus*, the new species can be further diagnosed by its unscaled (versus scaled over) tympana. From *D. mindanensis*, it can be distinguished on the basis of its greenish–yellow dewlap (versus tangerine–orange), the number of ribs supporting the patagium (six versus five), the absence (versus presence) of a lacrimal bone, its unscaled (versus scaled over) tympana, and in the position of its nostrils (oriented laterally rather than vertically). From *D. ornatus*, it can be further distinguished by its greenish–yellow dewlap (versus vivid chartreuse) and by its unscaled (versus scaled over) tympana. From *D. guentheri*, *D. palawanensis* can be further distinguished by the absence (versus presence) of an enlarged, thornlike superciliary tubercle, its yellow–green dewlap (versus reddish–brown), and by its pale gray dorsal body coloration in males (versus malachite green).

Because *D. palawanensis* has been treated by previous authors as conspecific with *D. volans sumatranus* and *D. cornutus* of the Greater Sunda Shelf (all three were recognized as *D. volans* by Inger, 1983), a proper diagnosis of *D. palawanensis* also requires comparison with these species. *Draco palawanensis* is easily distinguished from *D. cornutus* on the basis of its pale gray dorsal coloration in males (versus malachite green), the absence (versus presence) of an enlarged, thornlike superciliary scale, the absence (versus presence) of an ultramarine wash over the pectoral and ventral abdominal regions in both sexes, its ventral patagial coloration of pale yellow over the proximal one–third, dull orange over the distal two–thirds in males (versus blue–gray), and by its dorsal patagial color pattern; the dorsal patagium in *D. cornutus* males is malachite green over its proximal third, brick red over most of the distal two–thirds, with an ash–gray patch at the anterolateral edge, and an elongate black marginal patch. *Draco palawanensis* can be diagnosed from *D. volans sumatranus* on the basis of its patagial color pattern (the dorsal patagium of *D. volans sumatranus* is covered with round white, pale orange, or pale yellow spots over most of its surface, and over the distal half of patagium, there are extensive black pigments such that the base coloration is black over this portion of the wing). The ventral patagium of *D. volans sumatranus* males is blue–gray with large melanic blotches covering the entire ventral surface, whereas the ventral patagium of *D. palawanensis* males is pale yellow over its proximal one–third and dull orange over its distal two–thirds, with several large black marginal blotches. Furthermore, the morphology of the maxillary bone in *D. palawanensis* is distinctive (see above) and the frontal bone of *D. volans sumatranus* has a crenulated margin that is not present in *D. palawanensis*.

Description of holotype.—Dorsal head scales small to medium–sized, heterogeneous, keeled or rugose; rostral two times wider than high, bordered by six postrostrals; internasals, frontonasals, and prefrontals small except for a series of enlarged, strongly keeled scales arranged in shape of inverted "Y"; the base originating a few scales posterior to rostral, arms contacting supraorbitals; supraoculars granular laterally, grading to much larger size medially; medialmost supraoculars larger than all surrounding cephalic scales except parietals; frontoparietals and parietals slightly larger than scales of snout; interparietal much smaller than surrounding parietals, with opalescent lens; nasals turret–like, pierced centrally by external nares, nares point laterally and slightly dorsally; 3–3 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, except for two enlarged, keeled scales, similar in structure to anterior superciliaries, wider than high, not laterally compressed and thornlike; loreals and lorilabials immediately superior to supralabials relatively large, remaining loreals and lorilabials much smaller, but larger than adjacent palpebrals; an enlarged scale, wider than high, present immediately superior and slightly posterior to posteriormost supralabial; several pre–, sub–, and postoculars enlarged forming continuous subocular series; a series of three large keeled scales extending posteriorly from posterior border of orbit; supralabials 11–11, pentagonal, 1–3 times longer than high, posteriormost supralabial longest; infralabials 10–10, pentagonal or rectangular; tympanum not scaled over; tympanum surrounded by granular scales, a slightly enlarged tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for a tubercle superior to tympanum midway between tympanum and nuchal crest and a larger tubercle posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by four postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets enlarged distally; dewlap scales of males slightly enlarged at distal extremity.

Dorsal body scales small, slightly imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 18 scales in males; lateral nuchal crests composed of 3–4 scales; middorsals approximately two times larger than scales of lower flanks, a discontinuous series of enlarged keeled scales extending from lateral nuchal crests, along base of patagium, to sacral region; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal approximately 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series extending parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, approximately equal in size as largest dorsals; brachials imbricate, variable in size and degree of keeling; prebrachials about equal to largest dorsals in size, strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials weakly keeled, approximately equal to postbrachials in size, smaller than suprabrachials; antebrachials slightly larger than brachials, variably keeled, imbricate; infra–antebrachials smaller than other antebrachials; infracarpals granular, keeled or mucronate, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1–2 keels; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, unkeeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals, keeled; a series of enlarged, flaplike posterior infrafemorals forming conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of lower hind limb; tibials keeled, small proximally and distally, equal to or slightly larger than dorsals in size elsewhere, pretibials largest; infratarsals strongly keeled or mucronate, much smaller than supratarsals, proximal subdigital lamellae with 2–6 keels, distal subdigital lamellae with 1–2 keels, 24–28 fourth toe subdigital lamellae.

Patagia supported by 6 ribs; pleurodont teeth 7; lacrimal bone absent.

Coloration of holotype in preservative.—In preservative, dorsal coloration pale gray with dark brown and black mottling; head with extensive dark brown and black pigments on pale gray base, dorsal head with such extensive dark pigments that head appears dark brown with scattered pale gray flecks; a prominent transverse melanic bar crosses anterior orbital region, a melanic interorbital spot present within the transverse bar; orbital region suffused with dark brown pigments, ciliaries pale gray; the subocular region pale gray, bordered ventrally by horizontally–oriented melanic bar that lies just superior to supralabials; lateral surfaces of neck and dorsal surfaces of throat lappets pale gray, with brown reticulum; dorsal body pale gray with several diffuse, asymmetrical, brown blotches; tail banded with dark brown on pale gray; upper arm gray with dark brown mottling; forearm from elbow to tips of digits gray with dark brown banding; hind limbs gray with dark brown mottling over femoral and proximal portion of shank, from mid–shank to tips of digits banded; dorsal patagium orange–brown with several pale tan or gray longitudinal striations proximally, the entire dorsal surface covered with rectangular, block–like, black spots that are very small proximally (1 mm in diameter), but grade into larger blotches distally, the largest blotch near the patagial margin 9 mm in diameter, the dark blotches tending to follow the pale striations; ventral gular coloration white with fine, pale gray mottling anteriorly, nearly uniform gray posteriorly, entire dewlap appearing gray; ventral throat lappets gray–brown with diffuse white speckling; ventral surface of body and limbs pale gray–white, scattered brown flecks present over lateral pectoral region; ventral surface of tail with brown and pale gray bands over proximal half, with brown and tan bands over distal half; ventral patagium pale gray with 3–2 irregular black marginal blotches.

Variation.—A medium–sized species, maximum observed SVL in males = 82 mm, females = 84 mm; rostral 1–2 times wider than high, bordered by 4–8 postrostrals; internasals, frontonasals, and prefrontals small excepting a series of enlarged, strongly keeled scales arranged in shape of inverted "Y", sometimes scales that form "arms" of "Y" not enlarged leaving an "I" on snout; 2–3 canthals; an enlarged scale, wider than tall sometimes present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars may be enlarged forming continuous or discontinuous subocular series, remaining postoculars small; supralabials 8–14, rectangular, pentagonal, or with anterior border convex and posterior border concave, 1–3 times longer than tall, anteriormost supralabial usually smaller than others, posteriormost supralabial usually longest; infralabials 8–13, pentagonal or occasionally rectangular; 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and 1–

2 larger tubercles posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by 3–6 postmentals; dewlap scales of males slightly enlarged at distal extremity.

Middorsals 2–4 times larger than scales of lower flanks; midvertebral nuchal crest composed of 17–23 scales in males, 2–24 scales in females; lateral nuchal crests present in both sexes; a conspicuously enlarged series of keeled paravertebral scales rarely evident (one of 33); ventral body scales strongly keeled, may be slightly larger, equal in size, or smaller than largest dorsals; proximal subdigital lamellae of manus with 2–4 keels, distal subdigital lamellae of manus with 1–2 keels; proximal subdigital lamellae of pes with 2–4 keels, distal subdigital lamellae of pes with 1–2 keels, 24–30 subdigital lamellae on fourth toe.

Patagia supported by 6–6 ribs in 32 of 33 specimens, one with 5–6 ribs; pleurodont teeth usually 6 (14 of 32) or 7 (17 of 32), one with 8.

Coloration in life.—The dorsal pattern of *Draco palawanensis* is composed of brown, black, and tan pigments on a pale gray base. The dark pigments contrast sharply with the pale gray giving a mottled appearance. The tail is banded with dark brown and pale gray. The limbs are mottled proximally, banded distally. Both sexes have a melanic interorbital spot, but only females have a melanic nuchal spot. The orbital region of males is suffused with dark gray pigments, the ciliaries pale yellow. In females, the orbital region has a series of radiating melanic lines on a pale gray base. The ventral body coloration is white, and pale brown spots may be present over the pectoral region. In males, the gular pattern is composed of brown mottling on a pale tan field, which gives a reticulated appearance; the proximal one–third of the dewlap is grayish–brown, but appears orange during display because the tissues underlying the skin are bright orange; the distal two–thirds of the dewlap is uniform greenish–yellow. In females, the gular coloration is pale tan with faint white spots. The dorsal patagial coloration is similar in males and females. In males, the base coloration of the patagium is dull orange. Proximally, there are several pale tan or gray longitudinal striations. The entire dorsal surface of the patagium is covered with rectangular, block–like, black spots that are very small proximally (approximately 1 mm in diameter), but grade into larger blotches distally such that they are approximately 5–7 mm in diameter near the patagial margin. The dorsal patagium of females is similar to that of males, except that the base coloration is drab yellow rather than dull orange. The ventral patagium of males is yellow over the proximal one–third, dull orange over the distal two–thirds, with several large black marginal blotches. The ventral patagium of females is similar, but the base coloration of the entire ventral surface is pale yellow.

Distribution.—*Draco palawanensis* is known only from Palawan Island (Figure 1.1), but can be expected on larger land bridge islands separated from Palawan by shallow water. Likely candidates include Balabac, Dumaran, Linpacan, Culion, and Busuanga.

Natural History.—Little is known regarding the natural history of *Draco palawanensis*. The species is common on the trunks of coconut trees and *Casurina* trees, both of which represent heavily disturbed habitats. In natural dipterocarp rainforest, the species probably occupies forest edge and possibly forest canopy, as in *D. spilopterus* and *D. volans* (personal observation). During courtship, males first slowly extend the dewlap until the tip is projecting well forward of the snout, the dewlap is then slowly retracted, and finally 2–4 rapid double flicks of the dewlap are performed. During intensive courtship displays, the male also may open one of the patagia and orient its body perpendicular to that of the female. In addition to the movements of the dewlap and patagia, males also incorporate push–up displays, using the forelimbs only.

Etymology.—The specific epithet *palawanensis* refers to the island on which this endemic species occurs.

Comments.—As far as we are aware, every worker who has commented on the taxonomic status of the *Draco palawanensis* populations has considered them conspecific with Bornean *Draco volans* (*Draco volans sumatranus* of some authors). In addition to the morphological characters that distinguish *D. palawanensis* from *D. volans*, ND2 mitochondrial DNA sequence data (unpublished) also indicate that these are independent lineages. Indeed, the sequence data suggest that *D. palawanensis* is more closely related to the Philippine species *D. spilopterus*, *D. quadrasi*, *D. cyanopterus*, *D. reticulatus*, *D. ornatus*, and *D. guentheri*, as well as *D. cornutus* of the Greater Sunda shelf, than it is to *D. volans* (including Bornean populations). Thus, the phylogenetic relationships of *D. palawanensis* preclude us from treating the Palawan population as a synonym of *D. volans* (sensu stricto).

Draco bimaculatus Günther

Draco bimaculatus Günther, 1864:127. Type–locality: "Philippine Islands" (holotype: BM 24.1.g).

Draco lineatus De Witte, 1933:2.

Draco lineatus bimaculatus Hennig, 1936:197; fig. 11c.

Diagnosis.—*Draco bimaculatus* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) small adult size (maximum SVL of males = 70 mm [n=36], females = 71 mm [n=35]); (2) nostrils oriented laterally on the snout; (3) enlarged superciliary tubercle absent; (4) dorsal scales uniform in size and without keeling; (5) tympana unscaled; (6) five ribs supporting patagium; (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle present; (9) dorsal patagial coloration in males a lichenate blend of green, yellow, and dark brown; (10) dorsal patagial coloration in females a lichenate blend of green, yellow, and dark brown; (11) the ventral surface of male patagium blue with extensive black spotting; (12) ventral surface of female patagium yellow with extensive black spotting; (13) males with a small rounded dewlap off–white in coloration; (14) pale brown or tan dorsal body coloration in both sexes, with flecks of green, white, and black scattered throughout; (15) orbital region of males not heavily suffused with dark pigments.

Draco bimaculatus can be distinguished from all other species of *Draco* by the large black postrictal ocellus surrounding an enlarged white tubercle, by the lichenate dorsal patagial pattern found in both sexes, and by the unique dewlap of males (a small rounded dewlap, off–white in coloration) and females (a small rounded dewlap, black and white or black and ultramarine blue, see description below). *Draco bimaculatus* can be further distinguished from *D. cyanopterus*, *D. guentheri*, *D. jareckii*, *D. ornatus*, *D. quadrasi*, *D. reticulatus*, *D. spilopterus*, and *D. palawanensis* on the basis of the number of ribs supporting the patagium (five versus six). *Draco bimaculatus* can be further distinguished from *D. mindanensis* based on the orientation of the nostrils (oriented laterally versus posterodorsally) and in the absence (versus presence) of a lacrimal bone.

Description.—A small species, maximum observed SVL in males = 70 mm, females = 71 mm; dorsal head scales small, heterogeneous, variably keeled or rugose; rostral 1.2–3 times wider than high, bordered by 3–7 postrostrals; internasals, frontonasals, and prefrontals small except for 2–3 larger keeled scales that form lineate ridge down middle of snout parallel to long axis of body; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars larger than all surrounding cephalic scales; frontoparietals and parietals slightly larger than scales of snout; interparietal slightly larger than surrounding parietals, always with opalescent lens; nasals turret–like, pierced centrally by external nares, nares point laterally and slightly dorsally; 3–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, a slightly larger keeled scale sometimes present, no enlarged, thornlike superciliary scale; loreals and lorilabials immediately superior to supralabials relatively large, remaining loreals and lorilabials much smaller, granular, juxtaposed, only slightly larger than adjacent palpebrals; an enlarged scale, usually wider than tall, usually present immediately superior to posteriormost supralabial; a large tubercle occasionally present superior and slightly posterior to corner of mouth; a few pre–, sub–, and postoculars sometimes enlarged forming a discontinuous series, remaining postoculars granular; a series of 2–3 large scales extend posteriorly from posterior border of orbit; supralabials 7–11, pentagonal, 1–3 times longer than tall, anteriormost supralabial usually much smaller than others, posteriormost supralabial usually much longer than others; infralabials 7–11, pentagonal; tympanum unscaled, surrounded by granular scales, a large tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular except for enlarged, white tubercle approximately 3–5 scales posterior to corner of mouth; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and a third, larger tubercle posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by 3–5 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets slightly enlarged distally.

Dorsal body scales small, slightly imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales usually present, comprised of 14–20 scales in males, 0–16 scales in females; a lateral nuchal crest not present in either sex; middorsals approximately equal in size to scales of lower flanks, patches of slightly enlarged scales surrounding 1–3 much larger, keeled scales may be present along flanks near proximal edge of patagia; no conspicuously enlarged series of keeled paravertebral scales present; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series extending parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, approximately equal to dorsals in size; brachials slightly imbricate, variable in size and degree of keeling; prebrachials larger than dorsals, strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials granular, weakly keeled; infrabrachials approximately equal to suprabrachials in size, weakly keeled; antebrachials much larger than brachials, moderately keeled, juxtaposed; infra–antebrachials smaller than other antebrachials; infracarpals granular, keeled or mucronate, proximal subdigital lamellae with 2–3 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, unkeeled; postfemorals granular, strongly keeled, keels directed ventrally rather than distally; infrafemorals approximately equal to ventrals in size, weakly keeled; a series of enlarged, flaplike posterior infrafemorals forms conspicuous fringe along posterior edge of upper hind limb, continues along posterior edge of proximal half of lower hind limb; tibials keeled, granular proximally and distally, 3–4 times larger than dorsals elsewhere, pretibials largest; tarsals strongly keeled, infratarsals granular, proximal subdigital lamellae with 2 keels, distal subdigital lamellae with 1 keel, 22–28 subdigital lamellae on fourth toe.

Patagia usually supported by 5 ribs (14 of 15), occasionally 6 (one of 15); pleurodont teeth 7 (16 of 16); lacrimal bone absent.

Coloration in life.—The coloration of males and females is very similar, although subtle differences exist in the patagial coloration and more extreme differences are present in the coloration of the dewlap and throat lappets. The dorsum is pale brown or tan with flecks of green, white, and black scattered throughout. There are five pairs of enlarged presacral melanic blotches or chevrons that are arranged paravertebrally; the melanic blotches continue postsacrally for a short distance before grading into caudal banding. Smaller melanic spots may be present between the larger blotches. The five enlarged paravertebral blotches may be accompanied by complementary lateral blotches that continue as radially arranged bands on the patagium. The limbs are mottled with tan and brown proximally, with dark brown banding becoming increasingly distinct distally; the manus, pes, and digits with discrete brown bands. A pair of black patches posterior to the parietals may form an indistinct nuchal "loop" that extends from eye to eye. A large melanic interorbital spot is present in both sexes and a nuchal spot is present in females, but absent from males. A large melanic ocellus enclosing a conspicuous white central tubercle is present at the corner of the mouth. The orbits are not suffused with dark pigments. The ventral body coloration is greenish–white and brown spotting may be present over the pectoral region. In females, the coloration of the dewlap and ventral surfaces of the throat lappets is a vivid combination of black and white (usually tinged with ultramarine blue). The dewlap is mostly black, but the leading edge (that portion immediately overlying the second ceratobranchial elements of the hyoid apparatus) is bright white or aqua. There is also a prominent white or aqua crossband that extends between the distal edges of the throat lappets, bisecting the black gular coloration and giving the throat a banded appearance. This crossband is continuous with the white leading edge of the dewlap. An additional white band may also form the anterior border of the black gular area and an indistinct white blotch usually extends posteriorly from the leading edge of the dewlap into the center of the otherwise black dewlap. In males, the underlying pattern of the dewlap and throat lappets is similar to that of females (see below), but most of the coloration is absent, leaving only a pale tan or buffy remnant with scattered, indistinct, black central smudging. The coloration on the dorsal surface of the patagium is a lichenate blend of green and black and may or may not include a yellow component. The patagium is also covered with many white or pale yellow lines or striations that are oriented parallel with the body. The ventral surface of the patagium is covered with large melanic blotches in all *D. bimaculatus*, but the base coloration differs between the sexes. In males, the ventral patagium has a deep blue cast, whereas the ventral patagium is pale yellow in females.

Distribution.—*Draco bimaculatus* is known from the islands of Mindanao, Leyte, Samar, Bohol, Ponson, Basilan, Dinagat, Siargao, Tawitawi, Jolo, Sanga Sanga, and Lapac (Figure 1.2). These islands correspond to the Mindanao and Sulu Archipelago faunal complexes of Heaney (1986).

Natural History.—*Draco bimaculatus* appears to be a species of primary and secondary forest habitats, as well as of coconut groves immediately adjacent to forest habitats. Open coconut plantations far removed from forest (possibly more than just a few hundred meters) appear not to be inhabited by this species. *Draco bimaculatus* occurs in sympatry with *D. ornatus* on Samar, with *D. reticulatus* and *D. ornatus* on Bohol, and with *D. everetti*, *D. guentheri*, and *D. mindanensis* on Mindanao. As appears to be the case with all species of *Draco* in the Philippines, *D. bimaculatus* appears to feed primarily on ants.

Draco cyanopterus Peters

Draco reticulatus var. *cyanopterus*, 1867:15. Type–locality: "Mindanao" (no holotype designated).

Draco everetti Boulenger, 1885:258.

Draco volans reticulatus Hennig, 1936:179.

Draco volans Inger, 1983:8.

Diagnosis.—*Draco cyanopterus* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) moderately large size (maximum SVL of males = 89 mm [n=11], females = 95 mm [n=6]); (2) nostrils oriented laterally on snout; (3) presence of an enlarged, thornlike superciliary scale; (4) dorsal scales variable in size, often with strong keeling; (5) tympanum large, unscaled; (6) six or occasionally seven ribs supporting patagium; (7) lacrimal bone absent; (8) a large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) dorsal patagial coloration of males composed of large pale spots within a thin, dark brown to black reticulum with enlarged, unscaled, chartreuse patches between ribs; (10) dorsal patagial coloration of females with dark reticulum or dark mottling overlying peach to orange pigments proximally, medial portion of each wing mottled with black and either dark green or orange, distal third of patagium with several large black patches separated by gray bars that overlay ribs; (11) ventral surface of the patagium salmon in most males, sometimes yellow, immaculate or with a few small melanic spots proximally or near patagial margin; (12) ventral surface of patagium in females yellow, immaculate or with few small melanic spots proximally or near patagial margin; (13) males with triangular dewlap, reddish brown with white spots proximally, orange–yellow distally; (14) gray, tan, or brown dorsal body coloration in both sexes; (15) males with orbital region heavily suffused with dark pigments.

Draco cyanopterus can be distinguished from all other species of *Draco* on the basis of the unique patagial pattern of males (including large chartreuse blotches between the ribs) and females (the proximal portion of the patagium with a dark reticulum or mottling overlying peach to orange pigments, the medial portion mottled with black and either dark green or orange, and the distal third with several large black patches separated only by gray bars that overlay the ribs). *Draco cyanopterus* can be further distinguished from *D. bimaculatus* and *D. mindanensis* on the basis of the number of ribs supporting the patagium (six versus five). It can be further distinguished from *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. quadrasi*, and some populations of *D. spilopterus* on the basis of its unscaled tympana (versus scaled over). *Draco cyanopterus* can be further distinguished from *D. bimaculatus*, *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. palawanensis*, *D. quadrasi*, and *D. spilopterus* on the basis of its dewlap pattern, which is pale ruddy–brown over the proximal two–thirds and dark yellow over the distal third, the proximal one–third with several distinct white spots. It can be further distinguished from *D. mindanensis* on the basis of the orientation of its nostrils (oriented laterally versus posterodorsally) and the absence (versus presence) of a lacrimal bone. It can be further distinguished from *D. bimaculatus*, *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. palawanensis*, *D. quadrasi*, and *D. spilopterus* based on the presence (versus absence) of an enlarged, thornlike superciliary scale. *Draco cyanopterus* can be further distinguished from *D. guentheri* based on its brown or gray dorsal body coloration in males (versus malachite green).

Description.—A moderately large species, maximum observed SVL in males = 89 mm, females = 95 mm; dorsal head scales small to medium–sized, heterogeneous, variably keeled or rugose; rostral 1–2 times wider than high, bordered by 5–6 postrostrals; internasals, frontonasals, and prefrontals small excepting a series of enlarged, strongly keeled scales arranged in shape of inverted "Y", the base originates a few scales posterior to rostral, arms contacting supraorbitals; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars larger than all surrounding cephalic scales; frontoparietals and parietals slightly to much larger than scales of snout; interparietal slightly smaller than surrounding parietals, occasionally (3 of 11) with opalescent lens; nasals turret–like, pierced centrally by external nares, nares point laterally and slightly dorsally; 3–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, excepting a very large, laterally compressed thornlike superciliary scale, usually taller than wide; loreals and lorilabials immediately superior to supralabials relatively large, remaining loreals and lorilabials much smaller, juxtaposed, only slightly larger than adjacent palpebrals; an enlarged scale, usually wider than tall usually present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars sometimes enlarged forming discontinuous subocular series, remaining postoculars granular; a series of 2–3 large keeled scales extend posteriorly from posterior border of orbit; supralabials 9–12, anterior border convex, posterior border concave, 1–3 times longer than tall, anteriormost supralabial usually much smaller than others, posteriormost supralabial usually longest; infralabials 8–12, pentagonal; tympanum unscaled, surrounded by granular scales, a large tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and 1–3, larger tubercles posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by

3–5 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets enlarged distally; dewlap scales of males enlarged at distal extremity.

Dorsal body scales small, juxtaposed or slightly imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 19–25 scales in males, 5–14 scales in females; lateral nuchal crests present in both sexes; middorsals 2–4 times larger than scales of lower flanks, patches of slightly enlarged scales surrounding 1–3 much larger, keeled scales present along flanks near proximal edge of patagia, part of discontinuous series of enlarged keeled scales extending from lateral nuchal crests, along base of patagium, to sacral region; no conspicuously enlarged series of keeled paravertebral scales present; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal approximately 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series that extend parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, approximately equal to dorsals in size; brachials imbricate, variable in size and degree of keeling; prebrachials about equal to largest dorsals in size, strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials smaller than suprabrachials, weakly keeled; antebrachials slightly larger than brachials, variably keeled, juxtaposed or weakly imbricate; infra–antebrachials smaller than other antebrachials; infracarpals very small, keeled or mucronate, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, unkeeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals in size, weakly keeled; a series of enlarged, flaplike posterior infrafemorals forming conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of proximal half of lower hind limb; tibials keeled, small proximally and distally, equal to dorsals in size elsewhere, pretibials largest; tarsals strongly keeled or mucronate, infratarsals much smaller than supratarsals, proximal subdigital lamellae with 2 keels, distal subdigital lamellae with 1 keel, 26–31 subdigital lamellae on fourth toe.

Patagia supported by 6 ribs (12 of 12); pleurodont teeth usually 7 (6 of 10), sometimes 6 (4 of 10); lacrimal bone absent.

Coloration in life.—The dorsal body and limb coloration of both sexes is usually composed of pale gray, dark gray, tan, and brown mottling such that the overall coloration of the animal may appear gray or tan. Four indistinct dark gray or brown presacral dorsal blotches may be present. The pattern on the side of the neck usually is composed of a brown or gray reticulum surrounding pale gray blotches. The tail, which is encircled with dark brown bands, often has a distinct salmon cast, particularly ventrally where the salmon coloration may be quite vivid. A distinct melanic interorbital spot is present in both sexes, but the nuchal spot is restricted to females. In males, the orbital region (excepting only the ciliaries) is heavily suffused with dark pigments. The dewlap of males is pale ruddy–brown over the proximal two–thirds and dark yellow over the distal third. The proximal one–third of the dewlap includes several distinct white spots, each composed of approximately 10 scales. The ventral coloration in both sexes is white with varying amounts of tan or dark brown mottling or crossbanding over the pectoral region. The ventral surface of the patagium and tail is yellow in females, salmon in males, in both sexes either immaculate or with a few minute, widely scattered black spots. The same color that occurs on the ventral patagium may also be present as a wash down the middle of the chest and abdomen. Although the dorsal body coloration of males and females is similar, the sexes differ substantially in the coloration of the dorsal surface of the patagium. In males, the dorsal patagial pattern is composed of large pale cream spots within a thin, dark brown to black reticulum over the proximal one–third of the patagium, but distally there are 4–6 large patches of naked skin (without scales) that are vivid chartreuse in coloration; the green patches appear ultramarine blue in preserved specimens. In females, the proximal portion of the patagium has a dark reticulum or mottling overlying peach to orange pigments. The medial portion of each wing may be mottled with black and either dark green or orange. The distal third of the patagium has several large black patches separated only by gray bars that overlay the ribs.

Distribution.—*Draco cyanopterus* is known from the islands of Mindanao, Dinagat, and Camiguin Sur (Figure 1.3). These islands are land bridge to one another and form the southern portion of the Mindanao aggregate island complex of Heaney (1986). The northern islands of the Mindanao aggregate island complex are inhabited by *D. reticulatus*, the putative sister taxon of *D. cyanopterus* (McGuire, unpublished data).

Natural History.—*Draco cyanopterus* is a species of relatively open habitats and it seems likely that the species was found primarily along the edges of forest clearings and in relatively open areas in primary and secondary forests before logging of the Philippine forests commenced. Indeed, we have observed this species in just this sort of microhabitat in secondary forest. The species now occurs primarily in open coconut plantation habitats where it is usually the only species of *Draco* encountered. We have observed *D. cyanopterus* in sympatry with *D. guentheri*, *D. bimaculatus*, and *D. mindanensis* on Mindanao. At this locality, *D. cyanopterus* was occupying trees exposed to ample sunlight. As is the case with all species of Philippine *Draco* with which we are familiar, *D. cyanopterus* appears to feed primarily on ants.

Comments.—Peters (1867) did not designate a type 4specimen in his description of *Draco cyanopterus* (as a variety of *D. reticulatus*). Indeed, the description in Peters (1867) is brief, stating only that the new variety was collected by Semper on Mindanao and differs from the type of *D. reticulatus* only in the blue wing patches (in preservative). Nevertheless, given that *D. cyanopterus* is the only species of *Draco* in which preserved specimens have blue fields on the patagium, Peters' (1867) description is sufficient and a neotype need not be designated (ICZN, 1985). If designation of a neotype does become necessary at some future date, specimen ZFMK 20900 is available as this specimen was collected by Semper on Mindanao and was identified by Musters (1983) as being of the "*everetti* form."

Draco guentheri Boulenger

Draco guentheri Boulenger, 1885:257; pl. 20, fig. 2. Type–locality: "Philippine Islands" (holotype: BM 79.4.16.4).

Draco rizali Wandolleck, 1900:15.

Draco volans reticulatus Hennig, 1936:179.

Draco volans Inger, 1983:8.

Diagnosis.—The following diagnosis applies to all of the specimens of *Draco guentheri* that we have examined except for two specimens collected near the Malagos Eagle Station, Davao Province, Mindanao. These two specimens differ from all other specimens examined in a number of key characters and may warrant taxonomic recognition once larger samples are collected and geographic variation is better understood (see comments section below).

Draco guentheri can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) moderately large size (maximum SVL of males = 85 mm [n=8], females = 97 mm [n=9]); (2) nostrils oriented laterally on the snout; (3) enlarged, thornlike superciliary scale present; (4) dorsal scales variable in size, often with strong keeling; (5) presence of large, unscaled tympana; (6) six or occasionally seven ribs supporting patagium; (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) dorsal patagial coloration of males dark green with numerous spots of bluish or yellow–green, outer margin salmon (Taylor, 1922); (10) dorsal patagial coloration of females black, with slight gray wash, enclosing bright reddish to orange spots (Taylor, 1922); (11) in males, ventral surface of patagium salmon or brick red, usually with only one dark spot near outer margin (Taylor, 1922); (12) in females, ventral surface of patagium light yellow, with variable numbers of small dark spots; (13) males with triangular dewlap, bright purple or reddish with bright yellow tip (Taylor, 1922; Gaulke, 1993); (14) malachite green dorsal body coloration in males; females body coloration metallic, iridescent gray (Taylor, 1922b); (15) males with orbital region heavily suffused with dark pigments.

Draco guentheri can be distinguished from all other species of Philippine *Draco* except *D. ornatus* on the basis of the malachite green dorsal body coloration of males. *Draco guentheri* can be distinguished from *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. quadrasi*, and some populations of *D. spilopterus* based on its unscaled (versus scaled over) tympana. It can be further distinguished from *D. bimaculatus*, *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. palawanensis*, *D. quadrasi*, and *D. spilopterus* based on the presence (versus absence) of an enlarged, thornlike superciliary scale. It can be further distinguished from *D. bimaculatus* and *D. mindanensis* based on the number of ribs supporting the patagium (six versus five). It can be further distinguished from *D. mindanensis* based on the orientation of the nostrils (oriented laterally versus posterodorsally) and in the absence (versus presence) of a lacrimal bone.

Description.—A moderately large species, maximum observed SVL in males = 85 mm, females = 97 mm; dorsal head scales small to medium–sized, heterogeneous, variably keeled or rugose; rostral 1–3 times wider than high, bordered by 4–7 postrostrals; internasals, frontonasals, and prefrontals small except for a series of enlarged, strongly keeled scales arranged in shape of inverted "Y", the base originating a few scales posterior to rostral, arms contacting supraorbitals; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars almost as large as parietals; frontoparietals and parietals much larger than scales of snout; interparietal slightly smaller, equal, or slightly larger than surrounding parietals, usually (10 of 16) with opalescent lens; nasals turretlike, pierced centrally by external nares, nares point laterally and slightly dorsally; 3–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular except for usual presence of large, laterally compressed thornlike superciliary scale (see comments below), usually taller than wide; loreals and lorilabials immediately superior to supralabials relatively large, remaining loreals and lorilabials much smaller, juxtaposed, only slightly larger than adjacent palpebrals; an enlarged scale, usually wider than tall usually present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars may be enlarged forming discontinuous subocular series, remaining postoculars granular; a series of 2–3 large keeled scales extending posteriorly from posterior border of orbit; supralabials 7–12, pentagonal or with anterior border convex, posterior border concave, 1–4 times longer than tall, anteriormost supralabial usually much smaller than others, posteriormost supralabial usually longest; infralabials 9–13, pentagonal; tympanum usually unscaled (see comments below), surrounded by granular scales, a large tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and 2–4 tubercles posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone;

mental bordered by 3–5 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets enlarged distally; dewlap scales of males enlarged at distal extremity.

Dorsal body scales small, slightly imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 10–22 scales in males, 5–23 scales in females; lateral nuchal crests present in both sexes; middorsals 2–4 times larger than scales of lower flanks, patches of slightly enlarged scales surrounding 1–3 much larger, keeled scales present along flanks near proximal edge of patagia, part of discontinuous series of enlarged keeled scales extending from lateral nuchal crests, along base of patagium, to sacral region; a conspicuously enlarged series of keeled paravertebral scales rarely evident; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal approximately 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series that extend parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, approximately equal in size or smaller than largest dorsals; brachials imbricate, variable in size and degree of keeling; prebrachials about equal to largest dorsals in size, moderately or strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials weakly keeled, approximately equal to postbrachials in size, much smaller than suprabrachials; antebrachials slightly larger than brachials, variably keeled, juxtaposed or weakly imbricate; infra–antebrachials smaller than other antebrachials; infracarpals granular, keeled or mucronate, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, unkeeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals, keeled; a series of enlarged, flaplike posterior infrafemorals forms conspicuous fringe along posterior edge of upper hind limb, continues along posterior edge of proximal half of lower hind limb; tibials keeled, small proximally and distally, equal to dorsals in size elsewhere, pretibials largest; infratarsals strongly keeled or mucronate, much smaller than supratarsals, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel, 25–31 subdigital lamellae on fourth toe.

Patagia usually supported by 6 ribs (16 of 17), occasionally 7 (2 of 17); pleurodont teeth usually 7 (10 of 16), sometimes 6 (6 of 16); lacrimal bone absent.

Coloration in life.—Because the only live *Draco guentheri* that we have examined were males, the following color description will be more detailed for males than females. A detailed description of the female color pattern is available in Taylor (1922a) and we have included relevant aspects of his description following our description of male coloration. The dorsal coloration of free–living males is vivid malachite green. Unfortunately, this coloration rapidly fades to brown when the animals are handled and our color photographs (and thus our color illustrations) failed to capture the true nature of this coloration. In our sample, the green dorsal coloration of males is mottled with tan, white, and scattered flecks of black. The sides of the head and neck (including the dorsal surfaces of the neck lappets) are vivid green with many small black spots. The tail is banded with dark brown. The limbs are mottled with brown and green overlain with white spots. Forelimb banding is restricted to the fingers and hindlimb banding is present on the toes only. The orbital region is suffused with black pigments, excepting only the ciliaries, which are ultramarine blue. A large interorbital spot is present, but as in most members of the *Draco volans* group, males lack a nuchal spot. The ventral surface of the body and limbs is off–white; the ventral surface of the tail is salmon. The gular coloration is bright light green overlain with a dark green reticulum. The proximal one–fourth of the dewlap is vibrant green with closely set, fine black speckling; the remainder of the dewlap is immaculate green, although the distalmost one–fourth grades to white in some individuals (but see comments section below). The dorsal patagium is green, scattered with large paler green spots. Two or three black marginal blotches are present, separated from one another by green bars that overlay the ribs. One or a few green spots are visible within each black marginal patch where black pigments are lacking. The ventral patagium is buffy or pale green (see comments below), with one to several melanic spots present near the patagial margin. In some individuals, extensive black ventral spotting is present.

Taylor (1922a) described *D. guentheri* (as *D. rizali*) females as follows: dorsal coloration "metallic, iridescent gray, with dim, narrow, blackish reticulations, sometimes forming dim, irregular, brownish bands across back... shoulders with or without a greenish wash." The tail has dark brown bands on a paler brown base color. Taylor noted the presence of melanic interorbital and nuchal spots, dark markings or reticulations on the side of the head, and radiating lines from the eye. The ventral coloration is cream–white with the gular region reticulated with bluish. The dorsal patagium is described as "black, slightly washed with gray, enclosing bright reddish to orange spots" that are lightest nearer to the body and deeper red near the patagial margin. The ventral surface of the patagium is lightly washed with yellow, salmon, or red, with several small black spots near the anterolateral border. In some individuals, small black spots may be scattered over the entire ventral surface of the patagium.

Distribution.—*Draco guentheri* specimens are known from Mindanao, Basilan, Jolo, Siminor, Sanga Sanga, Siasi, and Bongao (Figure 1.4; Taylor, 1922; Gaulke, 1993). Taylor referred to *D. guentheri* (as *D. rizali*) as the common *Draco* of the Sulu Archipelago and it therefore seems likely that the species occurs on other islands within the archipelago, particularly the larger islands such as Tawitawi.

Natural History.—Little is known about the natural history of *Draco guentheri*. We found this species in second growth forest and on coconut trees adjacent to secondary forest near the Malagos Eagle Station, Mindanao. At this site, *D. guentheri* was in sympatry with *D. bimaculatus*, *D. cyanopterus*, and *D. mindanensis*. As Taylor (1918, 1922) indicated that *D. guentheri* is the common species of the Sulu Archipelago, it seems likely that the species occurs in open coconut groves, particularly in regions where *D. cyanopterus* is absent.

Comments.—*Draco guentheri* is known primarily from the Zamboanga region of Mindanao and from the Sulu Archipelago. Taylor (1922) and Gaulke (1993) both based their descriptions (as *D. rizali* and *D. reticulatus*, respectively) on specimens from these regions and most of the specimens that we have examined were collected in these areas. However, we have two male specimens collected near the Malagos eagle station, Davao Province, from the eastern portion of Mindanao. The Malagos specimens differ from the western specimens both in features of their scalation and coloration, but they are clearly closely related to this species. The Malagos specimens both have the tympana covered with small scales, whereas all of our material from Zamboanga, Jolo, and Siminor Islands have large, completely unscaled tympana. The Malagos specimens also lack the enlarged thornlike superciliary scale that is characteristic of all other *D. guentheri* we have examined. Like the Zamboanga and Sulu Archipelago specimens, the Malagos males were vivid malachite green in life which clearly distinguishes them from all other Philippines *Draco*. However, the dewlaps of the Malagos males were bright green and the ventral surfaces of the patagia were pale green, whereas Taylor (1922) and Gaulke (1993) describe the dewlap as bright purple or reddish with a bright yellow tip and the ventral surfaces of the patagia as salmon or brick red. Although we have noted several characteristics that appear to distinguish eastern and western *D. guentheri*, taxonomic adjustment would be premature at this time given that we have seen only two males (and no females) from eastern Mindanao.

Draco jareckii Lazell

Draco jareckii Lazell, 1992:488; fig. 9. Type–locality: "Basco, Batan Island, Batanes Province, Philippines" (holotype: PNM 1797).

Diagnosis.—*Draco jareckii* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics (color descriptions based on Lazell, 1992): (1) medium in size (maximum SVL of males = 90 mm [n=24], females = 90 mm [n=12]); (2) nostrils oriented laterally on snout;

(3) enlarged, thornlike superciliary scale absent; (4) dorsal scales variable in size, with strong keeling; (5) tympanum scaled over; (6) six ribs supporting patagium (*contra* Lazell, 1992); (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) dorsal patagial coloration in males mottled gray and brown with irregular concentric bands; (10) dorsal patagial coloration in females mottled gray and brown with irregular concentric bands; (11) ventral surface of patagium in males with substantial sooty black pigments on a gray base, diffuse yellow or greenish–yellow pigments also present; (12) ventral surface of patagium in females with substantial sooty black pigments on a gray base, diffuse yellow or greenish–yellow pigments also present; (13) males with triangular dewlap, primarily yellow but marbled gray basally, with beige–pink tip; (14) gray–brown dorsal body coloration in both sexes; (15) orbital region of males not heavily suffused with dark pigments.

Draco jareckii can be distinguished from all other species of *Draco* on the basis of its unique dorsal patagial color pattern (see below). *Draco jareckii* can be further distinguished from *D. bimaculatus*, *D. cyanopterus*, *D. guentheri*, *D. palawanensis*, and *D. reticulatus* on the basis of its scaled over (versus unscaled) tympana. It can be further distinguished from *D. bimaculatus* and *D. mindanensis* based on the number of ribs supporting its patagia (six versus five). It can be further distinguished from *D. mindanensis* based on the orientation of its nostrils (oriented laterally versus posterodorsally) and the absence (versus presence) of a lacrimal bone. It can be further distinguished from *D. cyanopterus*, *D. guentheri*, and *D. reticulatus* based on the absence (versus presence) of an enlarged, thornlike superciliary scale. It can be further distinguished from *D. bimaculatus*, *D.*

cyanopterus, *D. guentheri*, *D. mindanensis*, *D. ornatus*, *D. reticulatus*, and some populations of *D. spilopterus* based on the presence of a primarily yellow dewlap in males (versus white, orange, green, or brown).

Description.—A medium–sized species, maximum observed SVL in males = 90 mm, females = 90 mm (Lazell, 1992); dorsal head scales small to medium–sized, heterogeneous, variably keeled or rugose; rostral 2–3 times wider than high, bordered by 4–6 postrostrals; internasals, frontonasals, and prefrontals small excepting a series of enlarged, strongly keeled scales arranged in shape of inverted "Y", the base originates a few scales posterior to rostral, arms contact supraorbitals; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars larger than all surrounding cephalic scales; frontoparietals and parietals equal in size or slightly larger than scales of snout; interparietal slightly larger than surrounding parietals, always with opalescent lens; nasals turret–like, pierced centrally by external nares, nares point laterally and slightly dorsally; 3–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, excepting 1–2 enlarged, keeled scales, similar in structure to anterior superciliaries, wider than high, not laterally compressed and thornlike; loreals and lorilabials immediately superior to supralabials relatively large, remaining loreals and lorilabials much smaller, but substantially larger than adjacent palpebrals; an enlarged scale, wider than tall usually present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars sometimes enlarged forming continuous or discontinuous subocular series, remaining postoculars small; a series of 3–4 large keeled scales extending posteriorly from posterior border of orbit; supralabials 8–12, anterior border convex, posterior border concave, 1–3 times longer than tall, anteriormost supralabial usually smaller than others, posteriormost supralabial usually longest; infralabials 8–11, pentagonal or rectangular; tympanum covered with scales, 1–2 enlarged scales present centrally; tympanum surrounded by granular scales, a large tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and one, larger tubercle posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by 3–5 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets much enlarged distally; dewlap scales of males enlarged at distal extremity.

Dorsal body scales imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 17–25 scales in males, 17–18 scales in females; lateral nuchal crests present in both sexes; middorsals 2–4 times larger than scales of lower flanks, a discontinuous series of much enlarged, keeled scales present along flanks near proximal edge of patagia extending from lateral nuchal crests, along base of patagium, to sacral region; conspicuously enlarged series of keeled paravertebral scales present; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series that extend parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, slightly smaller than dorsals in size; brachials imbricate, variable in size and degree of keeling; prebrachials about equal to largest dorsals in size, strongly keeled, grading smoothly into slightly smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials weakly keeled, approximately equal to postbrachials in size, much smaller than suprabrachials; antebrachials slightly larger than brachials, variably keeled, juxtaposed or weakly imbricate; infra–antebrachials smaller than other antebrachials; infracarpals very small, keeled or mucronate, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, unkeeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals in size, keeled; a series of enlarged, flaplike posterior infrafemorals forms conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of proximal half of lower hind limb; tibials keeled, smallest proximally and distally, equal to dorsals in size elsewhere, pretibials largest; tarsals strongly keeled or mucronate, infratarsals much smaller than supratarsals, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel, 27–33 subdigital lamellae on fourth toe.

Patagia supported by 6 ribs (eight of eight); pleurodont teeth usually 7 (five of eight), sometimes 6 (three of eight); lacrimal bone absent.

Coloration in life.—Detailed descriptions of the color pattern of *Draco jareckii* in life were provided by Lazell (1992). Lazell (1992) described the dorsal body coloration of the holotype (male) as "dull fawn brown on the head and anterior trunk...broken by sooty to slate–gray brown tones, especially posteriorly. On mid–trunk and tail, brown gives way to shades of lead to ashy gray with a greenish tint posteriorly. Laterally the head was patterned in ash–gray and warm brown, shading to yellowish on the upper eyelid." The dewlap was described as "lemon yellow with a beige–pink tip and gray marbling basally" and the ventral surfaces of the throat lappets were described as "pale yellowish–gray with dark gray mottling." The dorsal patagial coloration was "mottled in shades of ash to slate–gray, with brown tones postero–basally, in irregularly concentric zones" and the ventral patagial coloration was said to be similar to that of the dorsal patagium, "but of a more contrasting ash and soot" in a "roughly concentric pattern". A yellow suffusion was evident between the posterior ribs.

Lazell (1992) described the female color pattern as darker than that of males with more gray and less brown tones. Females tended to show more "golden–yellow tints" on the head, trunk, and limbs. The much smaller dewlap was described as "pale yellow with sooty spots" and the ventral surfaces of the throat lappets were yellow. The dorsal patagial coloration was also described as darker than that of males and of a different pattern. In females, "a slatey to sooty intercostate pattern contained bold, near–white and gray–greenish blotches. There were prominent light, ash to lead gray radials" and a "brown tinge postero–basally." The ventral patagia of females was described as "more boldly marked than in males, approaching black and white with a considerable yellow or yellowish–green postero–basal wash."

Distribution.—*Draco jareckii* is known only from Batan Island, although other islands in the immediate vicinity, including two (Sabtang and Ibuhos) that are part of the same island bank, have not been surveyed (Figure 1.5).

Natural History.—Virtually nothing is published on the natural history of *Draco jareckii*. Lazell (1992) noted that the species occurs both in forest and in relatively denuded areas with sparse trees and tends to perch head downward (very unusual for *Draco*) on the trunks of these trees at a height of 1.5 to 6 meters.

Draco mindanensis Stejneger

Draco mindanensis Stejneger, 1908:677. Type–locality: "Datu Anib's place, near Catagan, northwest Mindanao, at base of Malindang Mountain, 1100 ft." (holotype: USNM 37388).

Draco fimbriatus mindanensis Hennig, 1936:203; fig. 10k.

Diagnosis.—*Draco mindanensis* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) large size (maximum SVL of males = 104.5 mm [n=9], females = 105.0 mm [n=6]); (2) posterodorsally oriented nostrils within turret–like nasal scales; (3) enlarged superciliary tubercle absent; (4) dorsal scales uniform in size and without keeling; (5) scaled over tympana; (6) 5 ribs supporting patagium; (7) lacrimal bone present; (8) large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) dorsal patagial coloration of males vivid red with small, scattered, white or pale red spots; (10) the dorsal patagial coloration of females black with conspicuous white spots over outer two–thirds and pale striations present over proximal one–third (Taylor, 1922b); (11) ventral patagial coloration of males red, with no black spots or blotches present; (12) ventral patagial coloration of females dusky, with no black spots or blotches present (Taylor, 1922b); (13) presence in males of a large attenuated dewlap, vivid tangerine orange in coloration, with same color present over entire ventral surfaces of throat lappets; (14) dorsal body coloration of males pale brown with slight greenish cast; (15) orbital region of males without melanic pigments.

Draco mindanensis can be distinguished from all other species of *Draco* by its red patagial coloration and vivid orange dewlap and ventral throat lappets in males. *Draco mindanensis* can be further distinguished from all other species of *Draco* occurring in the Philippines based on the orientation of its nostrils (oriented posterodorsally versus laterally) and in the presence (versus absence) of a lacrimal bone. *Draco mindanensis* can be further distinguished from all other species in the Philippines except *D. bimaculatus* based on the number of ribs supporting its patagium (five versus six).

Description.—A large species, maximum observed SVL in males = 104.5 mm, females = 105.0 mm; dorsal head scales small, homogeneous, variably keeled or rugose; rostral 1.8–4 times wider than high, bordered by 7–11 postrostrals; internasals, frontonasals, and prefrontals very small excepting a series of enlarged, strongly keeled scales arranged in the shape of an inverted "Y", the base originating several scales posterior to rostral, arms contact supraorbitals; in some the arms of "Y" not enlarged such that keeled scales of snout in shape of an "I"; supraoculars granular laterally, grading to slightly larger size medially, medialmost supraoculars only slightly larger than scales of snout; frontoparietals and parietals equal in size to much larger than scales of snout; interparietal larger than surrounding parietals, always with opalescent lens; nasals turret–like, pierced centrally by external nares, nares point dorsally and slightly posteriorly; 2–3 canthals, strongly keeled, separated from nasals by granular scales; anterior superciliaries elongate, keeled; posterior superciliaries granular, 1–2 slightly larger keeled scales sometimes present, no enlarged, thornlike superciliary tubercle; loreals and lorilabials granular, juxtaposed, only slightly larger than adjacent palpebrals, those immediately superior to supralabials only slightly enlarged; an enlarged scale usually not present immediately superior to posteriormost supralabial; in some individuals, an enlarged scale present superior and slightly posterior to corner of mouth; in some, 1–3 pre–, sub–, and postoculars enlarged forming a discontinuous series, remaining postoculars granular; in some, 1–3 moderately enlarged scales present posterior to orbit; supralabials 11–15, pentagonal, 1–2 times longer than tall, anteriormost supralabial not smaller than others, posteriormost supralabial not longer than others; infralabials 12–16, pentagonal; tympanum covered with small scales, an enlarged tubercle variably present anterior to tympanum; scattered enlarged tubercles sometimes present from corner of mouth posterior along side of neck and on dorsal surfaces of throat lappets; temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest; no enlarged tubercle present posterior and slightly superior to tympanum near the posterior border of quadrate bone; mental bordered by 4–6 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets slightly enlarged distally, scales of distal terminus of dewlap not enlarged.

Dorsal body scales small, homogeneous in shape, slightly imbricate, keeled; a distensible midvertebral nuchal fold present, but a crest composed of laterally compressed dorsal scales not present; lateral nuchal crests not present in either sex; middorsals 1–2 times larger than scales of lower flanks; series of greatly enlarged keeled scales extending from nape to sacral region along proximal edge of patagium composed of only 4–8 widely separated scales; no conspicuously enlarged series of keeled paravertebral scales present; caudals keeled; paired, enlarged middorsal caudals extending length of tail; paired, greatly enlarged subcaudals extending length of tail; over proximal 10% of tail, lateral caudals strongly keeled, forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series that extend parallel to axis of body; ventral patagium with flat, variably keeled, delicate scales; ventral body scales strongly keeled, larger than dorsals; brachials slightly imbricate, variable in size and degree of keeling; prebrachials larger than dorsals, strongly keeled, grading smoothly into smaller keeled suprabrachials, suprabrachials larger than dorsals; postbrachials small, weakly keeled or unkeeled; infrabrachials relatively large, larger than suprabrachials in some, unkeeled; antebrachials slightly larger than brachials, keeled, weakly imbricate; infra–antebrachials as large as supra–antebrachials; infracarpals granular, mucronate, proximal subdigital lamellae with 1–3 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, mucronate; postfemorals small, weakly keeled, keels directed ventrally rather than distally; infrafemorals much smaller than ventrals, unkeeled; a series of enlarged, flaplike posterior infrafemorals forming conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of proximal half of lower hind limb; tibials keeled, granular proximally, small distally, 1–2 times larger than dorsals elsewhere, pretibials largest; tarsals weakly keeled or mucronate, infratarsals granular, proximal and distal subdigital lamellae with 1 keel, 27–32 fourth toe subdigital lamellae.

Patagia usually supported by 5 ribs (14 of 15), occasionally 6 (1 of 15) or 4 (1 of 15 specimens with 5–4 ribs); pleurodont teeth 5–7 (2 of 12 specimens with 5; 4 of 12 specimens with 6; 6 of 12 specimens with 7); lacrimal bone present.

Coloration in life.—The only live specimens of *Draco mindanensis* seen by the authors were males and the following description by necessity applies primarily to this sex. The coloration of females has been briefly discussed in the literature (Taylor, 1922b), and color differences between males and females discussed therein will be incorporated into the following description. In males, the dorsal color is pale brown with a slight greenish cast; pale or dark brown spots or mottling is variably present. The tail and limbs have distinct brown banding; the bands on the limbs each may enclose a pale central band. Conspicuous white or pale spots are present on the sides of the neck and in the dark gray suffusion overlying the anterior gular region; the white spots may extend in a band across the nape immediately posterior to the parietals as well. Interorbital and nuchal spots are not present. The dewlap and ventral surfaces of the throat lappets of males are vivid tangerine orange. In females, the tip of the small dewlap is cream yellow, and the throat and the ventral surfaces of the lappets pale greenish yellow with scattered white spots (Taylor, 1922a). In males, the dorsal surface of the patagium is bright red with obscure, slightly paler red spots evident over the outer two–thirds and pale tan striations arranged parallel to the body present over the proximal one–third. In females, the patagium is black with conspicuous white spots over the outer two–thirds and pale striations present over the proximal one–third. The ventral surface of the patagium is red in males, dusky in females, with no black spots or blotches present in either sex.

Distribution.—*Draco mindanensis* is known from Mindanao, Dinagat, Leyte, and Samar islands (Figure 1.6), although it should be expected on Bohol if sufficient primary forest habitat remains on this island.

Natural History.—More so than any other species of *Draco* in the Philippines, *D. mindanensis* appears to be restricted to primary and possibly mature second growth forest. This species apparently cannot be found in coconut groves adjacent to forest and appeared to be absent from mature second growth forest on Bohol (the species is not known from this island, but is expected in primary forest habitats). In South Cotobato, Mindanao, *Draco mindanensis* was found only on the largest dipterocarp trees in primary forest, usually at great height (R. M. Brown, pers. comm.). Near Mt. Apo on Mindanao, *D. mindanensis* was found in sympatry with *D. bimaculatus*, *D. cyanopterus*, and *D. guentheri*.

Comments.—Given that *Draco mindanensis* appears to be dependent on primary or mature second growth forest habitats that are exceedingly rare in the Philippines, this may be the most seriously endangered species of *Draco*. Even when these habitats were common on Mindanao, these lizards were evidently difficult to find. Edward H. Taylor spent a considerable amount of time collecting on Mindanao, but had collected only two specimens at the time that he wrote Taylor (1922a).

Draco ornatus Gray

Dracunculus ornatus Gray, 1845:235. Type–locality: Philippines (lectotype [Musters, 1983]: BM 1946.8.27.30).

Draco ornatus Günther, 1864:124.

Draco spilopterus spilopterus Hennig, 1936:185.

Draco spilopterus Musters, 1983:72.

Draco volans Inger, 1983:8.

Diagnosis.—*Draco ornatus* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) medium in size (maximum SVL of males = 78.0 mm [n=11], females = 86.5 mm [n=18]); (2) nostrils oriented laterally on the snout; (3) enlarged, thornlike superciliary scale absent; (4) dorsal scales variable in size, often keeled or rugose; (5) tympana scaled over; (6) six or occasionally seven ribs supporting patagium; (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) dorsal patagial coloration of males uniform tan or gray, or the anterior half may be dull yellow–brown and the posterior half dull orange; entire dorsal surface overlain with scattered small brown spots and outer margin with large black or sooty patch enclosing several white spots; pattern similar to that of females, but much duller; (10) dorsal patagial coloration of females pale greenish proximally, grading into bright orange anterodistally and bright red posterodistally; entire dorsal surface covered with wavy black bars forming loosely arranged outwardly radiating bands; outer margin with a large black or sooty patch enclosing several crisp white spots; (11) in males, ventral surface of patagium covered with pale yellow or orange wash, with large black outer wing patch enclosing white spots (similar to patch present on dorsal surface of wing); (12) in females, ventral surface of patagium covered with pale yellow or orange wash, with large black outer wing patch enclosing white spots (similar to patch present on dorsal surface of wing); (13) males with triangular dewlap, brown overlain with white reticulum proximally, vivid chartreuse distally; (14) pale green and brown dorsal coloration in both sexes; (15) orbital region of males with radiating melanic bars or suffused with dark pigments.

Draco ornatus can be distinguished from all other species of *Draco* on the basis of the unique patagial color patterns of males and females (see descriptions below). The species can be further distinguished from all other species of *Draco* (with the possible exception of *D. guentheri*) based on the vivid chartreuse dewlap of males. This species can be further distinguished from *D. bimaculatus*, *D. cyanopterus*, *D. guentheri*, *D. palawanensis*, *D. reticulatus*, and some populations of *D. spilopterus* based on its scaled over (versus unscaled) tympana. This species can be further distinguished from *D. cyanopterus*, *D. guentheri*, and *D. reticulatus* based on the absence (versus presence) of an enlarged, thornlike superciliary scale. It can be further distinguished from *D. bimaculatus* and *D. mindanensis* based on the number of ribs supporting its patagia (six versus five). It can be further distinguished from *D. mindanensis* based on the orientation of its nostril (oriented laterally versus posterodorsally) and in the absence (versus presence) of a lacrimal bone.

Description.—A medium–sized species, maximum observed SVL in males = 78.0 mm, females = 86.5 mm; dorsal head scales small to medium–sized, heterogeneous, variably keeled or rugose; rostral 1–2.5 times wider than high, bordered by 3–6 postrostrals; internasals, frontonasals, and prefrontals small excepting a series of enlarged, strongly keeled scales arranged in shape of inverted "Y", the base originates a few scales posterior to rostral, arms contact supraorbitals; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars larger than all surrounding cephalic scales; frontoparietals and parietals substantially larger than scales of snout; interparietal may be smaller or larger than surrounding parietals, always with opalescent lens; nasals turret–like, pierced centrally by external nares, nares point laterally and slightly dorsally; 3–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, excepting 1–2 enlarged, keeled scales, similar in structure to anterior superciliaries, wider than high, not laterally compressed and thornlike; loreals and lorilabials immediately superior to supralabials relatively large, approximately 1/4 size of supralabials, remaining loreals and lorilabials much smaller, only slightly larger than adjacent palpebrals; 1–2 enlarged scales usually present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars may be enlarged forming discontinuous subocular series, remaining postoculars small; a series of 3–4 large keeled scales extending posteriorly from posterior border of orbit; supralabials 8–11, usually pentagonal or rectangular, but anterior border may be convex and posterior border may be concave, 1–3 times longer than tall, anteriormost supralabial usually smaller than others, posteriormost supralabial usually longest; infralabials 8–11, pentagonal or rectangular; tympanum covered with small scales; tympanum surrounded by granular scales, a large tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and one, larger tubercle posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by 2–5 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets much enlarged distally; dewlap scales of males enlarged at distal extremity.

Dorsal body scales imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 20–25 scales in males, 9–25 scales in females; lateral nuchal crests present in both sexes; middorsals 2–3 times larger than scales of lower flanks, a discontinuous series of much enlarged, keeled scales present along flanks near proximal edge of patagia extending from lateral nuchal crests, along base of patagium, to sacral region; conspicuously enlarged series of keeled paravertebral scales sometimes evident; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal approximately 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series that extend parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, equal to dorsals in size; brachials imbricate, variable in size and degree of keeling; prebrachials approximately twice the size of largest dorsals, strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials weakly keeled, larger than postbrachials, slightly smaller than suprabrachials; antebrachials slightly larger than brachials, variably keeled, juxtaposed or weakly imbricate; infra–antebrachials smaller than other antebrachials; infracarpals granular, keeled or mucronate, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, keeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals in size, keeled; a series of enlarged, flaplike posterior infrafemorals forming conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of proximal half of lower hind limb; tibials keeled, smallest proximally and distally, equal in size or slightly larger than dorsals elsewhere, pretibials largest; tarsals strongly keeled or mucronate, infratarsals much smaller than supratarsals, proximal subdigital lamellae with 1–2 keels, distal subdigital lamellae with 1 keel, 25–33 subdigital lamellae on fourth toe.

Patagia usually supported by 6 ribs (21 of 23), occasionally 7 (3 of 23); pleurodont teeth usually 6 (20 of 23), occasionally 7 (3 of 24); lacrimal bone absent.

Coloration in life.—The dorsal coloration of both sexes is a complex blend of green, brown, tan, black, and white pigments that together produce a lichenate pattern. The general color of the animal usually appears pale green and brown. Dark brown dorsal cross–bands with white anterior and posterior borders are sometimes evident. The tail is ringed with alternating dark brown and white to pale tan bands. The limbs are banded with dark brown, the bands becoming more distinct distally. In both sexes, there is a pale brown or pale gray, hourglass–shaped blotch on the dorsal surface of the head in the supraorbital region. The anterior border of the blotch is outlined in black and at the center of the black bar is a wedge–shaped, melanic interorbital spot. Females also have nuchal and postnuchal melanic spots. In both sexes, black lines radiate outward from the eye; in males, these lines may coalesce such that the orbital regions are suffused with dark pigments as in some other species of *Draco*. In both sexes, the ventral body coloration is white, with a lime–green wash present on the pectoral region. Scattered small brown spots usually are present on the pectoral and abdominal surfaces, but there is substantial individual variation in their intensity. The vent and ventral surface of the tail may be pale orange in males, pale brown in females. The mandibular and gular region either is white with small dark brown or black spots or brown with white spots (the brown component may be extensive, such that the pattern appears as white spots on a brown field). In males, the dark spots gradually expand along the base of the dewlap such that the pattern appears as a white reticulum on a brown base. The brown spots are largest at the base of the dewlap, grading smoothly into smaller spots before they disappear about half way down the dewlap. About one–third of the way down the dewlap, chartreuse pigments appear and this color intensifies distally such that the lower one–half to one–third of the dewlap is vivid chartreuse. In females, the same vivid chartreuse coloration is present on the small taglike dewlap. In both sexes, the ventral surfaces of the throat lappets are white with closely set, small, black or dark brown spots. The coloration of the dorsal surface of the patagium differs between the sexes. In males, the base color of the patagium may be uniform tan or gray, or the anterior half may be dull yellow–brown and the posterior half dull orange. The entire dorsal surface of the patagium is overlain with scattered brown spots similar to those present in male *D. spilopterus*. There is a large black patch encompassing nearly the entire distal third of each wing and this patch encloses several crisp, white spots. In females, the coloration on the dorsal surface of the patagium is much more vivid. The patagium is pale greenish proximally, but grades into bright orange anterodistally and bright red posterodistally. The entire dorsal surface is covered with wavy black bars that form loosely arranged outwardly radiating bands. As in males, there is a large black outer wing patch enclosing crisp white spots. In both sexes, the ventral surface of the patagium is covered with a pale yellow or orange wash. The ventral surface supports a large black outer wing patch enclosing white spots (similar to the patch that is present on the dorsal surface of the wing). The ventral patch is a distinct element and clearly is not the dorsal patch showing through the patagium. Aside from the black patch near the outer margin, the ventral patagium in both sexes is either devoid of black pigments or supports a few small black spots near its proximal edge.

Distribution.—*Draco ornatus* is known from the islands of Mindanao, Leyte, Samar, Bohol, and Dinagat (Figure 1.7). Statements in the literature suggesting that *D. ornatus* can be found on Luzon and Negros (Boulenger, 1885; Taylor, 1922) are almost certainly incorrect.

Natural History.—Like *Draco bimaculatus*, *D. ornatus* appears to be a species of primary and secondary forest habitats, as well as coconut groves immediately adjacent to forest. Open coconut plantations far removed from forest (possibly more than just a few hundred meters) appear not to be inhabited by this species. We have found *D. ornatus* in sympatry with *D. bimaculatus* on Samar and in sympatry with *D. reticulatus* and *D. bimaculatus* on Bohol. *Draco ornatus* appears to feed primarily on ants.

Draco quadrasi Boettger

Draco quadrasi Boettger, 1893:41. Type–locality: Sibuyan Island, Philippines
(syntypes: BM 1946.8.26.83-86).
Draco spilopterus spilopterus Hennig, 1936:185.
Draco spilopterus Musters, 1983:72.
Draco volans Inger, 1983:8.

Diagnosis.—*Draco quadrasi* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) medium in size (maximum SVL of males = 81.0 mm [n=11], females = 86.5 mm [n=7]); (2) nostrils oriented laterally on the snout; (3) enlarged, thornlike superciliary scale absent; (4) dorsal scales variable in size, often keeled or rugose; (5) tympana scaled over; (6) six or occasionally seven ribs supporting patagium; (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) in males, dorsal surface of patagium orange–yellow, devoid of brown spots, with sooty gray patch along outer margin; (10) in females, patagium mottled with tan and dark brown proximally, grading to yellow and black distally; dark pigments much more extensive than light pigments yielding a generally dark wing; (11) ventral surface of patagium of males uniform yellow with sooty outer margin; (12) ventral surface of patagium in females uniform yellow with sooty outer margin; (13) males with triangular, lemon yellow dewlap; (14) pale brown dorsal coloration in both sexes; (15) orbital region of males heavily suffused with dark pigments.

Draco quadrasi can be distinguished from all other species of *Draco* by its unique uniform yellow dorsal patagial coloration in adult males. *Draco quadrasi* can be further distinguished from *D. bimaculatus*, *D. cyanopterus*, *D. guentheri*, *D. reticulatus*, *D. palawanensis*, and some populations of *D. spilopterus* on the basis of its scaled over (versus unscaled) tympana. It can be further distinguished from *D. bimaculatus*, *D. cyanopterus*, *D. guentheri*, *D. mindanensis*, *D. ornatus*, *D. reticulatus*, and some populations of *D. spilopterus* on the basis of the yellow dewlap present in males (versus white, brown, green, or orange). It can be further distinguished from *D. cyanopterus*, *D. guentheri*, and *D. reticulatus* based on the absence of a an enlarged, thornlike superciliary scale. It can be further distinguished from *D. bimaculatus* and *D. mindanensis* based on the number of ribs supporting its patagia (six versus five). It can be further distinguished from *D. mindanensis* based on the orientation of its nostrils (oriented laterally versus posterodorsally) and the absence (versus presence) of a lacrimal bone.

Description.—A medium–sized species, maximum observed SVL in males = 81.0 mm, females = 86.5 mm; dorsal head scales small to medium–sized, heterogeneous, variably keeled or rugose; rostral 1–2 times wider than high, bordered by 3–7 postrostrals; internasals, frontonasals, and prefrontals small except for a series of enlarged, strongly keeled scales usually arranged in shape of inverted

"Y", base originating a few scales posterior to rostral, arms contacting supraorbitals; occasionally arms of "Y" incomplete with remaining scales forming "I" on snout; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars larger than all surrounding cephalic scales; frontoparietals and parietals substantially larger than scales of snout; interparietal may be smaller or larger than surrounding parietals, always with opalescent lens; nasals turret–like, pierced centrally by external nares, nares pointing laterally and slightly dorsally; 2–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, excepting 1–2 enlarged, keeled scales, similar in structure to anterior superciliaries, wider than high, not laterally compressed and thornlike; loreals and lorilabials immediately superior to supralabials relatively large, approximately 1/2 to 1/4 size of supralabials, remaining loreals and lorilabials much smaller, only slightly larger than adjacent palpebrals; 1–2 enlarged scales usually present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars may be enlarged forming discontinuous subocular series; remaining postoculars small; a series of 1–3 large keeled scales extend posteriorly from posterior border of orbit; supralabials 7–12, usually pentagonal or rectangular, but anterior border may be convex and posterior border may be concave, 1–3 times longer than tall, anteriormost supralabial usually smaller than others, posteriormost supralabial usually longest; infralabials 8–13, pentagonal or rectangular; tympanum covered with small scales; tympanum scaled over, 1–2 large tubercles present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and 1–2 tubercle posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by 4–6 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets much enlarged distally; dewlap scales of males enlarged at distal extremity.

Dorsal body scales imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 21–33 scales in males, 15–24 scales in females; lateral nuchal crests present in both sexes; middorsals 2–4 times larger than scales of lower flanks, a discontinuous series of much enlarged, keeled scales present along flanks near proximal edge of patagia extending from lateral nuchal crests, along base of patagium, to sacral region; conspicuously enlarged series of keeled paravertebral scales sometimes evident; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series extending parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, smaller than largest dorsals; brachials imbricate, variable in size and degree of keeling; prebrachials larger than largest dorsals, strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials weakly keeled, larger than postbrachials, slightly smaller than suprabrachials; antebrachials slightly larger than brachials, variably keeled, weakly imbricate; infra–antebrachials smaller than other antebrachials; infracarpals granular, keeled or mucronate, proximal subdigital lamellae with 2–5 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals equal in size or slightly larger than dorsals, strongly keeled; posterior suprafemorals granular, keeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals in size, keeled; a series of enlarged, flaplike posterior infrafemorals forming conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of proximal half of lower hind limb; tibials keeled, smallest proximally and distally, equal in size or slightly larger than dorsals elsewhere, pretibials largest; tarsals strongly keeled or mucronate, infratarsals much smaller than supratarsals, proximal subdigital lamellae with 2–5 keels, distal subdigital lamellae with 1 keel, 24–31 subdigital lamellae on fourth toe.

Patagia usually supported by 6 ribs (15 of 16), occasionally 7 (1 of 16); pleurodont teeth 6 (4 of 9) or 7 (5 of 9); lacrimal bone absent.

Coloration in life.—The dorsal pattern of *Draco quadrasi* is a lichenate blend usually including brown, tan, and pale green components. The tail is banded with dark brown and pale tan, although there is individual variation in the intensity of the bands. The limbs are mottled proximally, banded distally. Neither a melanic interorbital spot nor a nuchal spot is present in either sex. The orbital region of males is heavily suffused with dark brown or black pigments. The ventral body coloration is pale greenish white. In males, the gular pattern is composed of tan mottling on a pale green field, shading to pale blue–green posteriorly. The dewlap is lemon–yellow, although its base is tan anteriorly and bluish–green posteriorly. The ventral surfaces of the throat lappets are brown with white mottling. In females, the gular base color is ivory with a faint brown reticulum anteriorly, greenish white with fine black speckling posteriorly; the black speckling of the gular region is more extensive on the small dewlap such that the dewlap appears nearly uniform gray. The posterior gular pattern extends onto the ventral surfaces of the throat lappets. The dorsal patagial coloration of males is deep orange–yellow with faint, tan striations running parallel with the body. A large black and brown patch enclosing a few minute tan spots is present near the outer margin of the wing. The pattern on the ventral surface of the patagium of males is similar to the dorsal pattern in that it is yellow with a sooty gray outer blotch. In females, the dorsal patagial coloration is very different from that of males. The patagium is mottled with tan and dark brown proximally, grading to yellow and black distally. The dark pigments are much more extensive than the light pigments giving the wing a generally dark appearance. As in males, the ventral surface of the patagium is uniform yellow with a sooty outer margin.

Distribution.—*Draco quadrasi* occurs on the islands of Sibuyan, Mindoro, Romblon and Semirara (Figure 1.8). Only two *Draco* specimens from the island of Tablas were examined and this species could not be distinguished with confidence from *D. spilopterus*. On biogeographic grounds, the Tablas population would be expected to be *D. quadrasi* or a closely related endemic species. The proper designation of this population must await additional collecting.

Natural History.—*Draco quadrasi* appears to have the same habitat requirements as *D. spilopterus* and is abundant in open coconut groves on Mindoro.

Draco reticulatus Günther

Draco reticulatus Günther, 1864:125. Type–locality: "Philippine Islands" (holotype: BM 1946.8.27.28).

Draco volans reticulatus Hennig, 1936:179.

Draco volans Inger, 1983:8.

Diagnosis.—*Draco reticulatus* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) moderately large in size (maximum SVL of males = 90 mm [n=20], females = 91 mm [n=6]); (2) nostrils oriented laterally on the snout; (3) enlarged, thornlike superciliary scale present; (4) dorsal scales variable in size, often with strong keeling; (5) tympana unscaled; (6) six or occasionally seven ribs supporting patagium; (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) dorsal patagial coloration of males composed of large pale spots within thin, dark brown to black reticulum, without enlarged, unscaled, chartreuse patches between ribs; (10) dorsal patagial coloration of males composed of large pale spots within thin, dark brown to black reticulum; (11) ventral surface of patagium salmon in most males, occasionally yellow, immaculate or with few small melanic spots near patagial margin; (12) ventral surface of patagium yellow in females, immaculate or with few small melanic spots near patagial margin; (13) males with triangular dewlap, reddish brown with white spots proximally, orange–yellow distally; (14) gray, tan, or brown dorsal body coloration in both sexes; (15) males with orbital region heavily suffused with dark pigments.

Draco reticulatus can be distinguished from all other species of *Draco* based on its dorsal patagial color pattern (composed of large pale cream spots within a thin, dark brown to black reticulum). It can be further distinguished from *D. bimaculatus*, *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. palawanensis*, *D. quadrasi*, and *D. spilopterus* based on the presence (versus absence) of an enlarged, thornlike superciliary scale and in the coloration of the dewlap of males (brown with white spots proximally, yellow distally versus white, yellow, orange, or green). *Draco reticulatus* can be further distinguished from *D. jareckii*, *D. mindanensis*, *D. ornatus*, *D. quadrasi*, and some populations of *D. spilopterus* based on its unscaled (versus scaled over tympana). It can be further distinguished from *D. bimaculatus* and *D. mindanensis* based on the number of ribs supporting its patagia (six versus five). It can be further distinguished from *D. mindanensis* based on the orientation of its nostrils (oriented laterally versus posterodorsally) and the absence (versus presence) of a lacrimal bone.

Description.—A moderately large species, maximum observed SVL in males = 90 mm, females = 91 mm; dorsal head scales small to medium–sized, heterogeneous, variably keeled or rugose; rostral 1.2–3.0 times wider than high, bordered by 4–7 postrostrals; internasals, frontonasals, and prefrontals small excepting a series of enlarged, strongly keeled scales arranged in shape of inverted "Y", base originating a few scales posterior to rostral, arms contacting supraorbitals; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars larger than all surrounding cephalic scales; frontoparietals and parietals slightly to much larger than scales of snout; interparietal slightly smaller than surrounding parietals, sometimes (12 of 23) with opalescent lens;

nasals turret–like, pierced centrally by external nares, nares pointing laterally and slightly dorsally; 3–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, excepting a very large, laterally compressed thornlike superciliary scale, usually taller than wide; loreals and lorilabials immediately superior to supralabials relatively large, remaining loreals and lorilabials much smaller, juxtaposed, only slightly larger than adjacent palpebrals; an enlarged scale, usually wider than tall usually present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars may be enlarged, forming discontinuous subocular series, remaining postoculars granular; a series of 2–3 large keeled scales extend posteriorly from posterior border of orbit; supralabials 9–12, anterior border convex, posterior border concave, 1–3 times longer than tall, anteriormost supralabial usually much smaller than others, posteriormost supralabial usually longest; infralabials 9–12, pentagonal; tympanum unscaled, surrounded by granular scales, a large tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and 1–3; larger tubercles posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by 2–5 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets enlarged distally; dewlap scales of males enlarged at distal extremity.

Dorsal body scales small, juxtaposed or slightly imbricate, variably keeled; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 15–31 scales in males, 1–18 scales in females; lateral nuchal crests present in both sexes; middorsals 2–4 times larger than scales of lower flanks, patches of slightly enlarged scales surrounding 1–3 much larger, keeled scales present along flanks near proximal edge of patagia, part of discontinuous series of enlarged keeled scales extending from lateral nuchal crests, along base of patagium, to sacral region; no conspicuously enlarged series of keeled paravertebral scales present; caudals strongly keeled; paired, enlarged middorsal caudals extend length of tail; paired, enlarged, subcaudals extend length of tail; over proximal 10% of tail, lateral caudals strongly keeled forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series extending parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, approximately equal to dorsals in size; brachials imbricate, variable in size and degree of keeling; prebrachials about equal to largest dorsals in size, strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials smaller than suprabrachials, weakly keeled; antebrachials slightly larger than brachials, variably keeled, juxtaposed or weakly imbricate; infra–antebrachials smaller than other antebrachials; infracarpals very small, keeled or mucronate, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, unkeeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals in size, weakly keeled; a series of enlarged, flaplike posterior infrafemorals forming conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of proximal half of lower hind limb; tibials keeled, small proximally and distally, equal to dorsals in size elsewhere, pretibials largest; tarsals strongly keeled or mucronate, infratarsals much smaller than supratarsals, proximal subdigital lamellae with 2 keels, distal subdigital lamellae with 1 keel, 24–32 fourth toe subdigital lamellae.

Patagia usually supported by 6 ribs (24 of 25), occasionally 7 (1 of 25); pleurodont teeth usually 7 (12 of 20), sometimes 6 (9 of 20); lacrimal bone absent.

Coloration in life.—The coloration of male and female *Draco reticulatus* is similar in most respects. The dorsal body and limb coloration of both sexes is usually composed of pale gray, dark gray, tan, and brown mottling such that the overall coloration of the animal may appear gray or tan. Four indistinct dark gray or brown presacral dorsal blotches may be present. The pattern on the side of the neck usually is composed of a brown or gray reticulum surrounding pale gray blotches. The tail, which is encircled with dark brown bands, often has a distinct salmon cast, particularly ventrally where the salmon coloration may be quite vivid. A distinct melanic interorbital spot is present in both sexes, but the nuchal spot is restricted to females. In males, the orbital region (excepting only the ciliaries) is heavily suffused with dark pigments. The dewlap of males is pale ruddy brown over the proximal two–thirds and dark yellow over the distal third. The proximal one–third of the dewlap includes several distinct white spots, each composed of approximately 10 scales. The ventral coloration in both sexes is white with varying amounts of tan or dark brown mottling or cross–banding over the pectoral region. The ventral surface of the patagium and tail is generally yellow in females and salmon in males, although occasional males approach the yellow coloration of females. The ventral patagium is either immaculate, or a few minute and widely scattered black spots may be present. The same color that occurs on the ventral patagium may also be present as a wash down the middle of the chest and abdomen. In *D. reticulatus*, the dorsal patagial pattern of males and females is very similar, although females generally have more extensive black pigments near the patagial margin and the pale spots of the dorsal patagium are generally less discrete than in males. In both sexes, the dorsal patagial pattern is composed of large pale cream spots within a thin, dark brown to black reticulum. The thickness of the dark lines forming the reticulum and the size of the enclosed pale spots both tend to increase toward the outer edge of the patagium. There is regional variation in the distinctness of the pale spots and in the amount of black pigment present near the outer margin of the patagium. In males, there is a pale brick–red band near the outer edge of the wing.

Distribution.—*Draco reticulatus* is known from the islands of Leyte, Samar, Bohol, and Lapinin Chico (Figure 1.9). These islands are land bridge to one another and form the northern portion of the Mindanao aggregate island complex of Heaney (1986). *Draco reticulatus* does not occur on Mindanao Island proper, which is inhabited by its sister taxon, *D. cyanopterus* (McGuire, unpublished data).

Natural History.—As in *Draco cyanopterus*, *D. reticulatus* is a species of relatively open habitats and it seems likely that the species was found primarily along the edges of forest clearings and in relatively open areas in primary and secondary forests before logging of the Philippine forests commenced. The species now occurs primarily in open coconut plantation habitats where it is usually the only species of *Draco* encountered. We have observed *D. reticulatus* in sympatry with *D. bimaculatus* and *D. ornatus* on Bohol. On Bohol, *D. reticulatus* was occupying trees exposed to ample sunlight. As is the case with all species of Philippine *Draco* that we are familiar with, *D. reticulatus* appears to feed primarily on ants.

Comments.—Comparison of the holotype specimen of *Draco reticulatus* with other *Draco* specimens from the Philippines indicates that the type almost certainly was collected on Samar, Leyte, Bohol, or a smaller satellite island associated with one of these large islands. *Draco reticulatus* is closely related to *D. cyanopterus* and unpublished DNA sequence data unequivocally place these species as sister–taxa. Indeed, the species are very similar in most aspects of their scalation and color patterns, with the primary differences associated with the patagial coloration of both sexes.

Draco spilopterus Wiegmann

Draco spilopterus – Wiegmann, 1834:216; pl. 15. Type–locality: Manila, Luzon, Philippines (holotype: Plate 15 serves as the holotype [Lazell, 1992]).

Dracontoidis personatus Fitzinger, 1843:51.

Draco rostratus Günther, 1864:124.

Draco volans Inger, 1983:8.

Diagnosis.—*Draco spilopterus* can be distinguished from all other species of *Draco* in the Philippines by the following combination of characteristics: (1) large size (maximum SVL of males = 89.5 mm [n=101], females = 103.0 mm [n=62]); (2) nostrils oriented laterally on the snout; (3) enlarged, thornlike superciliary scale absent; (4) dorsal scales variable in size, often keeled or rugose; (5) scalation of tympanum variable, either unscaled, partially scaled, or completely scaled over; (6) six or occasionally seven ribs supporting patagium; (7) lacrimal bone absent; (8) large black postrictal ocellus surrounding an enlarged white tubercle absent; (9) males from all populations except Siquijor Island with dorsal patagium that is orange–yellow, with scattered small, brown spots; dorsal patagium of Siquijor males brown with pale cream reticulum; (10) females with dark brown dorsal patagium covered with pale tan striations, with or without pale yellow mottling; (11) in males, ventral surface of patagium yellow, usually with melanic patch near patagial margin (except Siquijor males, which may have more extensively distributed dark blotches); (12) in females, ventral surface of patagium yellow, usually with extensively distributed melanic blotches; (13) males with triangular, lemon–yellow or white dewlap; (14) pale brown dorsal coloration in both sexes; (15) orbital region either heavily suffused with dark pigments or with melanic lines radiating outward from eye.

Draco spilopterus can be distinguished from all other species of *Draco* in the Philippines on the basis of the presence in adult males of a yellow dorsal patagium with scattered small brown spots (sometime the spots are enlarged such that the pattern appears as a tan reticulum on a brown field). It can be further distinguished from *D. cyanopterus*, *D. guentheri*, and *D. reticulatus* based on the absence (versus presence) of an enlarged, thornlike superciliary scale. It can be further distinguished from *D. bimaculatus*, *D. cyanopterus*, *D. guentheri*, *D. mindanensis*, *D. ornatus*, and *D. reticulatus* on the basis of its large, triangular dewlap that is yellow or white in coloration (versus a small rounded white dewlap in *D. bimaculatus* or a brown, orange, or green dewlap in *D. cyanopterus*, *D. guentheri*, *D. mindanensis*, *D.*

ornatus, and *D. reticulatus*). It can be further distinguished from *D. bimaculatus* and *D. mindanensis* based on the number of ribs supporting its patagia (six versus five). It can be further distinguished from *D. mindanensis* based on the orientation of its nostrils (oriented laterally versus posterodorsally) and the absence (versus presence) of a lacrimal bone.

Description.—A large species, maximum observed SVL in males = 89.5 mm, females = 103.0 mm; dorsal head scales small to medium–sized, heterogeneous, variably keeled or rugose; rostral 1–3 times wider than high, bordered by 2–7 postrostrals; internasals, frontonasals, and prefrontals small excepting a series of enlarged, strongly keeled scales arranged in shape of inverted "Y", the base originates a few scales posterior to rostral, arms contact supraorbitals, sometimes scales that form "arms" of "Y" not enlarged leaving an "I" on snout; supraoculars granular laterally, grading to much larger size medially such that medialmost supraoculars larger than all surrounding cephalic scales except parietals; frontoparietals and parietals slightly larger or much larger than scales of snout; interparietal equal in size or smaller than surrounding parietals, usually with opalescent lens (108 of 114); nasals turretlike, pierced centrally by external nares, nares point laterally and slightly dorsally; 3–4 canthals, strongly keeled; anterior superciliaries elongate, keeled; posterior superciliaries granular, excepting 1–3 enlarged, keeled scales, similar in structure to anterior superciliaries, wider than high, not laterally compressed and thornlike; loreals and lorilabials immediately superior to supralabials relatively large, remaining loreals and lorilabials much smaller, but substantially larger than adjacent palpebrals; an enlarged scale, wider than tall sometimes present immediately superior to posteriormost supralabial; one to several pre–, sub–, and postoculars may be enlarged forming continuous or discontinuous subocular series, remaining postoculars small; a series of 3–4 large keeled scales extending posteriorly from posterior border of orbit; supralabials 7–13, rectangular, pentagonal, or with anterior border convex and posterior border concave, 1–3 times longer than tall, anteriormost supralabial usually smaller than others, posteriormost supralabial usually longest; infralabials 8–13, pentagonal or rectangular; tympanum either unscaled, partially scaled over, or completely scaled over; tympanum surrounded by granular scales, large tubercle present a few scales anterior to tympanum; scales surrounding corner of mouth granular; remaining temporals, occipitals, and nuchals granular except for 1–2 tubercles superior to tympanum midway between tympanum and nuchal crest and 1–3 larger tubercle posterior and slightly superior to tympanum immediately posterior to underlying quadrate bone; mental bordered by 2–6 postmentals; gular scales and scales of dewlap and ventral surfaces of throat lappets granular, scales of dorsal surfaces of throat lappets much enlarged distally; dewlap scales of males enlarged at distal extremity; dewlap exhibiting substantial interpopulational variation in length.

Dorsal body scales small, slightly imbricate, variably keeled, substantial interpopulational variation present in size of middorsals relative to more lateral dorsals; a midvertebral nuchal crest composed of laterally compressed dorsal scales present, comprised of 20–34 scales in males, 0–30 scales in females; lateral nuchal crests present in both sexes; middorsals 2–4 times larger than scales of lower flanks, patches of slightly enlarged scales surrounding 1–3 much larger, keeled scales present along flanks near proximal edge of patagia, part of discontinuous series of enlarged keeled scales extending from lateral nuchal crests, along base of patagium, to sacral region; a conspicuously enlarged series of keeled paravertebral scales rarely evident; caudals strongly keeled; paired, enlarged middorsal caudals extending length of tail; paired, enlarged, subcaudals extending length of tail; over proximal 10% of tail, lateral caudals strongly keeled, forming weak fringe; dorsal patagium with juxtaposed scales, variably keeled, keels arranged into linear series that extend parallel to axis of body; ventral patagium with flat, delicate scales, variably keeled; ventral body scales strongly keeled, equal in size or smaller than largest dorsals; brachials imbricate, variable in size and degree of keeling; prebrachials about equal to largest dorsals in size, moderately or strongly keeled, grading smoothly into smaller keeled suprabrachials; postbrachials much smaller than other brachials, weakly keeled or unkeeled; infrabrachials weakly keeled, approximately equal to postbrachials in size, much smaller than suprabrachials; antebrachials slightly larger than brachials, variably keeled, juxtaposed or weakly imbricate; infra–antebrachials smaller than other antebrachials; infracarpals granular, keeled or mucronate, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel; femorals highly variable in size and degree of keeling; prefemorals, anterior suprafemorals larger than dorsals, strongly keeled; posterior suprafemorals granular, unkeeled; postfemorals granular, variably keeled, keels directed posteriorly rather than distally; infrafemorals much smaller than ventrals, keeled; a series of enlarged, flaplike posterior infrafemorals forming conspicuous fringe along posterior edge of upper hind limb, continuing along posterior edge of proximal half of lower hind limb; tibials keeled, small proximally and distally, equal to dorsals in size elsewhere, pretibials largest; infratarsals strongly keeled or mucronate, much smaller than supratarsals, proximal subdigital lamellae with 2–4 keels, distal subdigital lamellae with 1 keel, 22–33 subdigital lamellae on fourth toe.

Patagia usually supported by 6 ribs, occasionally 7, rarely 5 (106 of 116 specimens with 6–6 ribs, 2 of 116 with 7–7 ribs, 6 of 116 with either 6–7 or 7–6 ribs, 1 of 116 with 5–6 ribs, and 1 of 116 with 5–5 ribs); pleurodont teeth usually 7 (82 of 111), sometimes 6 (27 of 111), rarely 5 (1 of 111) or 8 (1 of 111); lacrimal bone absent.

Coloration in life.—The dorsal coloration of *Draco spilopterus* may include tan, brown, black, cream, and greenish components, although the lizard generally appears tan from a distance. Four relatively discrete brown presacral cross-bands may or may not be present. The tail has dark brown banding and the limbs usually show some degree of banding, particularly distally. A melanic interorbital spot usually is present either as an independent marking or within a slender black band that crosses the supraorbital region. A well–developed nuchal spot usually is present in females, absent from males. The ventral body coloration is white or off–white, sometimes with a diffuse wash of ultramarine blue centered over the pectoral region. In some populations, the orbital region of males is heavily suffused with dark pigments, but in other populations, the orbital region of males may have melanic lines radiating outward from the eye; females exhibit the latter pattern. The coloration of the dewlap in males exhibits geographic variation. In live individuals from Luzon and Polillo, the dewlap is lemon yellow, and the distal terminus may or may not be washed with pink. In live individuals from Panay, Negros, and Siquijor the dewlap is white and may have a very faint wash of blue, green, or yellow. Live individuals from Cebu also have a dewlap that is mostly white, but there is more yellow present in the central portion of the dewlap than in individuals from Panay, Negros, and Siquijor. In females, the gular pattern (including that of the small dewlap) is composed of dark mottling or fine dark speckling on a cream or pale gray field. With the exception of the Siquijor population, the dorsal patagial pattern of males throughout the distribution of the species is characterized by brown spots on a bright yellow field. However, variation is present in the size and spacing of the brown spots and in the shade of yellow. In some *D. spilopterus* populations, the base coloration of the patagium is uniform yellow, whereas in other populations, the proximal portion of the wing may be orange–yellow grading to yellow distally. In most specimens, there is also a sooty gray to black patch near the outer margin of the wing, but this patch occasionally is absent in individuals from most populations, and is usually absent or faint in Lubang and Cebu specimens. Siquijor Island males have a very distinctive dorsal patagial pattern unlike that of any other *D. spilopterus* populations in that the patagium is brown with a pale tan or cream reticulum. In females throughout the distribution of the species, the patagia are dark brown or black, sometimes with yellow marbling, the pattern generally including pale striations that cover the proximal portion of the patagium. The extensiveness of the yellow marbling exhibits substantial variation. In some individuals, the patagium is nearly uniform brown with pale striations, the yellow marbling absent. In other individuals, the patagium may be mostly dark brown, with the yellow component present, but reduced to wavy yellow bars. Finally, the wings may exhibit extensive yellow pigments such that the brown and yellow components are equally represented. This variation can be observed within samples collected from the same site and there are no patagial patterns in females unique to one or more islands. In males, the ventral surface of the patagium is washed with yellow and there usually is a sooty gray patch near the outer margin of the wing; however, in Siquijor males, the melanic spots are more extensive, and are scattered over much of the ventral patagial surface. In females, the ventral patagium also has a yellow wash, but large melanic blotches are usually present over much of the patagium rather than confined to the outer margin.

Distribution.—*Draco spilopterus* is known from the islands of Luzon, Polillo, Kalotkot, Catanduanes, Marinduque, Lubang, Negros, Panay, Siquijor, Guimaras, Cebu, Bantayan, Masbate, Boracay, Carabao, Inampulugan, and possibly Tablas and Mindoro (Figure 1.10). As discussed in the *D. quadrasi* account, the Tablas Island population appears to be *D. spilopterus*, although the limited sample prevents an adequate examination of intra–island variation. Also, although it is clear that *D. quadrasi* occurs along the coastal areas of Mindoro, it appears that *D. spilopterus* also may occur on this island. We have examined one adult male specimen from Mt. Barawanan, Mindoro (CAS 20339) that cannot be distinguished from *D. spilopterus*. This specimen, collected by the Rabor expedition of 1954, is the only one that we have examined from the island that can be confidently identified as *D. spilopterus*, and we therefore entertain the possibility that the locality data associated with this specimen is in error. This issue will only be resolved once additional specimens are collected from upland areas of the island. If both species are to be found on Mindoro, we suggest that *Draco spilopterus* may be an upland species, with *D. quadrasi* found along the coast.

The distribution of *Draco spilopterus* generally corresponds to the Greater Luzon and Visayan Pleistocene aggregate islands, although the species also is found on at least two islands separated from these aggregate island complexes by deep submarine channels, Lubang and Siquijor. If *Draco spilopterus* does indeed occur on Mindoro, this would represent a third population not found on the Luzon or Visayan Pleistocene island complexes.

Natural History.—In forest habitats, *Draco spilopterus* is found along forest edges and on emergent trees that receive much direct sun. As with *D. cyanopterus* and *D. reticulatus*, *D. spilopterus* is abundant in coconut plantations. This species is not known to occur in sympatry with any other species of *Draco*. Alcala (1967) studied the ecology of *D. spilopterus* on Negros Island, providing data on many aspects of its biology including growth, reproduction, population structure, behavior, thermal biology, feeding, and predators.

Comments.—On biogeographic grounds, we might suspect *Draco spilopterus* to be composed of at least four independent lineages, one on Luzon and its satellite islands (including at least Kalatkot, Catanduanes, Marinduque, and Polillo), a second on the Visayan islands (including at least Negros, Panay, Cebu, Guimaras, Bantayan, Masbate, Boracay, Carabao, and Inampulugan), a third on Siquijor, and a fourth on Lubang. When sea levels were lower during the most recent glacial maximum (at the end of the Pleistocene, approximately 18,000 years ago), Philippine islands separated by shallow channels (less than 120m in depth) were joined by land bridges. Thus, this set of at least 17 islands now inhabited by *Draco spilopterus* was reduced to four independent islands (Greater Luzon, Greater Visaya, Siquijor, and Lubang) 18,000 years ago. Because these four paleo–islands are separated by deep channels, they have not been in contact for at least 160,000 years and possibly have never been connected (Heaney, 1985, 1986, and references cited therein). With the exception of the Siquijor population, which has a very distinctive patagial color pattern, *Draco* from the four regions are very similar with respect to their coloration, with the only obvious differences being the presence of bright yellow dewlaps in the Luzon group and primarily white dewlaps in the Visayan and Siquijor assemblages (except the Cebu population, which is characterized by a drab yellow dewlap). The dewlap coloration of the Lubang population is unknown. The modal number of pleurodont teeth differs between the Luzon and Lubang populations on the one hand, and Visayan and Siquijor populations on the other. The Greater Luzon and Lubang samples have a mode of six pleurodont teeth (17 of 20 specimens), whereas the Visayan and Siquijor samples have a mode of seven (79 of 90 specimens). Despite the substantial periods of isolation that *D. spilopterus* on these four Pleistocene islands may have incurred and the differences in dewlap coloration and pleurodont tooth number, a multivariate analysis of morphometric characters (unpublished data) was unable to discriminate between populations, suggesting that very little shape variation has evolved during the time that the populations have been isolated. Despite this lack of discrete morphometric variation, these populations may yet prove to be distinct evolutionary species. For example, an allozyme study might show that some of these insular populations of *D. spilopterus* are diagnosible, which would support the contention that *D. spilopterus* is composed of multiple distinct evolutionary species.

DISCUSSION

The distribution of *Draco* species in the Philippines is highly concordant with the aggregate island complexes formed during periods of reduced sea level during the Pleistocene. During the last glacial maximum (18,000 years ago), sea levels were reduced such that islands separated by sea channels less than 120m in depth were connected by dry land (Figure 1.11; Heaney, 1986 and references cited therein). Thus, Luzon was united with large adjacent islands including Polillo, Catanduanes, and Marinduque, but was not connected with any other large Philippine islands. The Visayan islands of Cebu, Masbate, Panay, and Negros were united; Mindanao, Bohol, Leyte, Samar, Basilan, Dinagat, and Biliran were connected; and Palawan was united with Busuanga, Culion, and Balabac. Large islands that remained independent of these aggregate island complexes include Romblon and Tablas (connected with one another, but apparently not with Panay or any other major island), Mindoro, Sibuyan, Siquijor, Lubang, and the bank of islands in the Sulu Archipelago extending between Jolo and Tawitawi (Heaney, 1985, 1986). Several small islands in the Babuyan group north of Luzon, including Batan and Camiguin Norte, also are separated from one another and from Luzon by deep water. As will be discussed below, most species of *Draco* are confined to sets of islands that are connected to one another by shallow sea channels because these species were presumably continuously distributed on these aggregate island complexes when they existed as single islands in the late Pleistocene. Distribution patterns concordant with Pleistocene aggregate island complexes have been documented for a variety of Philippine taxa, with many examples found in mammals

(Heaney, 1986), snakes (Leviton, 1963), and the scincid genera *Brachymeles* and *Sphenomorphus* (Brown and Alcala, 1980). Additional examples almost certainly can be found in virtually every group of organisms occurring in the Philippines.

The Mindanao aggregate island complex is inhabited by a greater diversity of *Draco* species than the other island complexes, with as many as five species occurring in sympatry on Mindanao proper. *Draco bimaculatus*, *D. cyanopterus*, *D. guentheri*, and *D. mindanensis* are known to occur in syntopy on Mindanao (McGuire, pers. obs.) and it seems very likely that *D. ornatus* also occurs in syntopy with these species as it also is widespread on the island. Three of the five species also occur on other islands on the Mindanao complex: *Draco bimaculatus* occurs on the major islands of Mindanao, Bohol, Leyte, and Samar, as well as several islands in the Sulu Archipelago that are separated by deep water from the Mindanao aggregate island complex; *Draco ornatus* is known from Mindanao, Bohol, Leyte, and Samar; and *Draco mindanensis* is known from Mindanao, Leyte, and Samar, and it seems likely that the species either occurs or once occurred (when adequate primary forest remained) on Bohol as well. Only *D. cyanopterus* and *D. guentheri* have distributions that seem unlikely to include land bridge islands north of Mindanao. The absence of *D. cyanopterus* is explained by the presence on these islands of its sister taxon, *D. reticulatus* (McGuire, unpublished data). *Draco guentheri* is known from few specimens in eastern Mindanao, but was described by Taylor (1922b) as the common species of the Zamboanga Peninsula (southwestern Mindanao) and the Sulu Archipelago. The distribution of *D. guentheri*, as currently understood, suggests that this species may not have reached the northern islands associated with Mindanao because the species does not occur in that portion of Mindanao (northeastern) connected with these islands by a shallow submarine shelf.

Aside from the bank of islands in the Sulu Archipelago occupied by *D. bimaculatus* and *D. guentheri*, the Mindanao complex, and possibly Mindoro Island (see above), all of the remaining Philippine aggregate island complexes are inhabited by single species of *Draco*. Greater Luzon, the Visayas, Lubang, and Siquijor are inhabited by *Draco spilopterus* (although each island bank may prove to be inhabited by a distinct species of "*D. spilopterus*"), Palawan (and presumably its associated islands) is inhabited by *D. palawanensis*, Sibuyan is inhabited by *D. quadrasi*, Batan is inhabited by *D. jareckii*, and Camiguin Norte is inhabited by an undescribed species (Lazell, 1992; Crombie, personal communication).

Draco quadrasi may have the most perplexing distribution of any of the Philippine species. This species is known from Mindoro, Sibuyan, Semirara, and Romblon. Although Romblon and Tablas appear to be connected by a shallow shelf and we would thus expect to see the same species of *Draco* present on both, the two specimens examined from Tablas appear to be *D. spilopterus*. Mitochondrial DNA sequence data (McGuire, unpublished data) indicate unequivocally that the Mindoro and Sibuyan populations form a natural group, but no tissue samples or sequence data are available for Romblon and Tablas populations. *Draco quadrasi* is distinguished from *D. spilopterus* of the Visayan islands only by its uniform yellow patagium (rather than yellow with extensive brown spotting) and by its yellow dewlap (versus white). Thus, the DNA sequence data may be more compelling evidence that the Sibuyan and Mindoro populations are conspecific (rather than populations with convergent color patterns) than are the color pattern features themselves. The specific identity of the Romblon and Tablas populations will be clarified when DNA sequence data for these populations are available. Regardless of the status of the Romblon and Tablas populations, the deep water separating Mindoro and Sibuyan together with the absence of geological data indicating a prior land–positive connection between the two islands suggests that overwater dispersal must be responsible for the unusual distribution of this species.

From a biogeographical perspective, Palawan Island has long been considered an extension of the Greater Sunda shelf. Palawan has been treated as an extension of Borneo because of its close geographic proximity to that island and because many mammalian groups (such as carnivores, pangolins, porcupines, and some insectivores) known from Borneo and Palawan are absent or poorly represented elsewhere in the Philippines (Everett, 1889; Heaney, 1986). Nevertheless, the channel that separates Palawan from Borneo is 145m in depth, indicating that Palawan has remained isolated from the Greater Sunda Shelf for at least 160,000 years (Heaney, 1985, 1986), if not longer. There are putative sister taxa shared by Palawan and other islands in the Philippines, particularly Mindoro and the western Visayas, that are not found on the Sunda Shelf (Brown, 1997; Everett, 1889; Ferner et al., 1997; Myers, 1951, 1953), indicating that the relationship between Palawan and the remainder of the Philippines may be understated in the biogeographical literature. *Draco* represents an excellent counter–example to the standard model that emphasizes a tight relationship between Palawan and Borneo. For example, there are nine species of *Draco* on Borneo, none of which occurs on Palawan. Furthermore, DNA sequence data indicate that *Draco* *palawanensis* is more closely related to Philippine species than to any species on the Greater Sunda Shelf (McGuire, unpublished data).

Key to the species of Philippine *Draco*

(adult males)

1a. Lacrimal bone present (palpable with a probe); nostrils oriented dorsally and slightly posteriorly; patagia bright red; dewlap and ventral surfaces of throat lappets vivid tangerine orange .... *mindanensis*

1b. Lacrimal bone absent; nostrils oriented laterally on snout; patagia not bright red; dewlap and ventral surfaces of throat lappets not tangerine orange 2

2a. Five ribs supporting patagium; dewlap small, rounded, off–white in color; a large melanic postrictal ocellus enclosing a white tubercle .... *bimaculatus*

2b. Six ribs supporting patagium; dewlap large, triangular, yellow, white, green, or brown in color; no melanic postrictal ocellus enclosing a white tubercle 3

3a. An enlarged, thornlike superciliary scale that is at least twice as high as wide 4

3b. No enlarged, thornlike superciliary scale 6

4a. Dorsal body coloration vivid green in life (often ultramarine blue in preservative) .... *guentheri*

4b. Dorsal body coloration tan or brown 5

5a. Dorsal patagium with 4–6 large vivid chartreuse blotches between the ribs .... *cyanopterus*

5b. Dorsal patagium without chartreuse blotches .... *reticulatus*

6a. Dorsal patagium with a large melanic marginal patch enclosing several crisp, white spots; distal half of dewlap vivid green .... *ornatus*

6b. Dorsal patagium with or without melanic marginal patch but lacking crisp white spots; dewlap yellow or white 7

7a. Dorsal patagium dull orange, overlain with rectangular, block–like, black spots that are small proximally (1 mm in diameter), but grade into larger blotches distally such that they are 5–7 mm in diameter near the patagial margin; tympana unscaled .... *palawanensis*

7b. Dorsal patagium "mottled in shades of ash to slate–gray, with brown tones postero–basally" (Lazell, 1992); tympana scaled over .... *jareckii*

7c. Dorsal patagium bright yellow, with or without scattered brown spots; tympana usually, but not always, scaled over 8

8a. Dorsal patagium yellow, lacking brown spots .... *quadrasi*

8b. Dorsal patagium either yellow (may be orange proximally) and overlain with many scattered brown spots, or brown with a pale cream reticulum (Siquijor) .... *spilopterus*

Key to the species of Philippine *Draco*
(adult females and juveniles of both sexes)

1a. Lacrimal bone present; nostrils oriented dorsally and slightly posteriorly .... *mindanensis*

1b. Lacrimal bone absent; nostrils oriented laterally on snout 2

2a. Five ribs supporting patagium; dewlap black with at least one white crossbar bar (tinged with ultramarine); a large melanic spot at corner of mouth enclosing a white tubercle .... *bimaculatus*

2b. Six ribs supporting patagium; if present, the small dewlap is unmarked or speckled, not black; no melanic postrictal ocellus enclosing a white tubercle 3

3a. An enlarged, thornlike superciliary scale that is at least twice as high as wide 4

3b. No enlarged, thornlike superciliary scale 5

4a. Dorsal patagium black, enclosing bright reddish to orange spots (Taylor, 1922b) .... *guentheri*

4b. Dorsal patagium black enclosing pale cream spots .... *reticulatus*

4c. Dorsal patagium pale orange with black marbling or tan with green and black marbling .... *cyanopterus*

5a. Dorsal patagium dull yellow, overlain with rectangular, block–like, black spots that are small proximally (1 mm in diameter), but grade into larger blotches distally such that they are 5–7 mm in diameter near the patagial margin; tympana unscaled .... *palawanensis*

5b. Dorsal patagium vivid orange and red with black marbling, a large melanic marginal patch enclosing several crisp, white spots; tympana scaled over .... *ornatus*

5c. Dorsal patagium with a "slatey to sooty" base coloration containing "bold near–white and gray–greenish blotches" and "prominent light, ash to lead gray radials" (Lazell, 1992); tympana scaled over .... *jareckii*

5d. Dorsal patagium black or dark brown with pale cream striations or pale cream marbling; tympana scaled over (*quadrasi*) or usually scaled over (*spilopterus*) .... *quadrasi* or *spilopterus*

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Table 1.1. Synopsis of the specific epithets that have been applied to Philippine *Draco* species. The authors listed were the first to use the taxonomic combination presented.

Prior Usage or New Combination	Authority	Current Status (With Respect to Philippine Populations)
Draco bimaculatus	Günther, 1864	*Draco bimaculatus*
Draco cyanopterus	this study	*Draco cyanopterus*
Draco everetti	Boulenger, 1885	*Draco cyanopterus*
Draco fimbriatus mindanensis	Hennig, 1936	*Draco mindanensis*
Draco guentheri	Boulenger, 1885	*Draco guentheri*
Draco jareckii	Lazell, 1992	*Draco jareckii*
Draco lineatus bimaculatus	Hennig, 1936	*Draco bimaculatus*
Draco mindanensis	Stejneger, 1908	*Draco mindanensis*
Dracunculus ornatus	Gray, 1864	*Draco ornatus*
Draco palawanensis	this study	*Draco palawanensis*
Dracontoidis personatus	Fitzinger, 1843	*Draco spilopterus*
Draco quadrasi	Boettger, 1893	*Draco quadrasi*
Draco reticulatus	Günther, 1864	*Draco reticulatus*
Draco reticulatus var. *cyanopterus*	Peters, 1867	*Draco cyanopterus*
Draco rizali	Wandolleck, 1900	*Draco guentheri*
Draco rostratus	Günther, 1864	*Draco spilopterus*
Dracunculus spilopterus	Wiegmann, 1834	*Draco spilopterus*
Draco volans	Linnaeus, 1758	*Draco cyanopterus* *Draco guentheri* *Draco ornatus* *Draco palawanensis* *Draco spilopterus* *Draco quadrasi* *Draco reticulatus*
Draco volans sumatranus	Musters, 1983	*Draco cyanopterus* *Draco guentheri* *Draco palawanensis* *Draco reticulatus*

Figure 1.1 Distribution of *Draco palawanensis*. The stippled area represents the known distribution of the species.

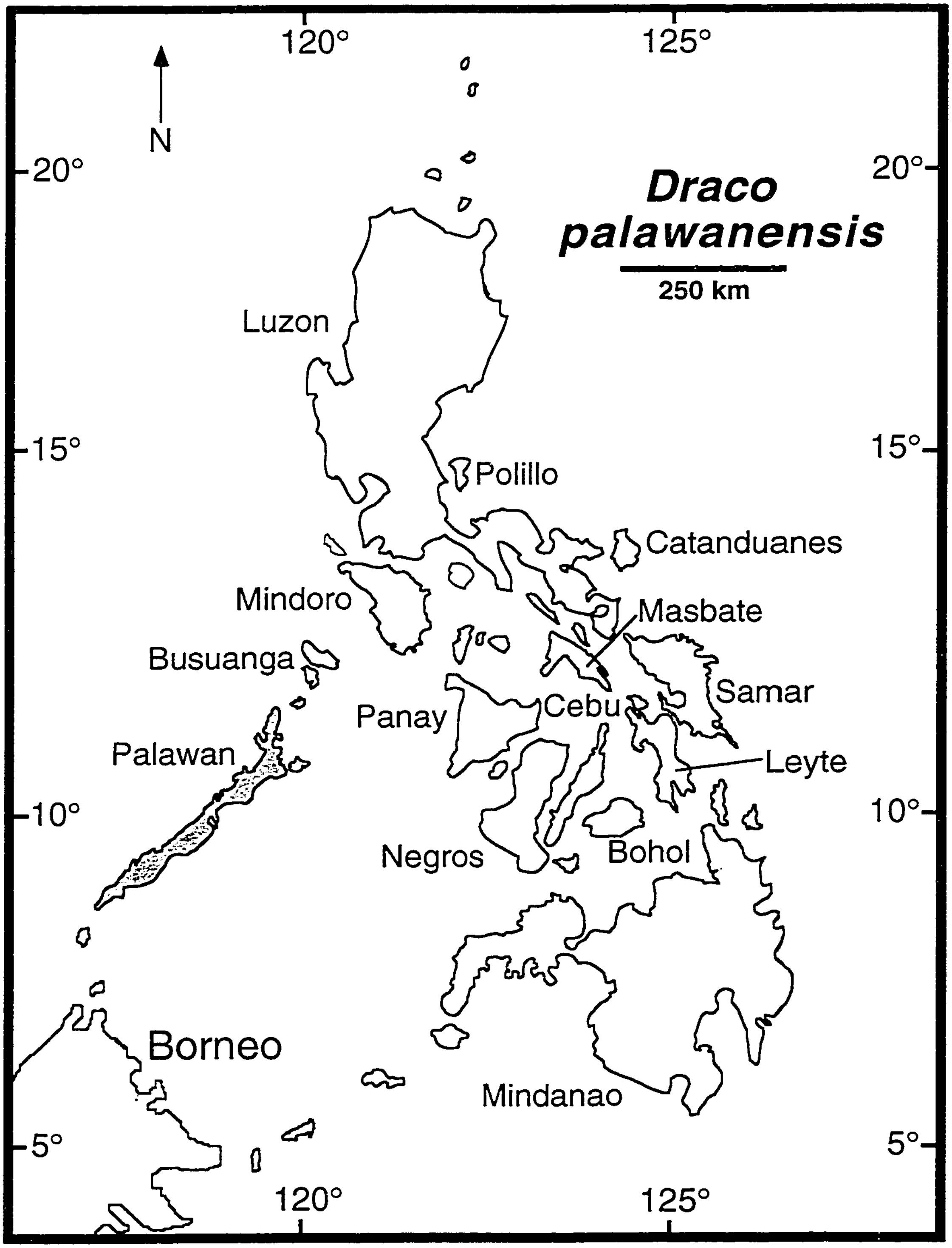
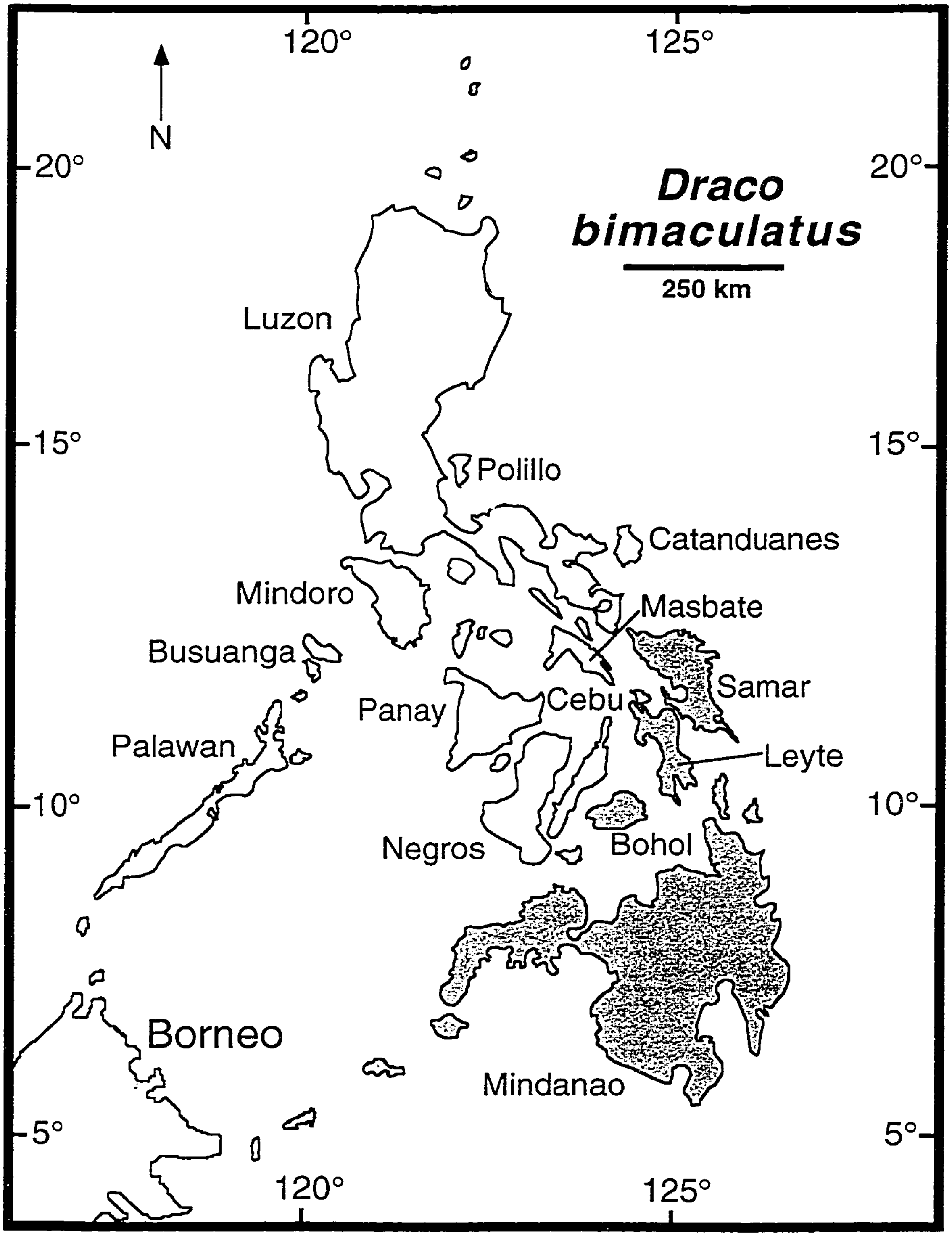

120°
125°
N
20°
15°
10°
5°
Draco palawanensis
250 km
Luzon
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
Negros
Bohol
Borneo
Mindanao

Figure 1.2. Distribution of *Draco bimaculatus*. The stippled area represents the known distribution of the species.



120°
125°
N
20°
20°
Draco bimaculatus
250 km
Luzon
15°
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Cebu
Panay
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Mindanao
5°
5°
120°
125°

Figure 1.3. Distribution of *Draco cyanopterus*. The stippled area represents the known distribution of the species.

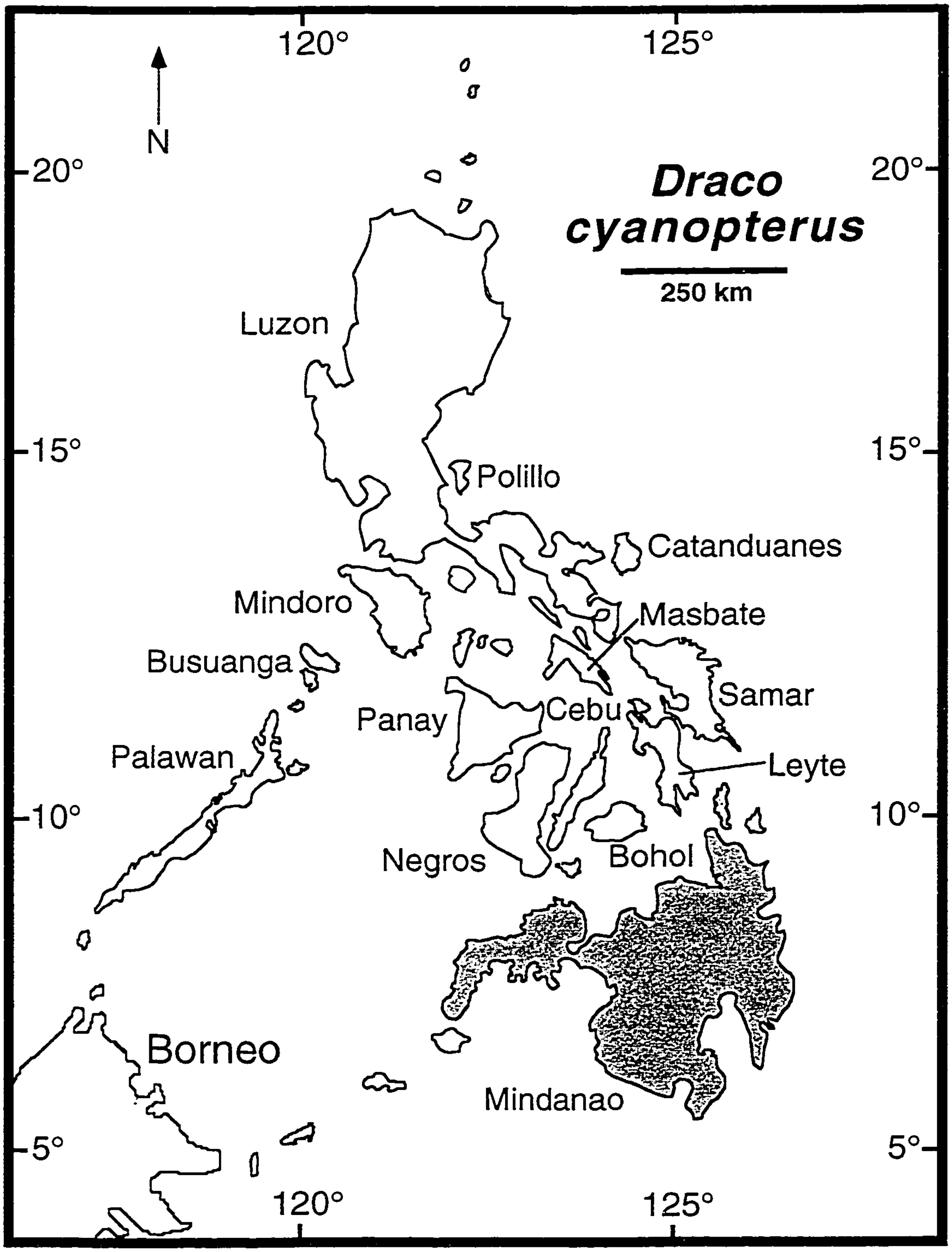

120°
125°
N
20°
Draco cyanopterus
250 km
Luzon
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
10°
Negros
Bohol
Borneo
Mindanao
5°

Figure 1.4. Distribution of *Draco guentheri*. The stippled area represents the known distribution of the species.

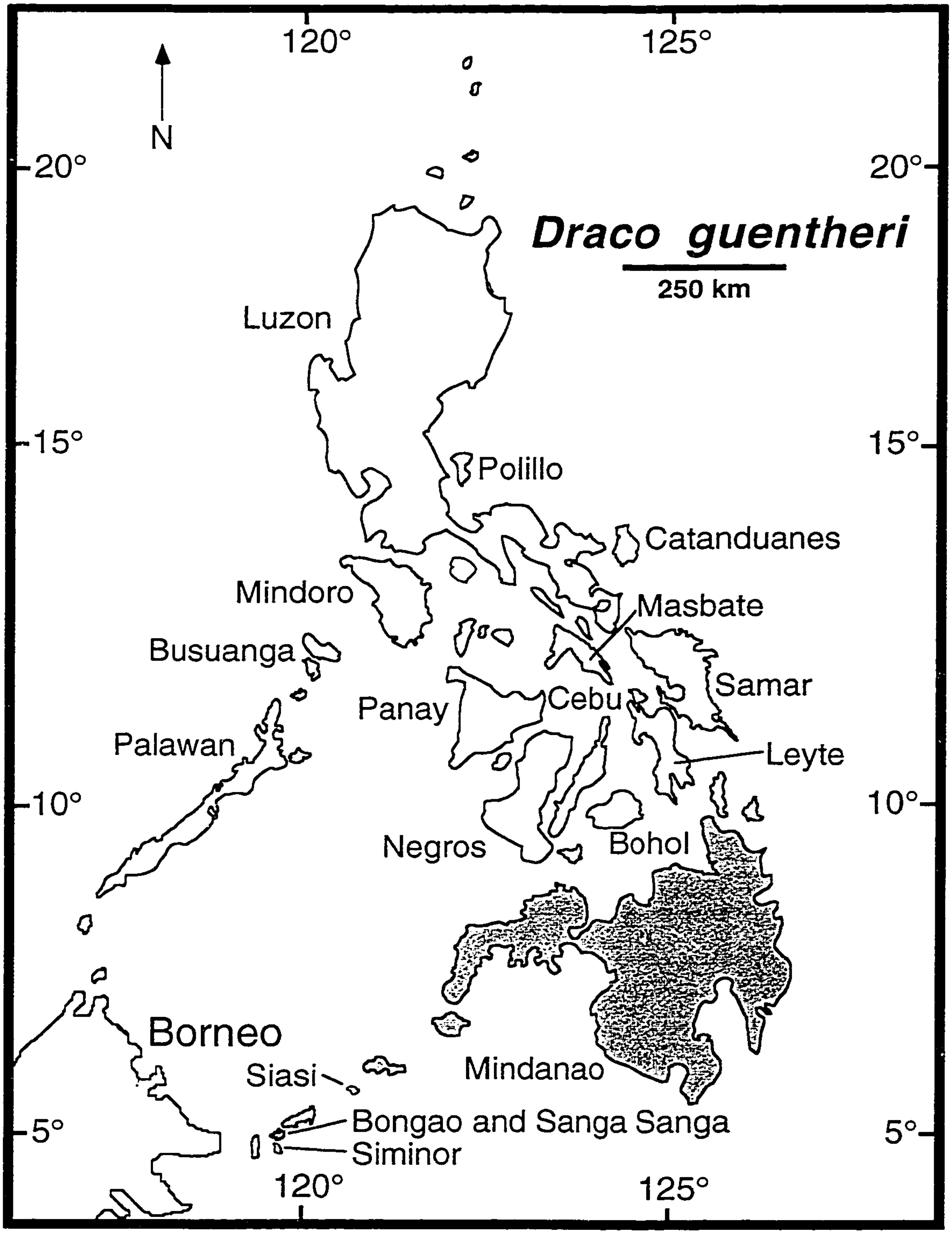

120°
125°
N
20°
20°
Draco guentheri
250 km
Luzon
15°
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Siasi
Mindanao
Bongao and Sanga Sanga
5°
5°
Siminor
120°
125°

Figure 1.5. Distribution of *Draco jareckii*. The stippled area represents the known distribution of the species.

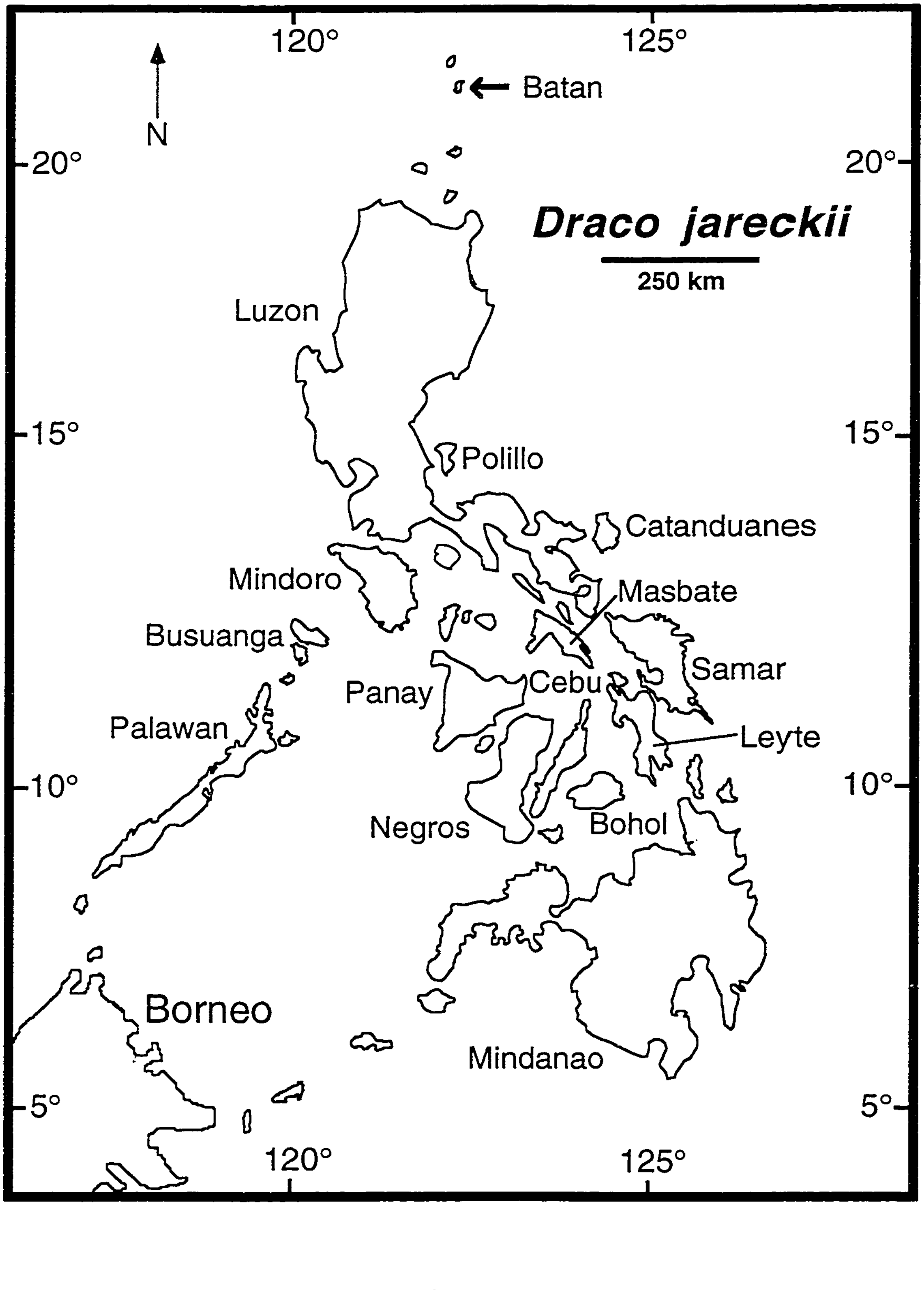

120°
125°
Batan
N
20°
20°
Draco jareckii
250 km
Luzon
15°
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Mindanao
5°
5°
120°
125°

Figure 1.6. Distribution of *Draco mindanensis*. The stippled area represents the known distribution of the species.

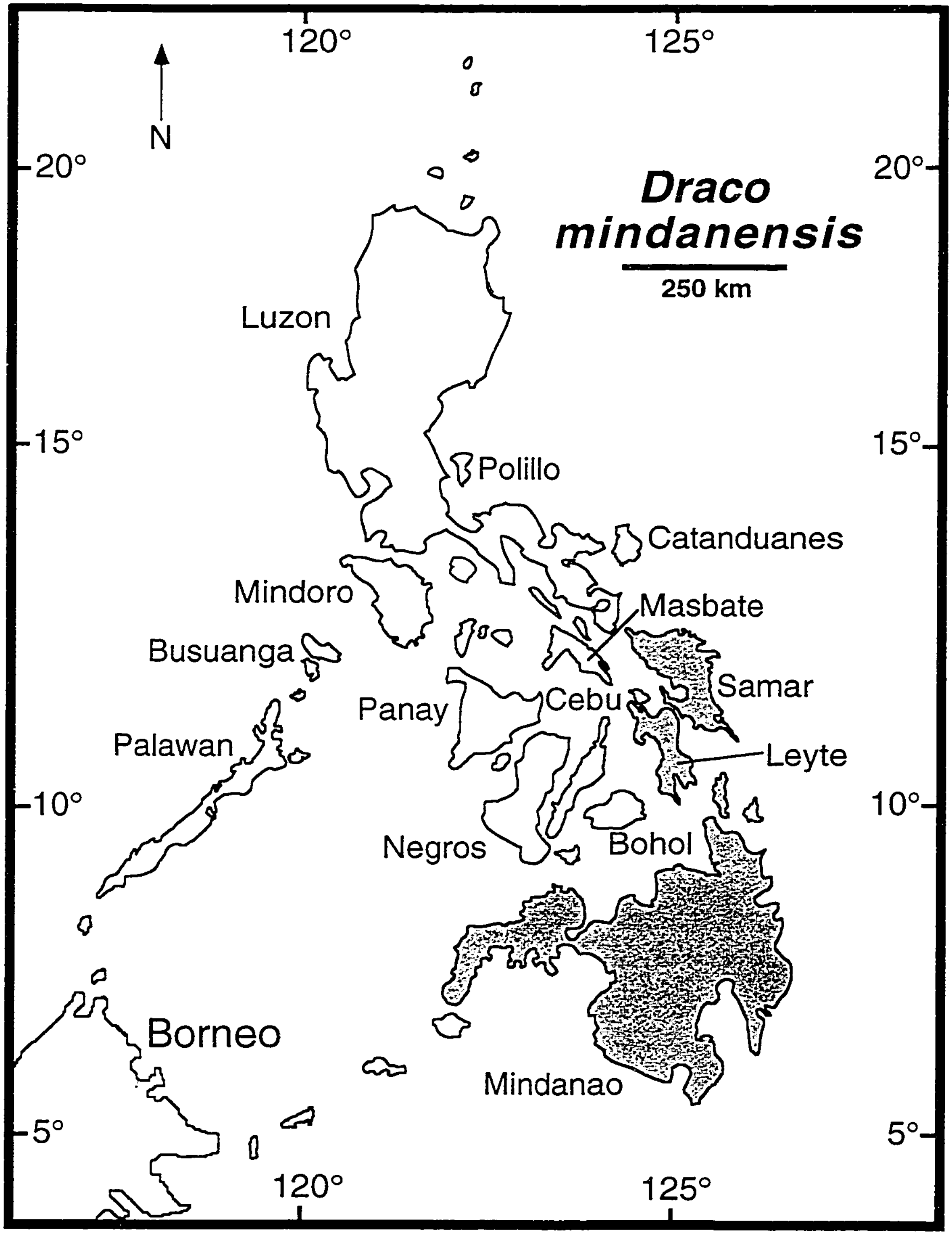

120°
125°
N
20°
20°
Draco
mindanensis
250 km
Luzon
15°
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Cebu
Panay
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Mindanao
5°
5°
120°
125°

Figure 1.7. Distribution of *Draco ornatus*. The stippled area represents the known distribution of the species.

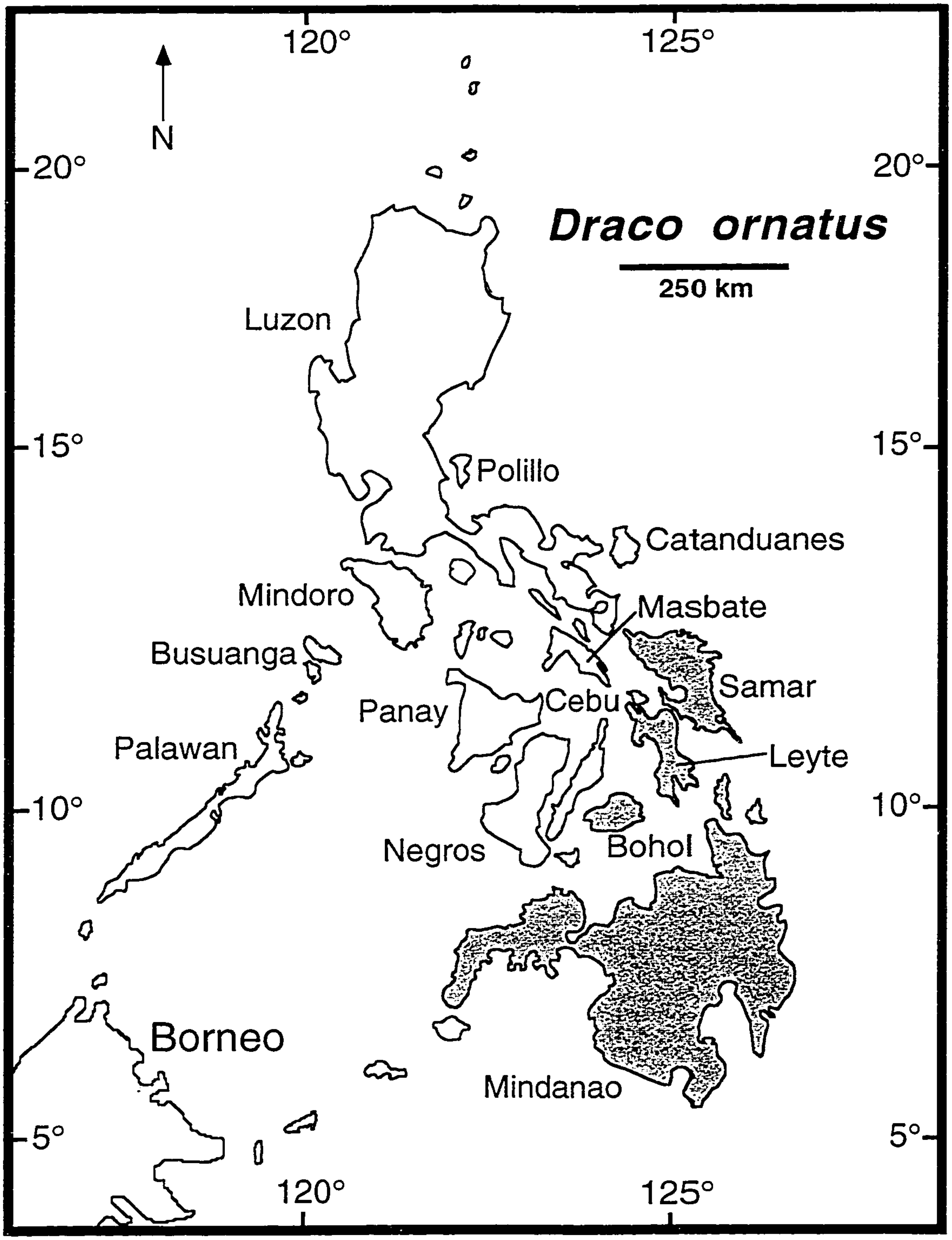

120°
125°
N
20°
20°
Draco ornatus
250 km
Luzon
15°
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Mindanao
5°
5°
120°
125°

Figure 1.8. Distribution of *Draco quadrasi*. The stippled area represents the known distribution of the species.

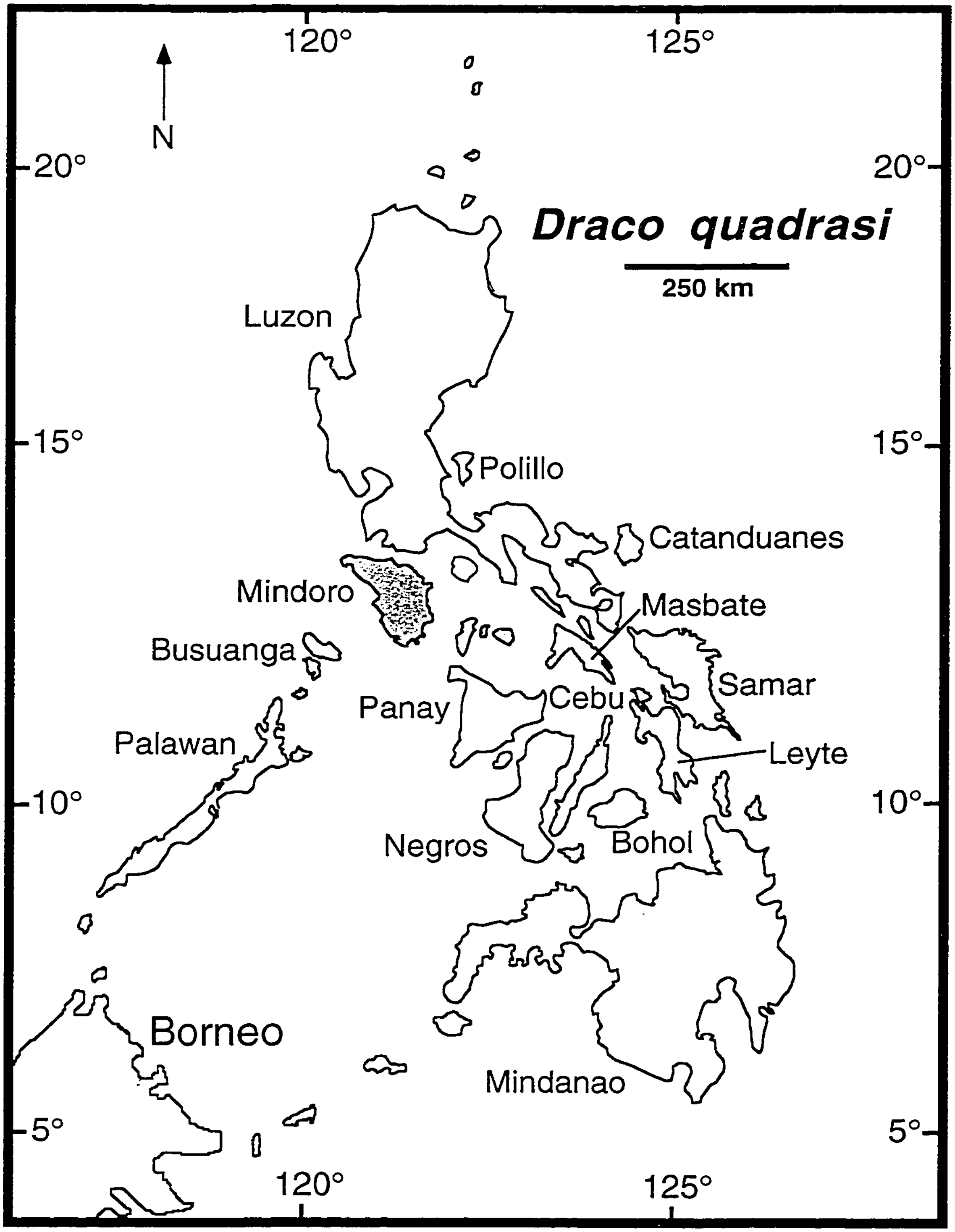

120°
125°
N
20°
20°
Draco quadrasi
250 km
Luzon
15°
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Mindanao
5°
5°
120°
125°

Figure 1.9. Distribution of *Draco reticulatus*. The stippled area represents the known distribution of the species.

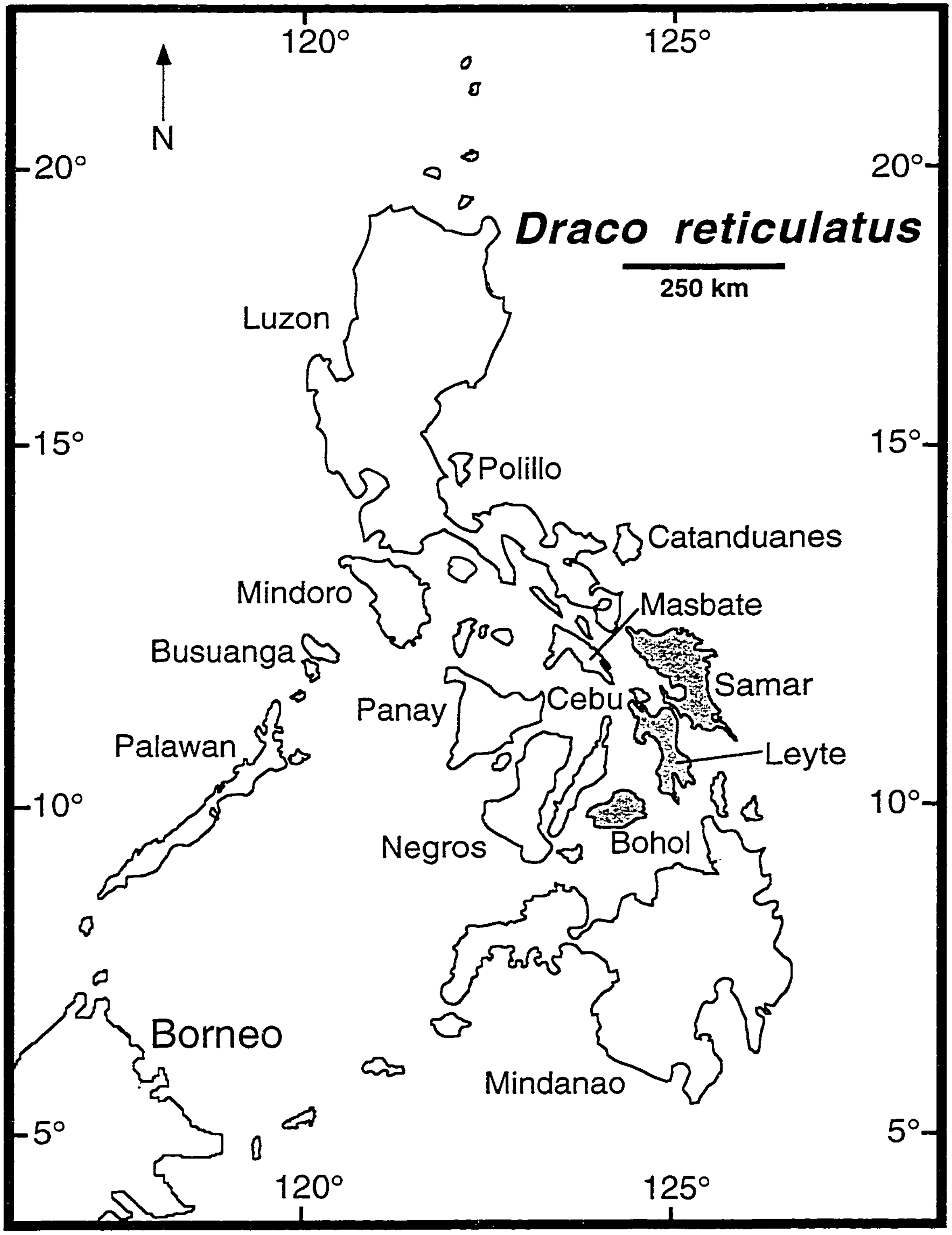

120°
125°
N
20°
20°
Draco reticulatus
250 km
Luzon
15°
15°
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Mindanao
5°
5°
120°
125°

Figure 1.10. Distribution of *Draco spilopterus*. The stippled area represents the known distribution of the species.

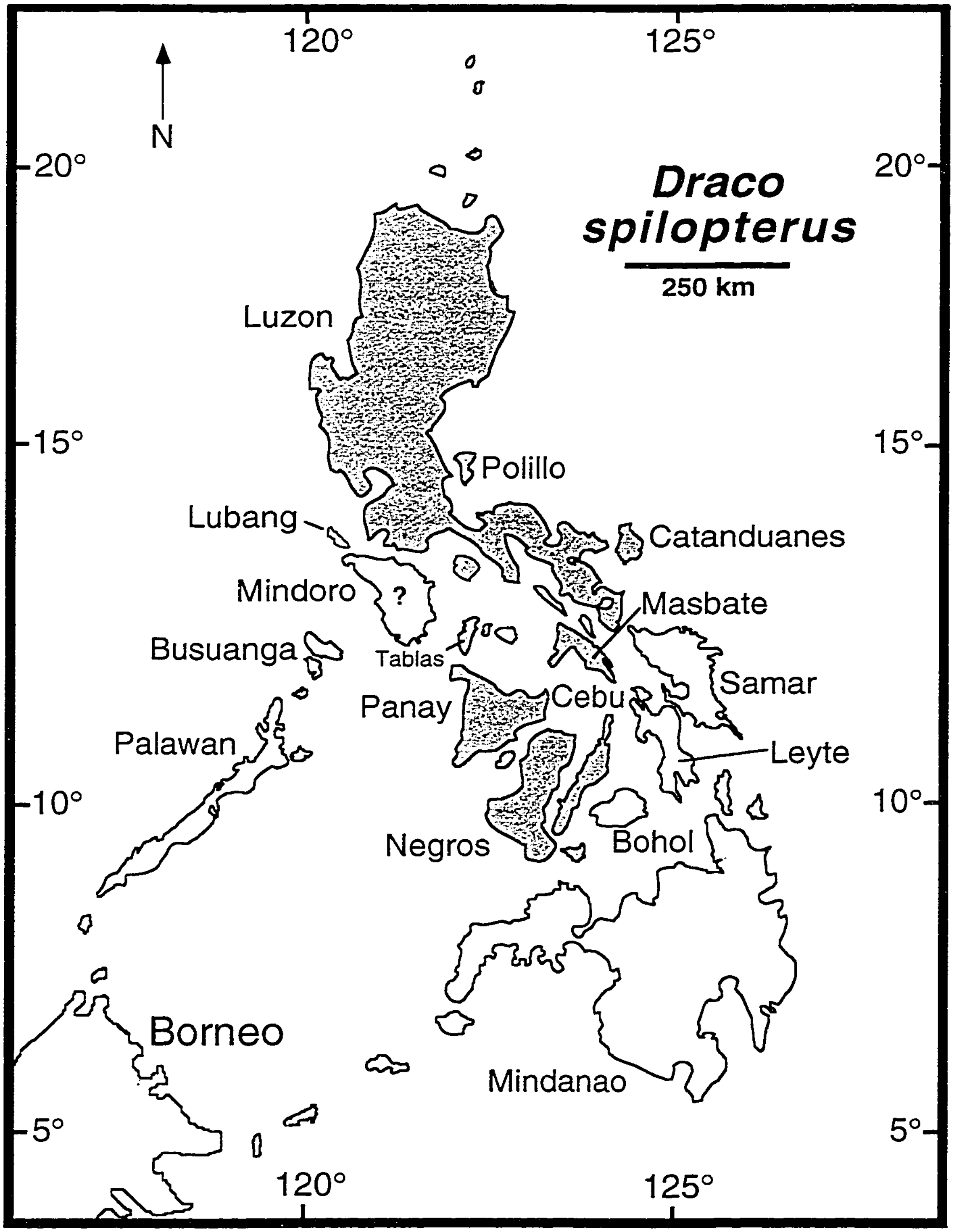
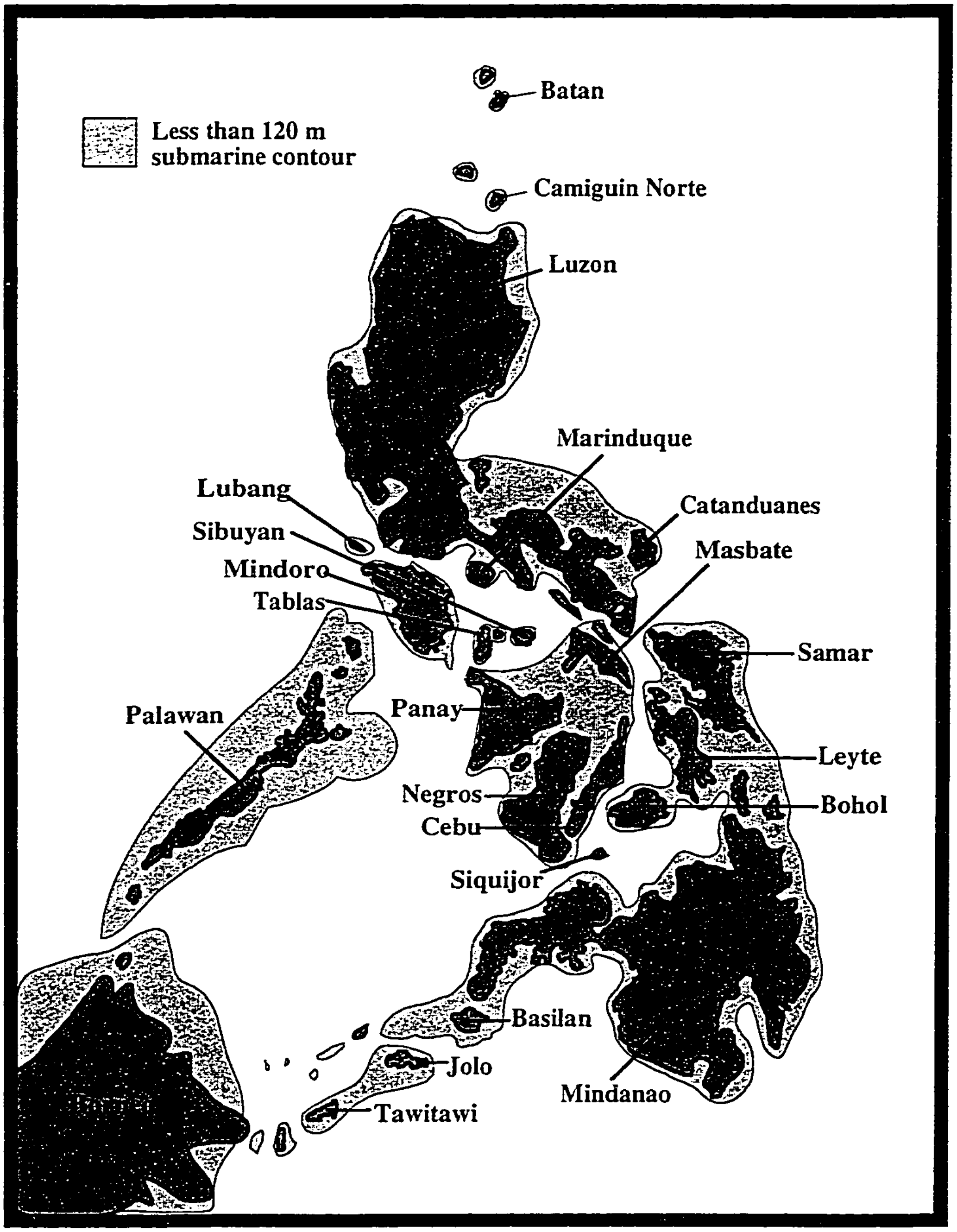

120°
125°
N
20°
20°
Draco spilopterus
250 km
Luzon
15°
15°
Polillo
Lubang
Catanduanes
Mindoro
?
Masbate
Busuanga
Tablas
Samar
Cebu
Panay
Palawan
Leyte
10°
10°
Negros
Bohol
Borneo
Mindanao
5°
5°
120°
125°

Figure 1.11. Map illustrating the extent of the Philippine islands during the late Pleistocene (18,000 years before present) when sea-levels were approximately 120 m lower; from Heaney (1986).


Batan
Less than 120 m submarine contour
Camiguin Norte
Luzon
Marinduque
Lubang
Catanduanes
Sibuyan
Masbate
Mindoro
Tablas
Samar
Palawan
Panay
Leyte
Negros
Bohol
Cebu
Siquijor
Basilan
Jolo
Mindanao
Tawitawi

CHAPTER 2

PHYLOGENETIC SYSTEMATICS OF SOUTHEAST ASIAN FLYING LIZARDS (GENUS *DRACO*) BASED ON MITOCHONDRIAL DNA SEQUENCE DATA

The flying lizards (genus *Draco*) of Southeast Asia are remarkable in their ability to glide large distances using an airfoil formed by wing-like patagial membranes supported by elongate thoracic ribs (Colbert, 1967; Herre, 1958; Klingel, 1965). Although these lizards are famous for their gliding ability, their potential as a model system for comparative studies has remained unexplored. *Draco* exhibit a number of characteristics that make them an appealing group with which to study a variety of evolutionary phenomena. One of the most attractive characteristics of the genus is that it is composed of approximately 40 species, and thus exhibits sufficient species-richness to allow for statistical power in comparative studies. The following types of comparative studies are possible with this group: 1) *Draco* species exhibit substantial size variation, and this variation has important consequences for the evolution of gliding performance. A study of *Draco* gliding performance including species spanning the entire size distribution of the genus would allow one to test hypotheses relating to the consequences of size evolution for locomotor performance; 2) like the New World anoles, *Draco* males have well–developed dewlaps that are used in social displays. The presence of substantial interspecific variation in terms of shape, coloration, and scalation of the dewlap, as well as in their display repertoires, suggests that *Draco* would be an excellent group with which to investigate the evolution of dewlap morphology and display characteristics across a group of closely related, yet interspecifically variable species; 3) as many as six species of *Draco* can be found in sympatry at many localities (Inger, 1983; pers. obs.), suggesting that these lizards would provide an excellent system for the study of niche partitioning. Each of the comparative studies outlined above must be conducted in a phylogenetic context. However, to date, an explicit phylogenetic analysis of this group has not been published. The purpose of the present paper is to provide a phylogenetic estimate of *Draco* relationships based on mitochondrial DNA sequence data. The phylogenetic estimate here provided will serve as the historical framework for several comparative analyses currently in progress.

MATERIALS AND METHODS

Taxonomic Sampling

Mitochondrial DNA sequence data were obtained for 51 *Draco* species and/or populations and four outgroup taxa (Appendix 2). Taxonomic representation includes all currently recognized species of *Draco* except *D. dussumieri* and *D. jareckii*. However, I also lack sequence data for three currently recognized subspecies (*D. lineatus modigliani*, *D. l. ochropterus*, and *D. l. rhytisima*) that I will argue should be recognized as distinct species on the basis of diagnostic morphological characteristics and their occurrence in allopatry with respect to other

Draco taxa (Musters, 1983). As alluded to above, the *Draco* taxonomy followed here differs in many respects from the taxonomies presented in the most recent systematic treatments of the entire genus (Inger, 1983; Musters, 1983). Much of this disagreement is associated with Philippine taxa; therefore, a modified taxonomy for the Philippine assemblage (McGuire and Alcala, submitted) will be followed here. However, there remain several additional cases of taxonomic disagreement, including my recognition of the following species: *D. indochinensis*, *D. formosus*, *D. beccarii*, *D. bourouniensis*, *D. spilonotus*, "Tahulandang," *D. sumatranus*, *D. boschmai*, and *D. timoriensis*. Justifications for the recognition of these species are provided below.

Inger (1983) considered *Draco indochinensis* to be a synonym of *D. blanfordi*, whereas Musters (1983) recognized it as a subspecies of *D. blanfordi*. I treat *D. indochinensis* as a distinct evolutionary species because it is both allopatrically distributed and clearly diagnosable from *D. blanfordi*. The most compelling character state differences are associated with the dewlap of males. The dewlap of *D. indochinensis* is widest at its base, decreases in width over its entire length, and terminates in a sharp point. In contrast, the dewlap of *D. blanfordi* is distally expanded with a basal constriction, and terminates in a rounded distal edge. The latter type of dewlap is characteristic not only of *D. blanfordi*, but also of *D. formosus*, *D. obscurus*, and *D. taeniopterus* and suggests that *D. blanfordi* and *D. indochinensis* may not even be sister taxa, let alone conspecifics. *Draco indochinesis* also differs from *D. blanfordi* in the presence (in both sexes) of a thick black transverse band that extends across the posterior gular region from one throat lappet to the other, and in the presence of dark radial bands on the dorsal surfaces of the patagia in both sexes rather than in females only.

Inger (1983) considered *Draco formosus* to be a synonym of *D. obscurus*, and Musters (1983) recognized *D. formosus* as a subspecies of *D. obscurus*. Because these taxa are diagnosable and allopatrically distributed (*D. formosus* occurs on the Malay peninsula, *D. obscurus* on Borneo and Sumatra), I treat them as distinct species. *Draco formosus* and *D. obscurus* differ in the degree of distal expansion of the dewlap in males (greatly expanded in *D. formosus*, unexpanded or only slightly expanded in *D. obscurus*), in maximum body size (*D. formosus* reaches 114 mm SVL [n=62], whereas *D. obscurus* reaches only 100 mm SVL [n=25]), in the presence or absence of a caudal crest in males (present in *D. formosus*, absent in *D. obscurus*) and in several color pattern features (*D. obscurus* males lack the dark radial bands on the dorsal patagium that are present in *D. formosus* males, have a peach–colored eye ring that is lacking in *D. formosus*, and either lack or express only faintly the broad maroon band around the patagial margin that is present in *D. formosus*). I have not examined specimens of *D. obscurus* from Sumatra, and my recognition of Sumatran populations as *D. obscurus* follows Musters (1983).

Draco beccarii, *D. bourouniensis*, and *D. spilonotus* were considered to be synonyms of *D. lineatus* by Inger (1983), whereas Musters (1983) recognized each as subspecies of *D. lineatus*. I recognize each as full species on the basis of their allopatric distributions and because they are clearly diagnosable (see Musters, 1983). Although they are unrepresented in this analysis, I recognize *D. modigliani*, *Draco ochropterus*, and *D. rhytisima* on the same basis (see Musters, 1983).

"Tahulandang" represents an undescribed species from Tahulandang island (in the Sangir-Talaud island group) that is closely related to *D. biaro*, *D. caerhulians*, and *D. spilonotus* (McGuire, unpublished data).

Draco sumatranus, *D. boschmai*, and *D. timoriensis* were considered to be synonyms of *D. volans* by Inger (1983), whereas each was recognized as a distinct subspecies of *D. volans* by Musters (1983). *Draco boschmai*, *D. sumatranus*, *D. timoriensis*, and *D. volans* are each allopatrically distributed and diagnosable, and I therefore recognize each as distinct species. However, I should point out that *D. boschmai* itself is composed of several diagnosable, allopatric lineages and further taxonomic modification of this group will be necessary (McGuire, unpublished data). Each of the four taxa have distinct patagial color patterns, and only *D. boschmai* exhibits substantial intraspecific variation (between island populations separated by deep water channels). Populations of *D. sumatranus* from the Malay Peninsula, Borneo, and Sumatra all share the same dorsal color pattern. The dorsal patagium of both sexes is characterized by large, rounded white, pale yellow, or pale orange spots over most of its surface, with the base color of the distal half of the patagium black. *Draco volans* (from both Java and Bali) are sexually dichromatic with respect to the patagial color pattern. The patagia of males are characterized by a pale tan to pale orange base coloration overlain with several thick, black, concentrically arranged radial bands. Females lack the discrete black radial bands, instead having irregular, black sinuous blotches that are small and relatively diffuse proximally, grading to large and distinct distally. *Draco boschmai* and *D. timoriensis* can be distinguished from both *D. sumatranus* and *D. volans* based on the presence of an enlarged series of keeled paraveterbral scales and very different color patterns. *Draco timoriensis* are sexually dichromatic. The dorsal patagium of males is bright yellow, overlain with a diffuse series of gray radial bands, and the ventral patagium lacks melanic pigments. In *D. timoriensis* females, the dorsal patagium is black or dark brown with white horizontally oriented striations and the entire ventral patagial surface is saturated with melanic pigments. *Draco boschmai* exhibits substantial interisland variation in the dorsal color pattern, but none of the populations for which I have examined specimens approach the color patterns present in *D. timoriensis*, *D. sumatranus*, or *D. volans*. Like *D. volans* and *D. timoriensis*, *D. boschmai* are sexually dichromatic. In some *D. boschmai* populations, both the dorsal and ventral surfaces of the patagia of males are entirely suffused in melanic pigments. Females from these populations have patagia characterized by large pale spots on a dark base and lack ventral patagial melanic pigments. In other populations of *D. boschmai*, neither males nor females have extensive melanic pigments on either the dorsal or ventral surfaces of the patagium. I should emphasize that the color pattern differences listed here are not intended to be exhaustive and a thorough evaluation of the status of these taxa is beyond the scope of this paper. A taxonomic revision *D. boschmai* and *D. timoriensis* will be published elsewhere (McGuire, in preparation).

Choice of Outgroup Taxa

A recent molecular phylogenetic analysis of agamine relationships (Macey et al., submitted) found strong support for a clade composed primarily of Southeast Asian taxa. Their Southeast Asian clade included *Draco*, *Acanthosaura*, *Aphaniotis*, *Bronchocoela*, *Calotes*, *Ceratophora*, *Gonocephalus*, and *Japalura*. In their study, a clade including *J. tricarinata* and *J. variegata* was placed as the sister group of *Draco* with very strong support (100 bootstrap proportion, decay value of 24). However, *Japalura* was found to be paraphyletic, with a clade composed of *J. fasciatus*, *J. flaviceps*, and *J. splendida* relatively distantly related to *Draco*. In this analysis, I have relatively broad sampling from within the Southeast Asian clade. Representative outgroup taxa include *J. tricarinata*, *J. splendida*, *Aphaniotis fuscus*, and *B. cristatella*. *Aphaniotis fuscus* and *B. cristatella* also were suggested to be closely related to *Draco* in the unpublished dissertation of Moody (1980).

DNA Sequencing

DNA was prepared using phenol/chloroform (Maniatis et al., 1982) or Chelex (Walsh et al., 1991) extraction. Amplification of the entire ND2 protein coding gene, together with portions of three flanking tRNAs, was performed using the polymerase chain reaction (Saiki et al. 1988) following the protocol of Palumbi (1996). The external primers employed in this analysis include METf.1: 5'–AAGCAGTTGGGCCCATRCC–3' and ALAr.2m: 5'–AAAGTGTCTGAGTTGCATTCRG–3' and the internal primers used included ND2f.5: 5'–AACCAAACCCAACTACGAAAAT–3' and ND2r.6: 5'–ATTTTTCGTAGTTGGGTTTGRTT–3' (Macey et al. 1997). The external primers amplify a fragment that corresponds to positions 4437–5617b in the human genome (Anderson et al., 1981). Single-stranded PCR products were purified using Promega Wizard™ PCR Prep kits, sequenced using ABI Prism™ terminator cycle sequencing kits, purified again using Princeton Separations centri-sep spin columns, and visualized on an ABI 377 automated sequencer following standard protocols.

Alignment of the ND2 gene was performed by eye, although MacClade 3.04 (Maddison and Maddison, 1992) was used to verify that the sequence remained in frame throughout its length. Gaps in the ND2 gene were detected in five sequences, two of which are three bases in length and represent autapomorphies for their respective taxa. The remaining three gaps are six bases in length and occur in the same position in the ND2 gene, suggesting that they represent a single deletion event. The tRNAs were aligned according to secondary structural models (Kumazawa and Nishida, 1993; Macey and Verma, 1997). Those regions that could not be aligned with confidence were excluded from the analysis. The excluded regions totalled approximately 16 nucleotide positions within the D–loop and T–loop of $tRNA^{Trp}$ and a short spacer region between $tRNA^{Trp}$ and $tRNA^{Ala}$.

Data Analyses

Phylogenetic analyses were performed using a beta version of PAUP* (version 4.0d64 provided by D. L. Swofford) and GAML (Lewis, 1998). All parsimony analyses employed the heuristic search option with tree bisection-reconnection (TBR) branch swapping, MULPARS, and random addition of taxa (100 replicates). Parsimony analyses were performed under a variety of character weighting protocols to assess the effect that differential character weighting has on the phylogenetic estimate. In addition to applying equal weights to all base positions, I also estimated the transition–transversion bias using maximum–likelihood and reweighted transversions proportionally using step matrices. Frequencies of nucleotide substitutions at each codon position were also estimated from the data and used as a basis for differential weighting. Finally, analyses were conducted in which differential weighting was based on both transitions/transversion bias and codon position bias. Single–site gaps were treated as a fifth base in all analyses and were weighted equivalently with transitions. Phylogenetic signal for each treatment of the data set was evaluated using the g_1 statistic (Fitch, 1979, 1984; Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992), which measures the skewness of the distribution of random trees (10,000 random trees were used for each analysis). Tree support was assessed using the nonparametric bootstrap (Felsenstein, 1985; 1000 replicates). Bootstrap analyses utilized random addition of taxa, but with only one addition-sequence replicate per bootstrap replicate.

The sequence data also were analyzed under a maximum–likelihood optimality criterion. The protocol of Huelsenbeck and Crandall (1997) was followed such that less parameter–rich models of sequence evolution were employed initially and more complex models were applied thereafter, unless a likelihood–ratio test could not detect a significant increase in the likelihood scores of the phylogenetic estimates. The likelihood–ratio tests were evaluated using the c^2 distribution. Maximum–likelihood is computationally intensive and, following standard procedures, can require extensive CPU time to complete likelihood analyses of 55 taxa using all but the simplest models of evolution. Therefore, I employed two procedures in an attempt to reduce computation time of likelihood analyses. I used GAML (Lewis, 1998) to perform likelihood analyses under the HKY85 model and PAUP* 4.0d64 for all other models employed. All PAUP* likelihood analyses utilized the following set of procedures. First, the optimal tree under a weighted parsimony analysis (transversions weighted three times greater than transitions) was used as a starting tree for further branch swapping following optimization of model parameters on the parsimony tree. These model parameters were fixed in this analysis such that PAUP* was only required to optimize branch lengths during the swapping procedure. Once an optimal topology was discovered, the process was undertaken again by reoptimizing model parameters on the new likelihood tree. The procedure was continued until PAUP* could no longer find an alternative tree with a higher likelihood score.

GAML analyses were run on the University of Texas' Cray T3e massively-parallel supercomputer, which allowed me to complete 55-taxon likelihood analyses under the HKY85+G model in less than one day. Because GAML does a poor job of optimizing branch-lengths (Lewis, 1998), the topology recovered by GAML was then imported into PAUP for optimization of branch-lengths and HKY85+G (with proportion of invariant sites estimated from the data) model parameters. The ability of GAML to find globally optimal topologies remains largely untested and, in an attempt to avoid locally optimal solutions, I performed three separate GAML runs, each beginning with a different starting seed (following the same procedures used by Lewis [1998] in his initial assessment of his program using a data set of similar size). I then chose the best reoptimized GAML tree as a starting point for further branch swapping using PAUP*.

RESULTS

Phylogenetic Signal

The results of the g_1 analyses indicate that under each of the four weighting procedures employed in the parsimony analyses, the data set contains substantial phylogenetic structure. For each treatment, the g_1 values were significantly left-skewed at $P < 0.01$ (Hillis and Huelsenbeck, 1992).

Parsimony Analyses

After ambiguously aligned gap regions and the primer sequences are excluded from consideration, the mitochondrial DNA data set contained 1121 base positions. Of the 1121 included sites, 231 were constant and 211 were variable, yet parsimony–uninformative, leaving a total of 679 parsimony–informative characters.

Parsimony analysis of the data set with all base positions and gap characters equally weighted resulted in five equally parsimonious trees each of length 4926, the strict consensus of which is presented in Figure 2.1. The nonparametric bootstrap analysis results in a different topology, which is presented in Figure 2.2.

Analysis of the data set with transversions weighted three times greater than transitions resulted in two equally parsimonious trees of length 6350, the strict consensus of which is presented in Figure 2.3. The nonparametric bootstrap analysis results in a different topology, which is presented in Figure 2.4.

Analysis of the data with second codon positions weighted two times greater than first and third positions resulted in a single most parsimonious tree of length

6085 (Figure 2.5). The results of the nonparametric bootstrap analysis, which results in a different topology, are presented in Figure 2.6.

Analysis of the data with transversions weighted three times greater than transitions and second codon positions weighted two times greater than first and third codon positions resulted in 10 equally parsimonious trees of length 7849, the strict consensus of which is presented in Figure 2.7. Four islands of equally parsimonious trees were discovered in this analysis. The results of the nonparametric bootstrap analysis are presented in Figure 2.8.

Maximum–Likelihood Analyses

Maximum–likelihood analyses were conducted under four models of sequence evolution (all of which included estimation of the number of invariant sites from the data): the Jukes-Cantor model (JC69; Jukes and Cantor, 1969; Figure 2.9), the Felsenstein model (F81; Felsenstein, 1981; Figure 2.10), the Hasegawa–Kishino–Yano model with gamma–distributed rates (HKY85+G; Hasegawa et al., 1985; Figure 2.11), and the general–time–reversible model with gamma distributed rates (GTR+G; Lanave et al., 1984; Figure 2.12). The JC69 model is the least complex in that equal nucleotide frequencies are assumed and transitions and transversions are assumed equally likely. The F81 model adds three additional parameters in that the nucleotide frequencies are allowed to vary. The HKY85+G model incorporates two additional parameters because transitions and transversions are allowed to occur at unequal rates and because the model allows for gamma distributed rate heterogeneity among sites. Finally, the GTR+G model adds four more parameters by allowing six types of character state changes to occur at unequal rates, rather than the two types of changes (transitions and transversions) allowed by the HKY85+G model. Likelihood–ratio tests were used to assess whether the incorporation of additional model parameters significantly improved the estimated maximum–likelihood scores. The results of the likelihood–ratio tests are presented in Table 2.1. These analyses show that the incorporation of increased model complexity significantly increases the likelihood scores and, based on these results, the tree estimated under the GTR+G model is considered to be the preferred maximum–likelihood tree.

DISCUSSION

Parsimony Analyses

Parsimony analyses undertaken with four alternative sets of weighting procedures resulted in phylogenetic estimates that were largely, but not completely, congruent with one another. Thirty-seven of 50 nodes present on the strict consensus tree obtained with all characters weighted equally were also supported in the three analyses that employed differential character weighting. Not surprisingly, most (36 of 37) of the nodes that were common to all four analyses were relatively strongly supported (bootstrap values ≥ 62, $\bar{x} = 90.3$). Only the *D. cornutus* + *D. guentheri* clade was common to the four analyses despite weak bootstrap support ($\bar{x} = 39.3$).

Several major clades were strongly supported under all four weighting procedures. For ease of discussion, I will refer to these clades informally as the "*fimbriatus*", "lacrimal bone" (because the constituent species have lacrimal bones that are absent in the remaining species of *Draco*), "dorsal nostril" (all taxa characterized by dorso-posteriorly oriented nostrils), "*lineatus*", "*volans*", "Lesser Sunda" (endemic to the Lesser Sunda island group of Indonesia), and "Philippine *volans*" groups (see Figure 2.1). With the exception of the Philippines *volans* group, all of these clades were strongly supported in each of the four analyses (minimum bootstrap value of 80, $\bar{x}$ = 95.2). Relationships within these major clades generally were well–resolved and strongly supported (Figures 2.2, 2.4, 2.6, 2.8). However, relationships within the Philippines *volans* group proved particularly difficult to recover. Indeed, interspecific relationships within this clade remain essentially unresolved, with only the *D. reticulatus* + *D. cyanopterus* clade strongly supported. Furthermore, monophyly of *D. spilopterus*, which is readily diagnosed morphologically, was unsupported in each of the four analyses with three strongly supported *D. spilopterus* subclades placed variably throughout the Philippines *volans* clade depending on the weighting procedure employed.

Maximum–Likelihood Analyses

The maximum–likelihood analyses and likelihood–ratio tests indicate that an analysis employing the parameter–rich general–time–reversible model with gamma distributed rates explains the data significantly better than do analyses based on the JC69, F81, or HKY85+G models. The GTR+G phylogenetic estimate is largely congruent with the parsimony estimates, sharing 35 of the 37 nodes common to the four parsimony analyses. Those nodes that are strongly supported in the parsimony analyses also are recovered in the GTR+G maximum–likelihood analysis, and the few areas of disagreement are concentrated within the Philippine *volans* group.

Indeed, just as was the case with the parsimony analyses, maximum–likelihood also appears to have difficulty resolving relationships within the Philippines *volans* group and this appears to result from short internal branches together with long terminal branches (see Figures 2.9–2.12). Cunningham et al. (1998) investigated the performance of likelihood and distance methods under alternative branch length conditions and found that maximum–likelihood under the GTR model substantially outperformed likelihood under simpler models of evolution (as well as distance methods under simple or complex models) when the true underlying tree had short internal branches and long terminal branches. Their findings suggest that the GTR+G likelihood results are more likely to reflect the evolutionary history of the Philippine *volans* group than are the parsimony results or the likelihood results based on less complex models of evolution. Interestingly, only the GTR+G likelihood analysis supported the monophyly of *D. spilopterus*, despite the fact that *D. spilopterus* populations are virtually indistinguishable morphologically.

The GTR+G likelihood analysis also suggests that *Draco cornutus* and *D. palawanensis* are sister taxa and together places them as the sister taxon of the remaining members of the Philippine *volans* group. This finding is of interest because *D. cornutus* and *D. palawanensis* are the only members of the Philippine *volans* clade that one could argue do not occur in the Philippines biogeographic province. *Draco cornutus* is found on Borneo and *D. palawanensis* is endemic to Palawan, which generally is considered to be an extension of the Greater Sunda shelf and thus more closely related biogeographically to Borneo than to other Philippine islands (Figure 2.13; Everett, 1889; Heaney, 1985, 1986). The placement of *D. cornutus* and *D. palawanensis* is surprising because *D. cornutus* is very similar phenotypically to *D. guentheri*, a species that occurs on Mindanao and the islands of the Sulu Archipelago. These two species, which are placed as sister taxa in all four of the parsimony analyses and in the JC69 and F81 likelihood analyses, are characterized by malachite green dorsal coloration in males and an enlarged, thornlike superciliary scale. The similarities are sufficient that *D. guentheri* specimens have been misidentified as *D. cornutus* by herpetologists familiar with *D. cornutus* populations in adjacent Borneo (see Taylor, 1922). In contrast, *D. palawanensis* and *D. cornutus* are phenotypically dissimilar, with *D. palawanensis* males pale gray or tan in color and lacking an enlarged, thornlike superciliary scale. Before being elevated to full species status by McGuire (Chapter 1), *D. palawanensis* generally was thought to be conspecific with *D. sumatranus* rather than *D. cornutus* (Musters, 1983).

Comparison With Previous Phylogenetic Hypotheses

The only explicit phylogenetic hypothesis for *Draco* thus far presented in the literature was that of Musters (1983; Figure 2.14). However, Musters' (1983) hypothesis was not based on an empirical analysis of data, but rather on a thoughtful consideration of a small number of conspicuous and unpolarized morphological characters. In his defense, Musters made it clear from the outset that he considered his hypothesis to be highly speculative and at best a starting point for a more rigorous phylogenetic study. That said, it is not too surprising that the results of the present analysis disagree in many respects with those of Musters (1983). Indeed, only two of the 12 nodes on Musters' tree were recovered in the present study. The shared nodes represent the two clades that are most easily diagnosed on the basis of external morphology. The first shared clade is the dorsal nostril group, which is characterized by unique turret-like nostrils that are oriented dorsally and posteriorly on the snout. The second clade, composed of *D. blanfordi*, *D. formosus*, *D. obscurus*, and *D. taeniopterus*, is characterized by the presence in males of a distally expanded dewlap that is overlain with greatly enlarged scales. Muster's (1983) also suggested that *D. melanopogon* and *D. haematopogon* are sister taxa. If *D. indochinensis* is ignored (Musters considered *D. indochinensis* to be a subspecies of *D. blanfordi* and, consequently, did not include this taxon on his phylogenetic tree), this hypothesis is consistent with the likelihood analyses as well as two of the four parsimony analyses (the analysis that assumed equal weighting of characters and the analysis in which second codon positions were weighted twice that of first and third positions). The remaining nodes on the Musters (1983) phylogenetic tree are not consistent with any of the analyses conducted here.

Although Musters (1983) provided the only explicit phylogenetic hypothesis, he and others have implied relationships with their taxonomies. For example, Musters (1983) followed Hennig (1936) in recognizing *Draco bimaculatus* as a subspecies of *D. lineatus*. This taxonomy implies that *D. bimaculatus* and the *lineatus* group taxa form a clade. Although the F81 maximum–likelihood analysis is consistent with this hypothesis, all other analyses, including the preferred GTR+G maximum–likelihood analysis indicate that *D. bimaculatus* is neither the sister taxon of, nor nested within, the *D. lineatus* group (Figures 2.1–2.12).

Inger (1983) treated all of the members of the *volans* group as a single species, *Draco volans*. His conservative taxonomy is consistent with the phylogenetic results presented here in that all of the taxa that he synonymized with

D. volans form a monophyletic group. Other clades recovered here that Inger (1983) treated as single species include *D. formosus* + *D. obscurus* (recognized as *D. obscurus* by Inger), and the lineatus group (recognized as *D. lineatus* by Inger).

The phylogenetic data also provide evidence that *Draco indochinensis* should not be treated as a synonym of *D. blanfordi* (Inger, 1983), or as a subspecies of *D. blanfordi* (Musters, 1983), as it is neither the sister taxon of *D. blanfordi* nor a member of the clade that includes *D. blanfordi*, *D. taeniopterus*, *D. formosus*, and *D. obscurus* (Figures 2.1–2.12). The phylogenetic data are consistent with the morphological and distributional data (see above) indicating that *D. indochinensis* is a distinct evolutionary species.

CONCLUSIONS

The phylogenetic analysis of a mitochondrial DNA sequence data set provides the first robust estimate of *Draco* phylogenetic relationships. Although the maximum parsimony and maximum–likelihood analyses are not entirely congruent, it is nevertheless clear which nodes are well supported by referring to the nonparametric bootstrap results conducted under the parsimony optimality criterion. Furthermore, consideration of each of the alternative trees in comparative analyses will not be prohibitive computationally given the small number of alternative phylogenetic estimates that were obtained. The phylogenetic study discovered several major *Draco* clades that are strongly supported. Relationships within the major clades are generally well–resolved and strongly supported, although this is not the case for the Philippine *volans* group.

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Musters, C. J. M. 1983. Taxonomy of the genus *Draco* L. (Agamidae, Lacertilia, Reptilia). Zool. Verhandelingen 199:1–120.

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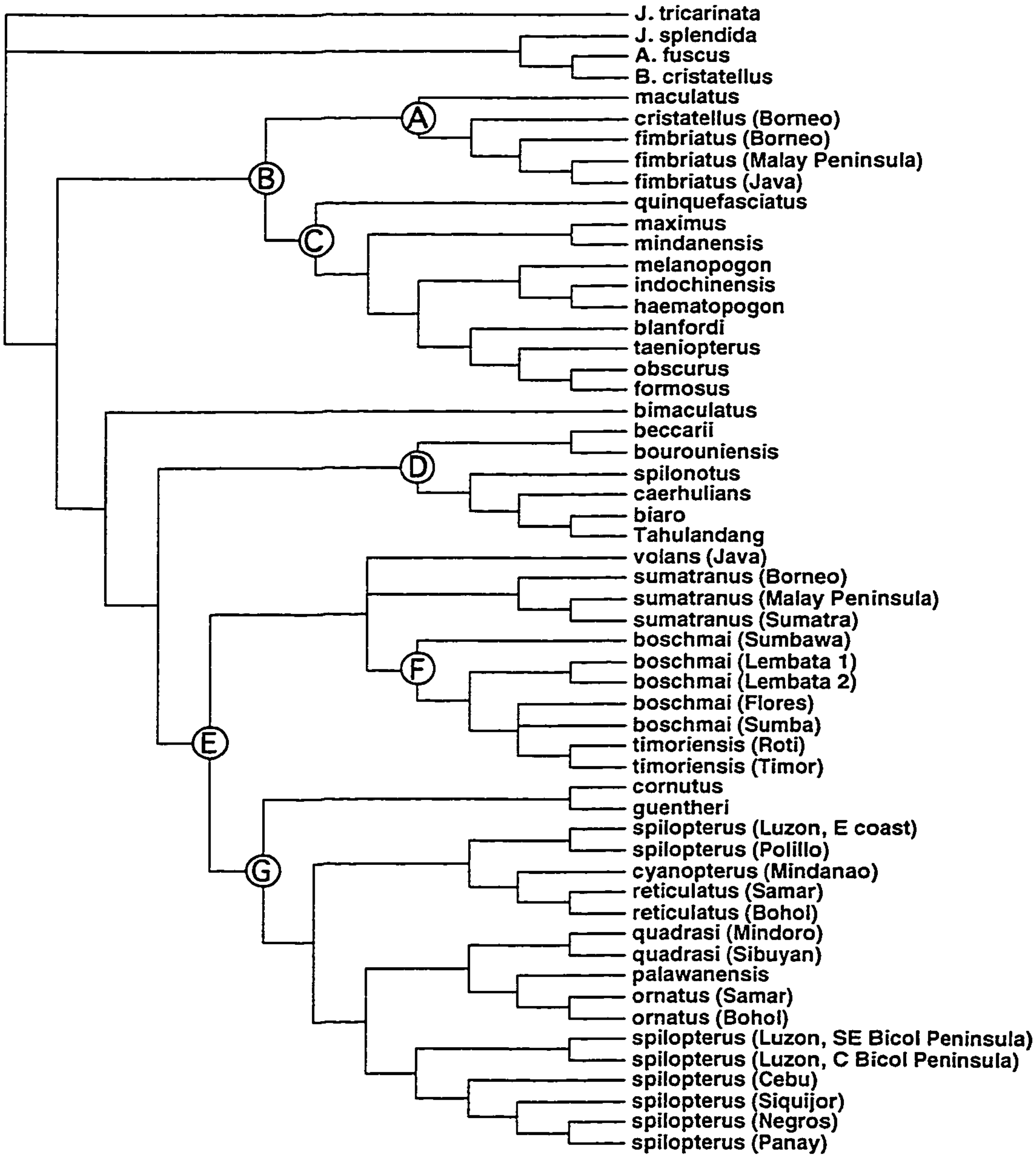
Taylor, E. H. 1922. The lizards of the Philippine Islands. Bureau of Science, Manila.

Walsh, S. P., D. A. Metzger, and R. Higuchi. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques 10:506–513.

Table 2.1. Results of the likelihood ratio tests. JC69 = Jukes-Cantor model, F81 = Felsenstein model, HKY85+G = Hasegawa–Kishino–Yano model with gamma distributed rates, GTR+G = general time reversible model with gamma distributed rates. Following Bonferroni correction, the significance level for rejection of the null hypothesis is set to 1.67 x 10^{-2}.

Models Compared	$\log L_0$	$\log L_1$	–2 log L	d.f.	*P*
H0: JC69 H1: F81	24,296.93	24,163.32	267.22	3	$p<0.0001$
H0: F81 H1: HKY85+G	24,163.33	21,526.42	5,273.82	2	$p<0.0001$
H0: HKY85+G H1: GTR+G	21,526.42	21,498.24	56.36	4	$p<0.0001$

Figure 2.1. Strict consensus of five trees obtained in a parsimony analysis with all sites equally weighted. CI (excluding uninformative characters) = 0.276; RI (excluding uninformative characters) = 0.554; RC = 0.164. The nodes identified by letters refer to the following informally recognized clade names: A = *fimbriatus* group, B = lacrimal bone group, C = dorsal nostril group, D = *lineatus* group, E = *volans* group, F = Lesser Sunda group, G = Philippine *volans* group.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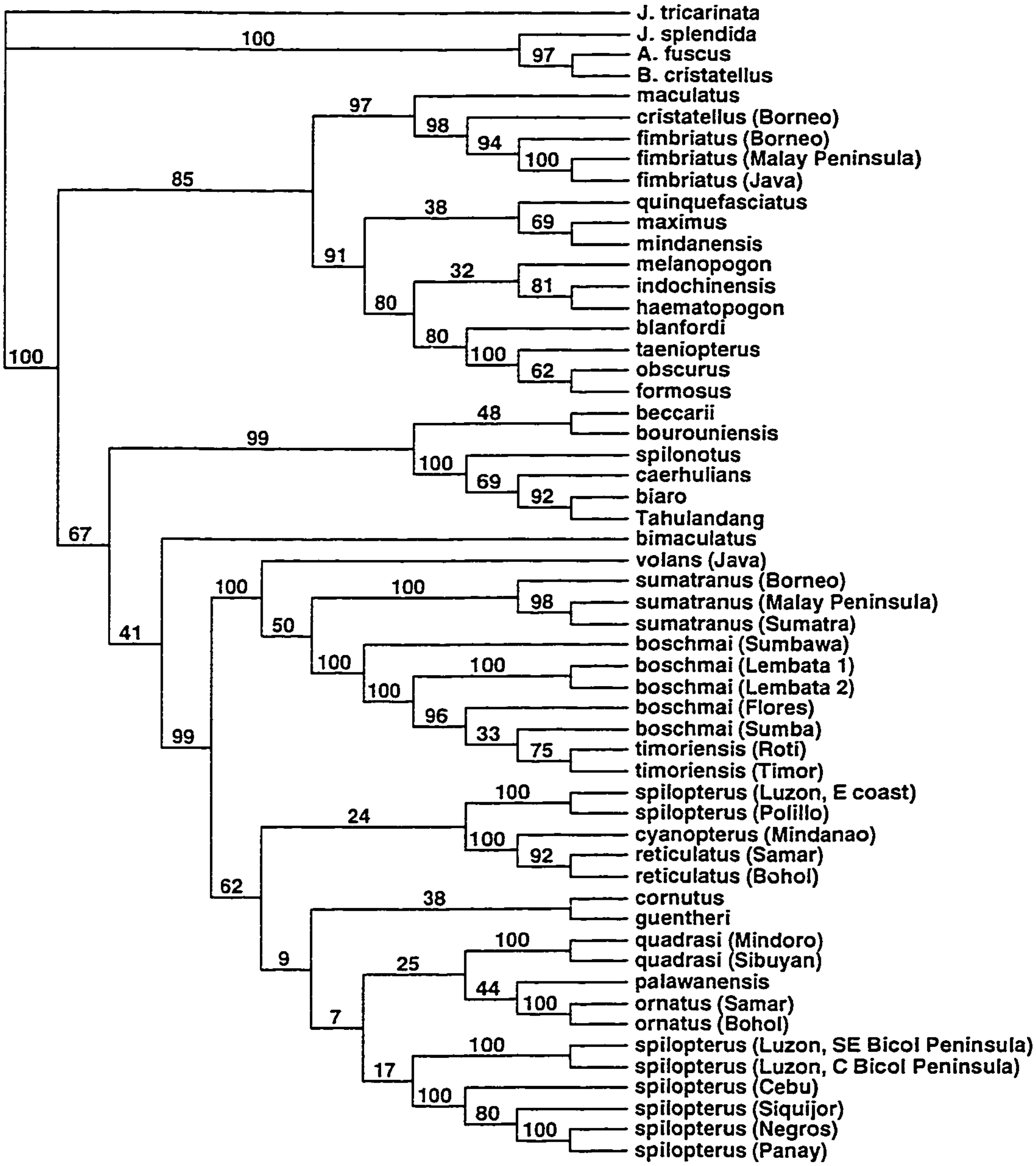
J. splendida
A. fuscus
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
quinquefasciatus
maximus
mindanensis
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Flores)
boschmai (Sumba)
timoriensis (Roti)
timoriensis (Timor)
cornutus
guentheri
spilopterus (Luzon, E coast)
spilopterus (Polillo)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
palawanensis
ornatus (Samar)
ornatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)
A
B
C
D
E
F
G

Figure 2.2. 50% majority rule consensus tree obtained in the nonparametric bootstrap analysis with all characters equally weighted.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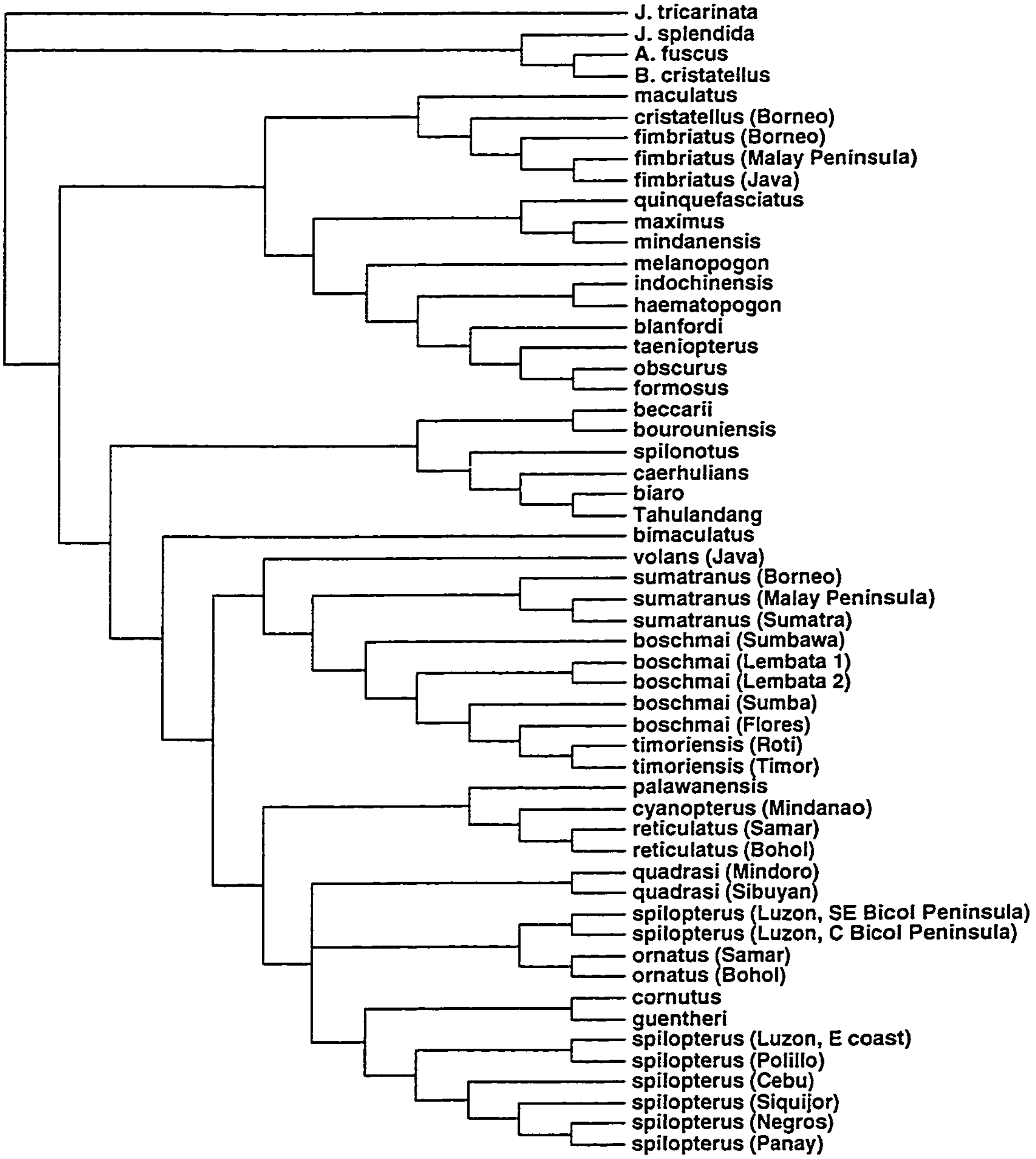
J. splendida
97
A. fuscus
B. cristatellus
97
maculatus
98
cristatellus (Borneo)
94
fimbriatus (Borneo)
85
100
fimbriatus (Malay Peninsula)
fimbriatus (Java)
38
quinquefasciatus
69
maximus
mindanensis
91
32
melanopogon
81
indochinensis
80
haematopogon
80
blanfordi
100
100
taeniopterus
62
obscurus
formosus
48
beccarii
bourouniensis
99
spilonotus
100
caerhulians
69
92
biaro
Tahulandang
67
bimaculatus
volans (Java)
100
100
sumatranus (Borneo)
98
sumatranus (Malay Peninsula)
50
sumatranus (Sumatra)
41
boschmai (Sumbawa)
100
100
boschmai (Lembata 1)
100
boschmai (Lembata 2)
boschmai (Flores)
96
33
boschmai (Sumba)
99
75
timoriensis (Roti)
timoriensis (Timor)
100
spilopterus (Luzon, E coast)
24
spilopterus (Polillo)
cyanopterus (Mindanao)
100
92
reticulatus (Samar)
62
reticulatus (Bohol)
38
cornutus
guentheri
100
quadrasi (Mindoro)
9
25
quadrasi (Sibuyan)
palawanensis
44
100
ornatus (Samar)
7
ornatus (Bohol)
100
spilopterus (Luzon, SE Bicol Peninsula)
17
spilopterus (Luzon, C Bicol Peninsula)
spilopterus (Cebu)
100
80
spilopterus (Siquijor)
100
spilopterus (Negros)
spilopterus (Panay)

Figure 2.3. Strict consensus of five trees obtained in a parsimony analysis with transversions weighted three times greater than transitions. CI (excluding uninformative characters) = 0.288; RI (excluding uninformative characters) = 0.595; RC = 0.183.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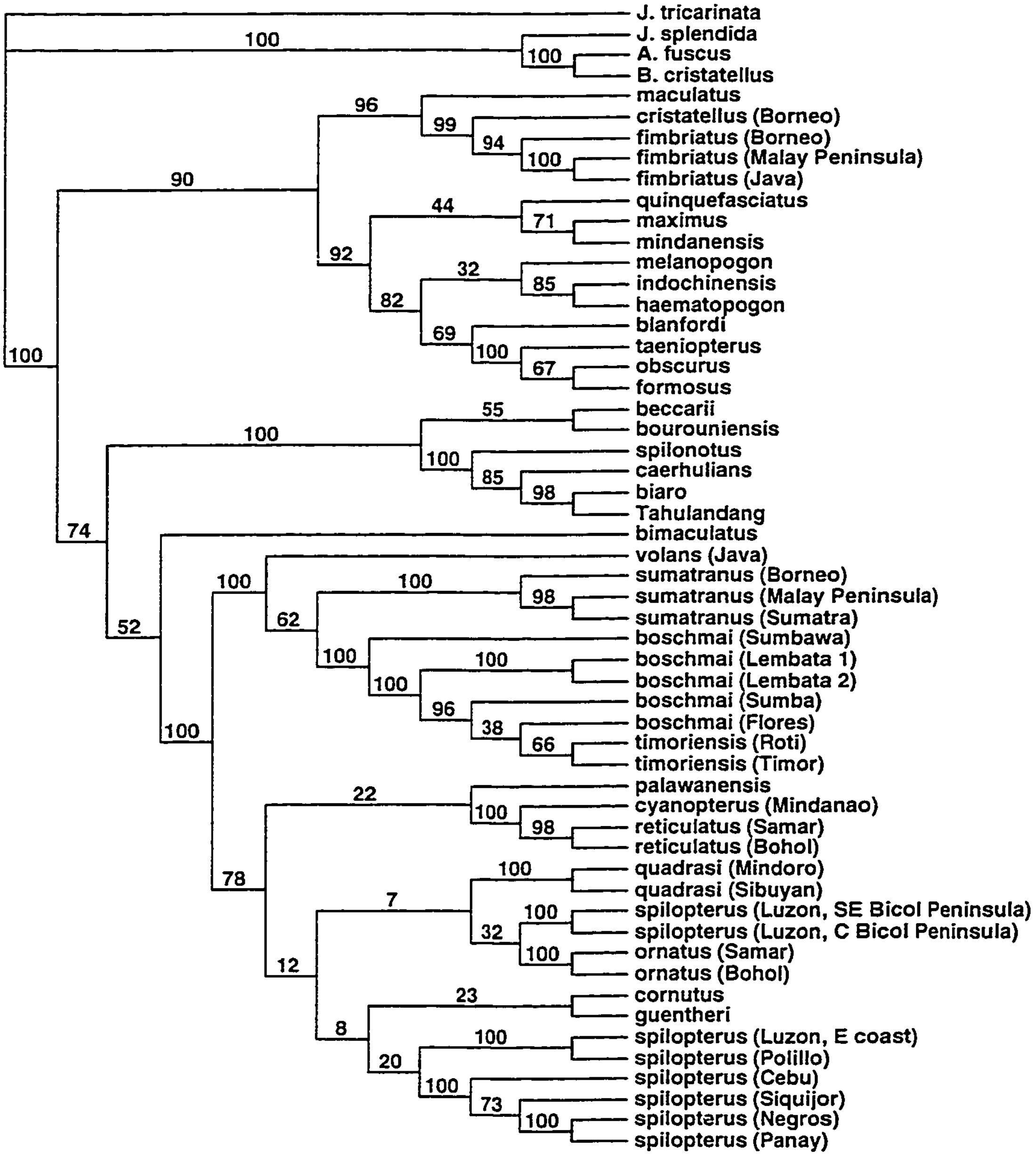
J. splendida
A. fuscus
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
quinquefasciatus
maximus
mindanensis
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
bimaculatus
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Sumba)
boschmai (Flores)
timoriensis (Roti)
timoriensis (Timor)
palawanensis
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
ornatus (Samar)
ornatus (Bohol)
cornutus
guentheri
spilopterus (Luzon, E coast)
spilopterus (Polillo)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)

Figure 2.4. 50% majority rule consensus tree obtained in the nonparametric bootstrap analysis with transversions weighted three times greater than transitions.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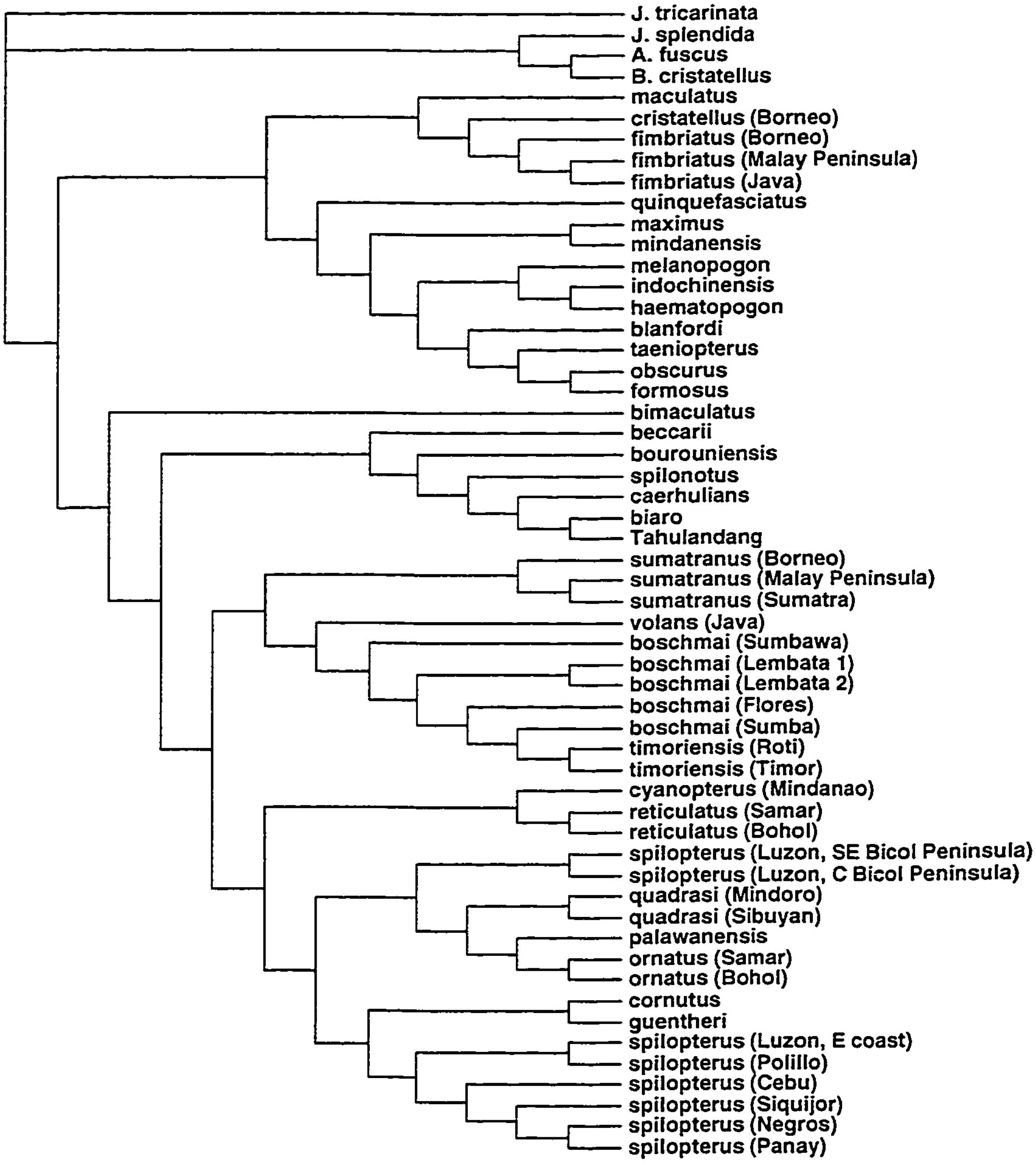
100
J. splendida
100
A. fuscus
B. cristatellus
96
maculatus
99
cristatellus (Borneo)
94
fimbriatus (Borneo)
90
100
fimbriatus (Malay Peninsula)
fimbriatus (Java)
44
quinquefasciatus
71
maximus
92
mindanensis
32
melanopogon
85
indochinensis
82
haematopogon
69
blanfordi
100
100
taeniopterus
67
obscurus
formosus
55
beccarii
100
bourouniensis
spilonotus
100
caerhulians
85
98
biaro
Tahulandang
74
bimaculatus
volans (Java)
100
100
sumatranus (Borneo)
98
sumatranus (Malay Peninsula)
52
62
sumatranus (Sumatra)
boschmai (Sumbawa)
100
100
boschmai (Lembata 1)
100
boschmai (Lembata 2)
96
boschmai (Sumba)
100
38
boschmai (Flores)
66
timoriensis (Roti)
timoriensis (Timor)
22
palawanensis
100
cyanopterus (Mindanao)
98
reticulatus (Samar)
reticulatus (Bohol)
100
quadrasi (Mindoro)
78
quadrasi (Sibuyan)
7
100
spilopterus (Luzon, SE Bicol Peninsula)
32
spilopterus (Luzon, C Bicol Peninsula)
100
ornatus (Samar)
12
ornatus (Bohol)
23
cornutus
guentheri
8
100
spilopterus (Luzon, E coast)
20
spilopterus (Polillo)
100
spilopterus (Cebu)
73
spilopterus (Siquijor)
100
spilopterus (Negros)
spilopterus (Panay)

Figure 2.5. Strict consensus of five trees obtained in a parsimony analysis with second codon positions weighted two times greater than first and third codon positions. CI (excluding uninformative characters) = 0.285; RI (excluding uninformative characters) = 0.563; RC = 0.172.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J. splendida
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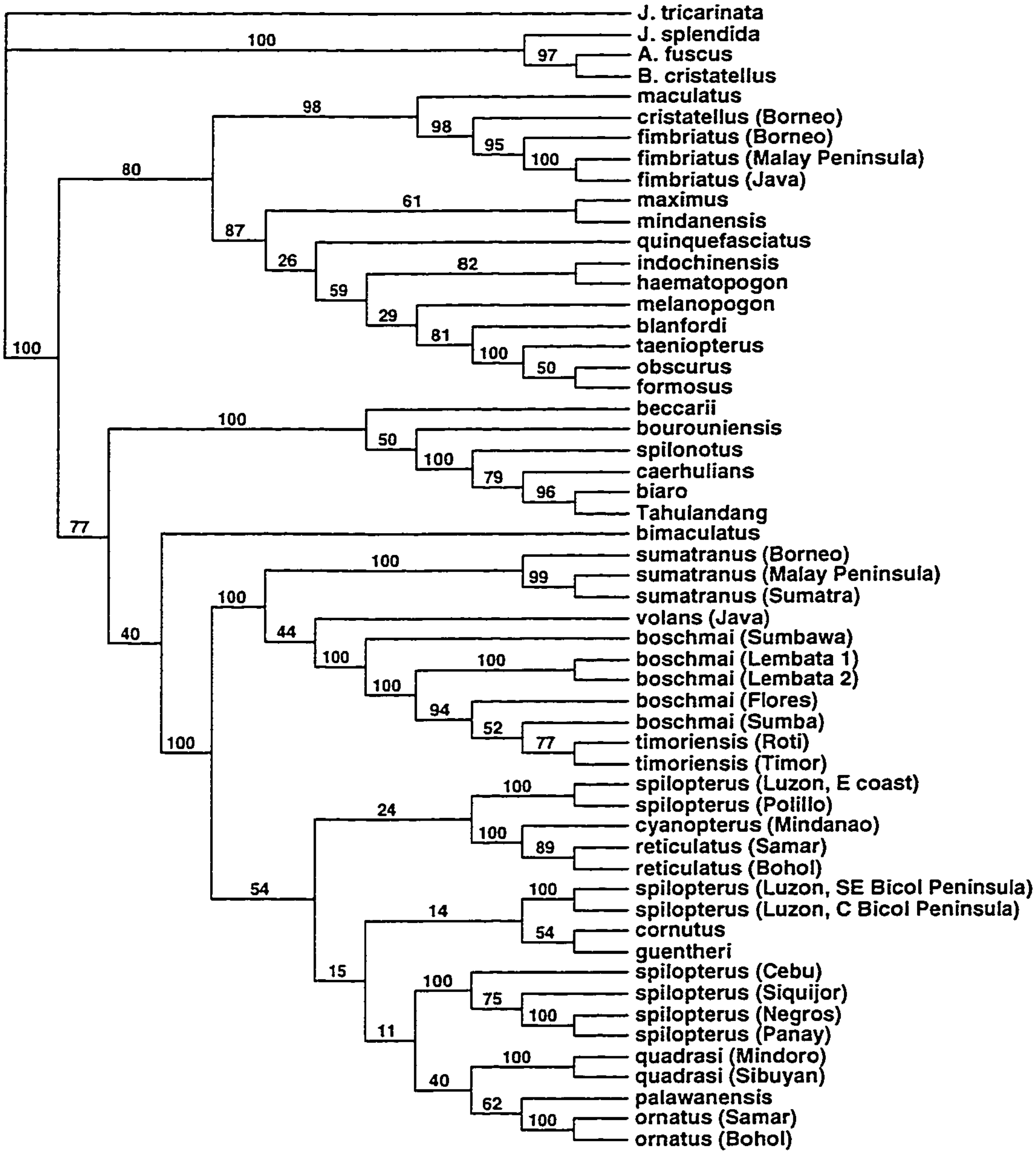
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
quinquefasciatus
maximus
mindanensis
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
volans (Java)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Flores)
boschmai (Sumba)
timoriensis (Roti)
timoriensis (Timor)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
quadrasi (Mindoro)
quadrasi (Sibuyan)
palawanensis
ornatus (Samar)
ornatus (Bohol)
cornutus
guentheri
spilopterus (Luzon, E coast)
spilopterus (Polillo)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)

Figure 2.6. 50% majority rule consensus tree obtained in the nonparametric bootstrap analysis with second codon positions weighted two times greater than first and third codon positions.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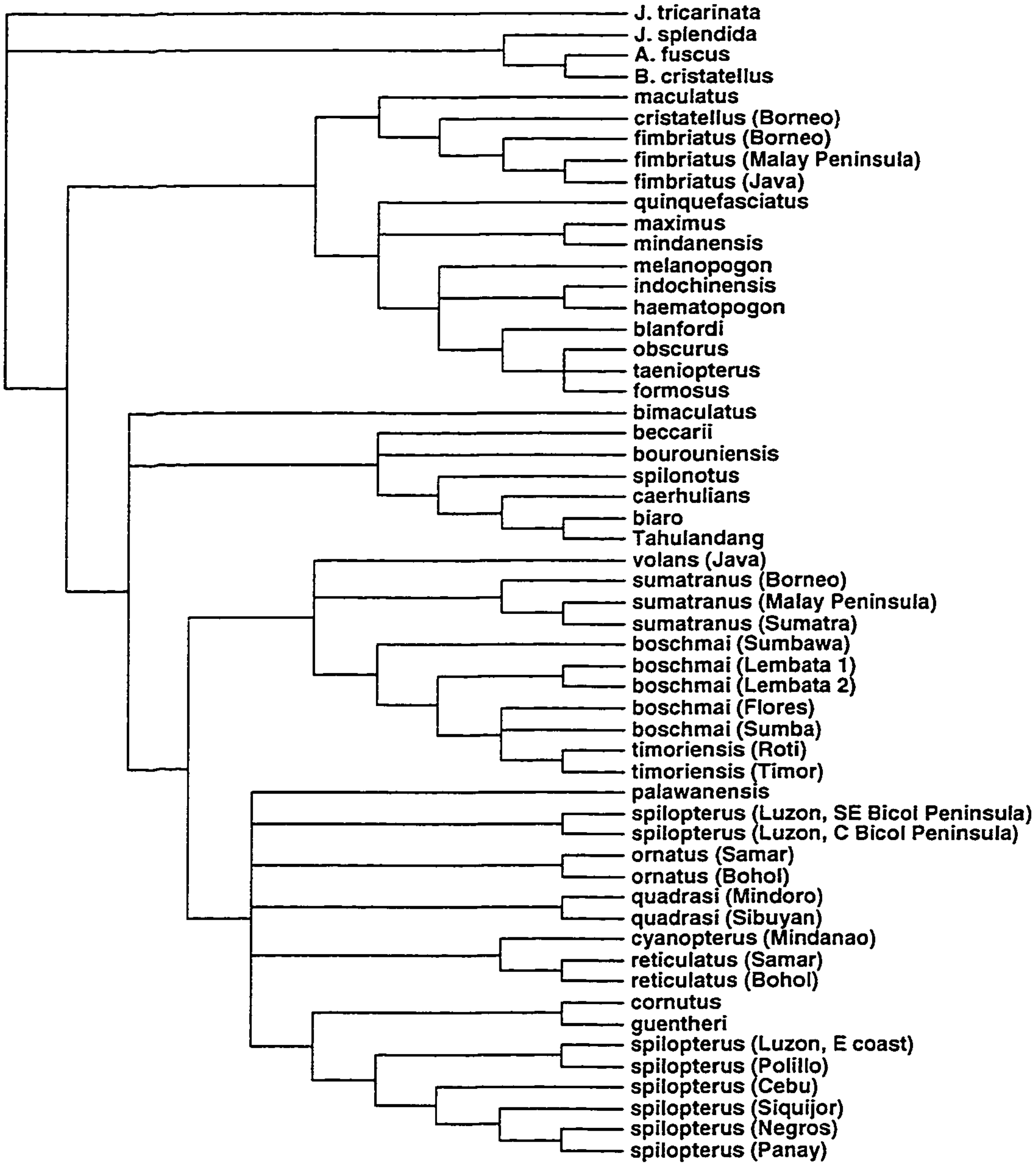
100
J. splendida
97
A. fuscus
B. cristatellus
98
maculatus
98
cristatellus (Borneo)
95
fimbriatus (Borneo)
100
fimbriatus (Malay Peninsula)
80
fimbriatus (Java)
61
maximus
87
mindanensis
quinquefasciatus
26
82
indochinensis
haematopogon
59
melanopogon
29
blanfordi
81
100
taeniopterus
100
50
obscurus
formosus
100
beccarii
50
bourouniensis
100
spilonotus
79
caerhulians
96
biaro
Tahulandang
77
bimaculatus
100
sumatranus (Borneo)
99
sumatranus (Malay Peninsula)
100
sumatranus (Sumatra)
volans (Java)
44
boschmai (Sumbawa)
40
100
100
boschmai (Lembata 1)
boschmai (Lembata 2)
100
boschmai (Flores)
94
52
boschmai (Sumba)
100
77
timoriensis (Roti)
timoriensis (Timor)
100
spilopterus (Luzon, E coast)
24
spilopterus (Polillo)
cyanopterus (Mindanao)
100
89
reticulatus (Samar)
reticulatus (Bohol)
54
100
spilopterus (Luzon, SE Bicol Peninsula)
14
spilopterus (Luzon, C Bicol Peninsula)
54
cornutus
guentheri
15
100
spilopterus (Cebu)
75
spilopterus (Siquijor)
100
spilopterus (Negros)
11
spilopterus (Panay)
100
quadrasi (Mindoro)
40
quadrasi (Sibuyan)
palawanensis
62
100
ornatus (Samar)
ornatus (Bohol)

Figure 2.7. Strict consensus of five trees obtained in a parsimony analysis with transversions weighted three times greater than transitions and second codon positions weighted two times greater than first and third codon positions. CI (excluding uninformative characters) = 0.299; RI (excluding uninformative characters) = 0.603; RC = 0.194.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J. splendida
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B. cristatellus
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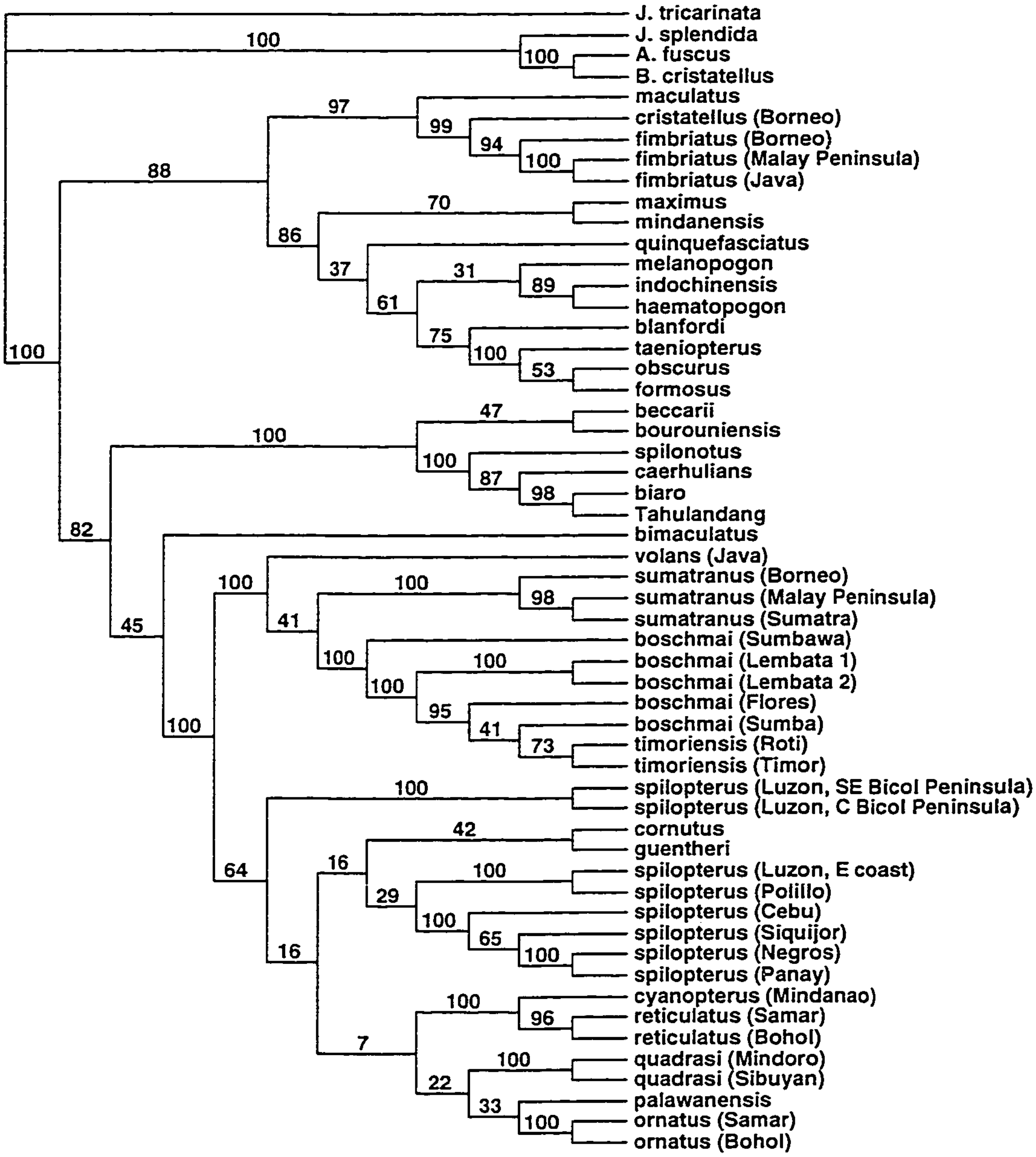
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
quinquefasciatus
maximus
mindanensis
melanopogon
indochinensis
haematopogon
blanfordi
obscurus
taeniopterus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Flores)
boschmai (Sumba)
timoriensis (Roti)
timoriensis (Timor)
palawanensis
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
ornatus (Samar)
ornatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
cornutus
guentheri
spilopterus (Luzon, E coast)
spilopterus (Polillo)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)

Figure 2.8. 50% majority rule consensus tree obtained in the nonparametric bootstrap analysis with transversions weighted three times greater than transitions and second codon positions weighted two times greater than first and third codon positions.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J. splendida
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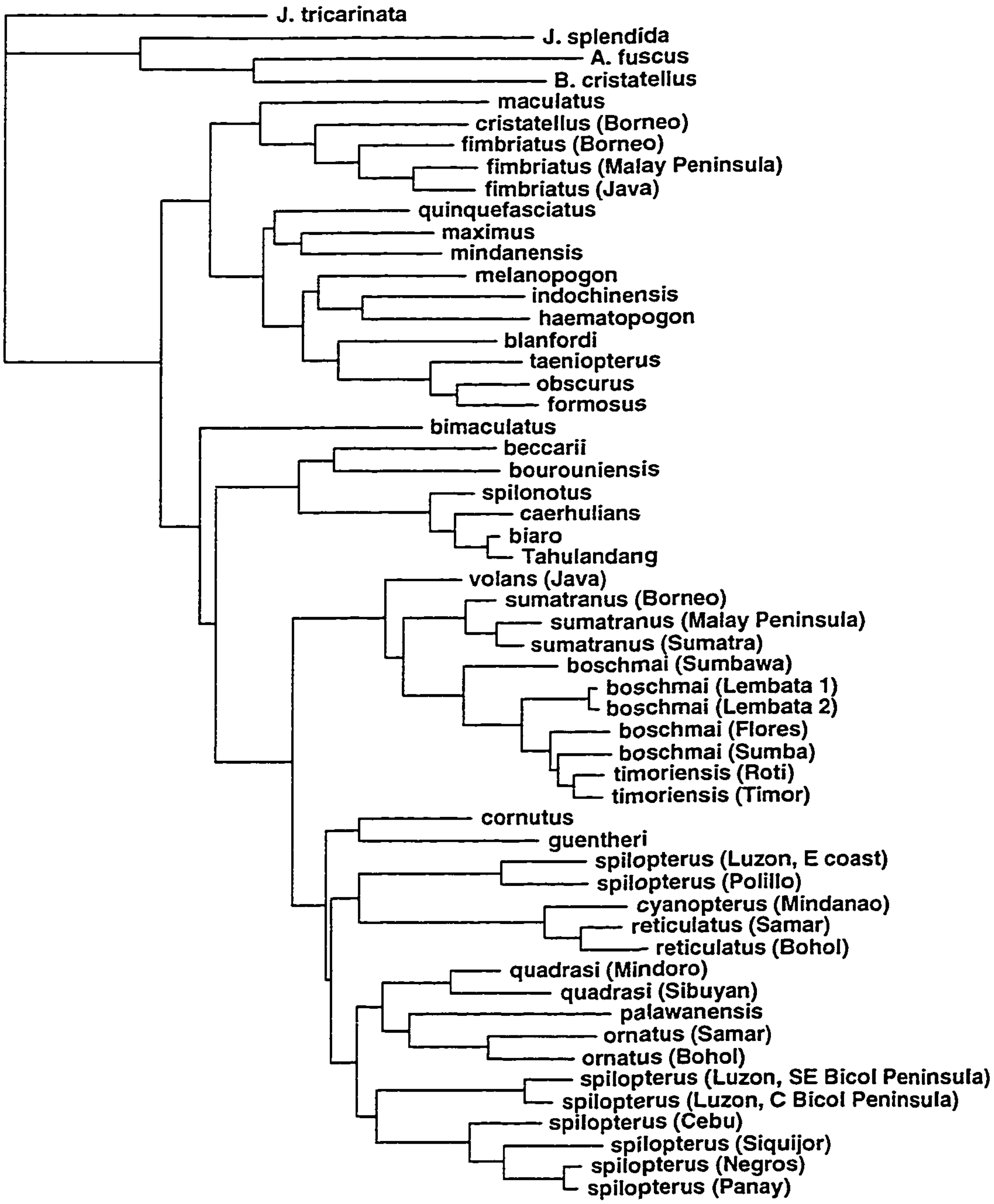
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
maximus
mindanensis
quinquefasciatus
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
bimaculatus
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Flores)
boschmai (Sumba)
timoriensis (Roti)
timoriensis (Timor)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
cornutus
guentheri
spilopterus (Luzon, E coast)
spilopterus (Polillo)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
palawanensis
ornatus (Samar)
ornatus (Bohol)
100
100
97
99
94
100
88
70
86
37
31
89
61
75
100
53
100
47
100
100
87
98
82
100
100
41
100
98
45
100
100
100
95
41
73
100
100
64
42
16
100
29
100
65
100
16
100
96
7
100
22
33
100

Figure 2.9. Results of the maximum–likelihood analysis under the JC69 model. The -log likelihood score obtained in this analysis was 24,296.93.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J. splendida
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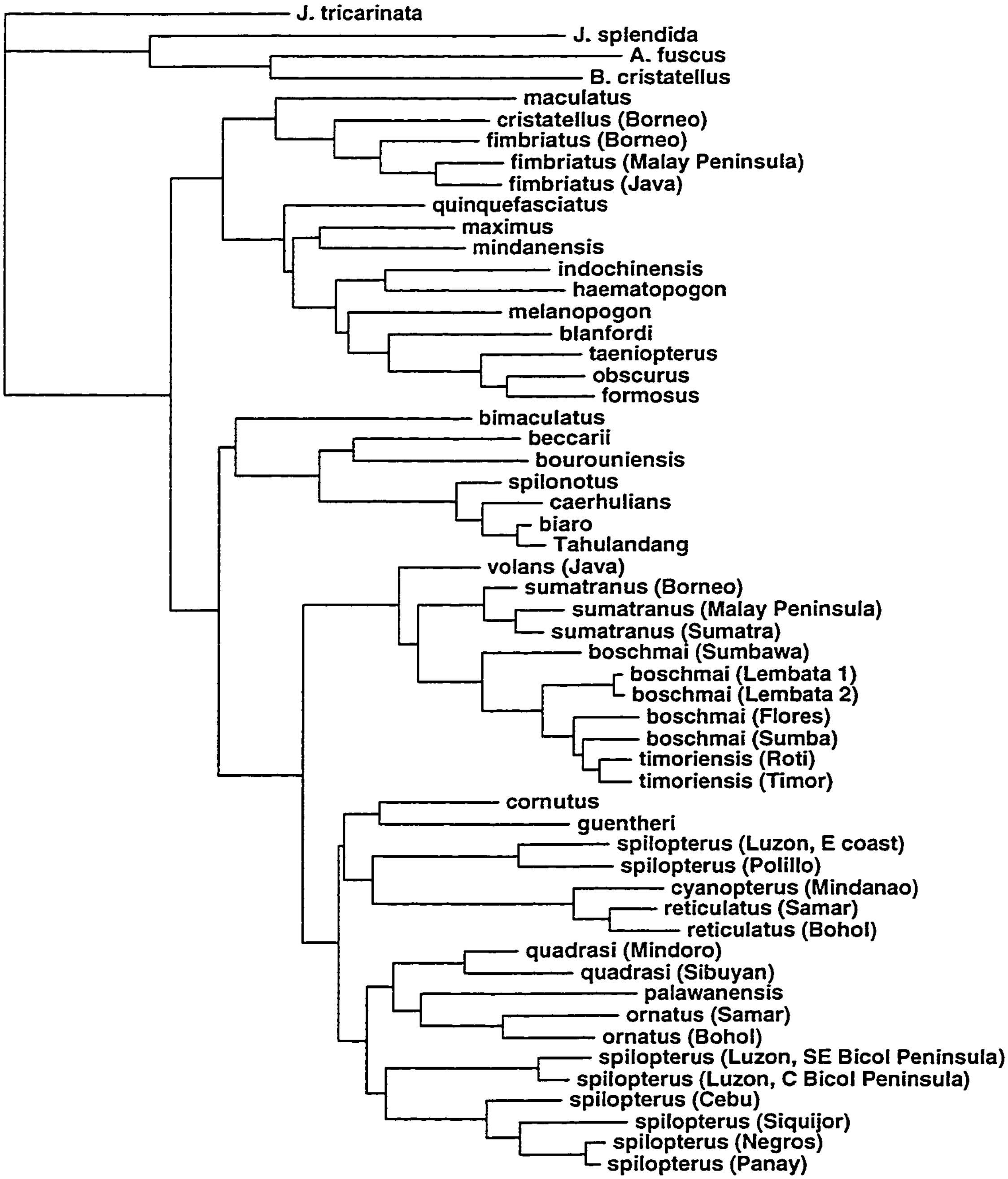
fimbriatus (Malay Peninsula)
fimbriatus (Java)
quinquefasciatus
maximus
mindanensis
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Flores)
boschmai (Sumba)
timoriensis (Roti)
timoriensis (Timor)
cornutus
guentheri
spilopterus (Luzon, E coast)
spilopterus (Polillo)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
palawanensis
ornatus (Samar)
ornatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)

Figure 2.10. Results of the maximum–likelihood analysis under the F81 model. The -log likelihood score obtained in this analysis was 24,163.32.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J. splendida
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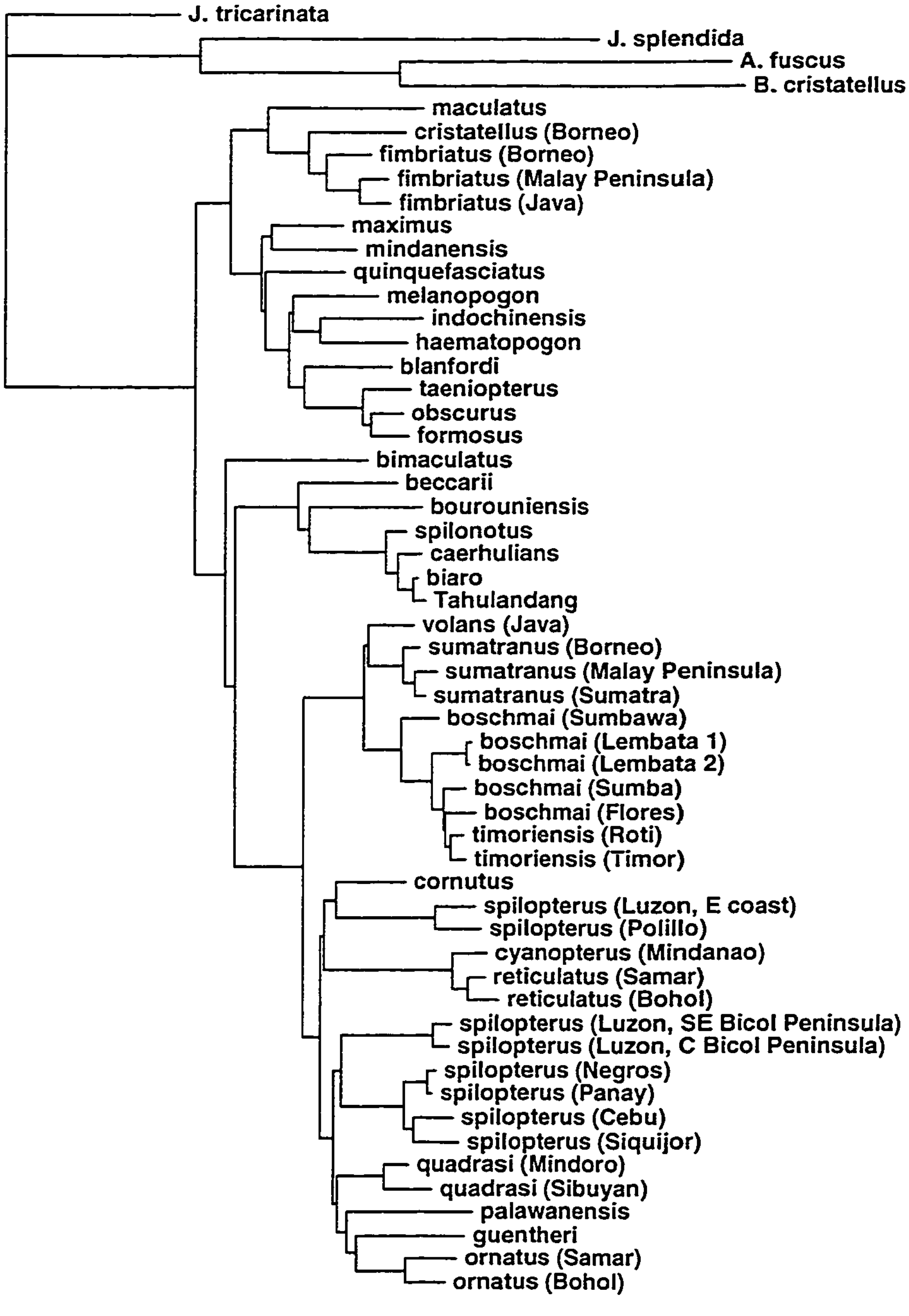
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
quinquefasciatus
maximus
mindanensis
indochinensis
haematopogon
melanopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Flores)
boschmai (Sumba)
timoriensis (Roti)
timoriensis (Timor)
cornutus
guentheri
spilopterus (Luzon, E coast)
spilopterus (Polillo)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
palawanensis
ornatus (Samar)
ornatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)

Figure 2.11. Results of the maximum–likelihood analysis under the HKY85+G model. The -log likelihood score obtained in this analysis was 21,528.40.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J. splendida
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B. cristatellus
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fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
maximus
mindanensis
quinquefasciatus
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Sumba)
boschmai (Flores)
timoriensis (Roti)
timoriensis (Timor)
cornutus
spilopterus (Luzon, E coast)
spilopterus (Polillo)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
spilopterus (Negros)
spilopterus (Panay)
spilopterus (Cebu)
spilopterus (Siquijor)
quadrasi (Mindoro)
quadrasi (Sibuyan)
palawanensis
guentheri
ornatus (Samar)
ornatus (Bohol)

Figure 2.12. Results of the maximum–likelihood analysis under the GTR+G model. The -log likelihood score obtained in this analysis was 21,498.24.

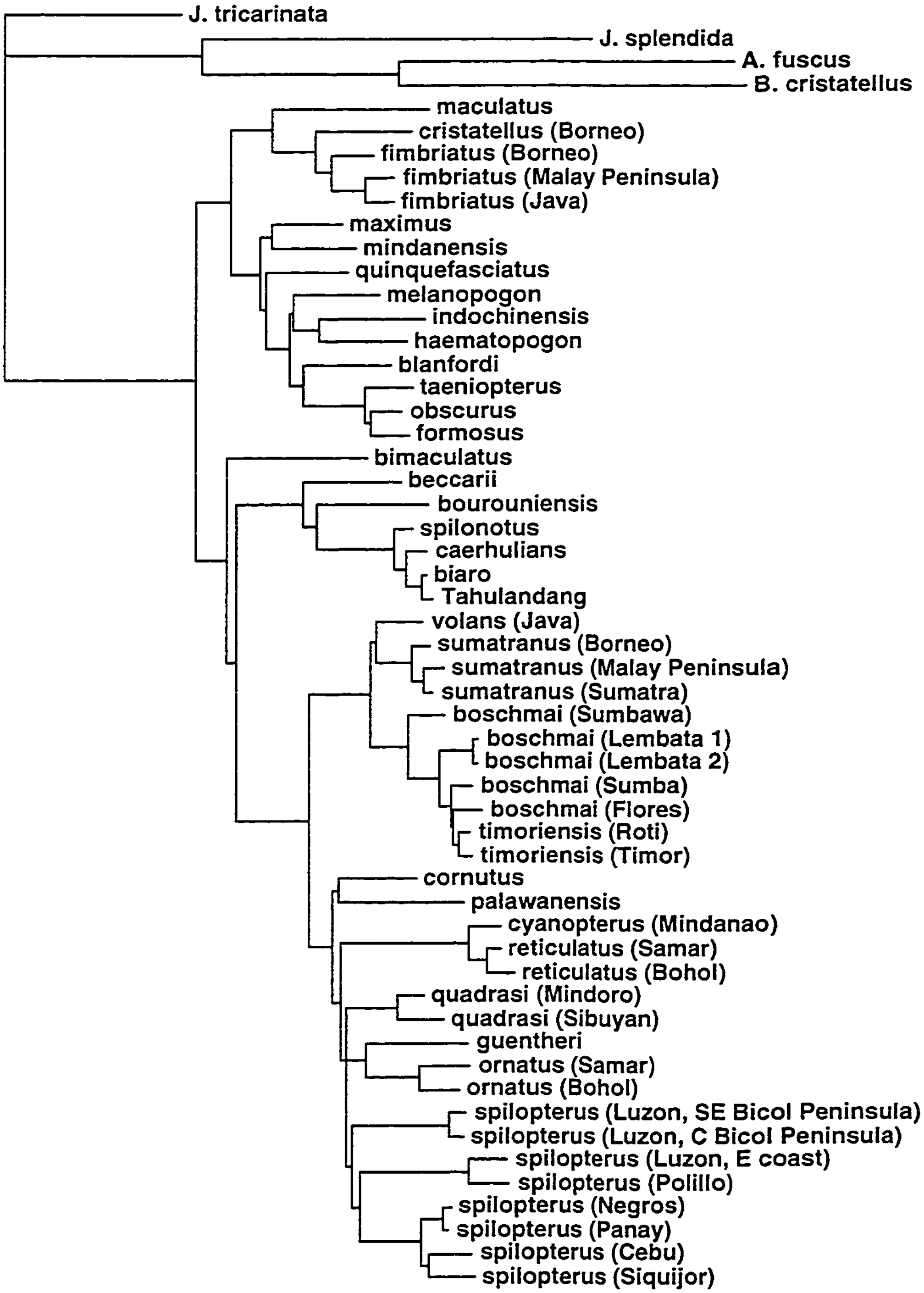

J. tricarinata
J. splendida
A. fuscus
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
maximus
mindanensis
quinquefasciatus
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Sumba)
boschmai (Flores)
timoriensis (Roti)
timoriensis (Timor)
cornutus
palawanensis
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
guentheri
ornatus (Samar)
ornatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
spilopterus (Luzon, E coast)
spilopterus (Polillo)
spilopterus (Negros)
spilopterus (Panay)
spilopterus (Cebu)
spilopterus (Siquijor)

Figure 2.13. Distribution map for *Draco cornutus*, *D. guentheri*, and *D. palawanensis*.

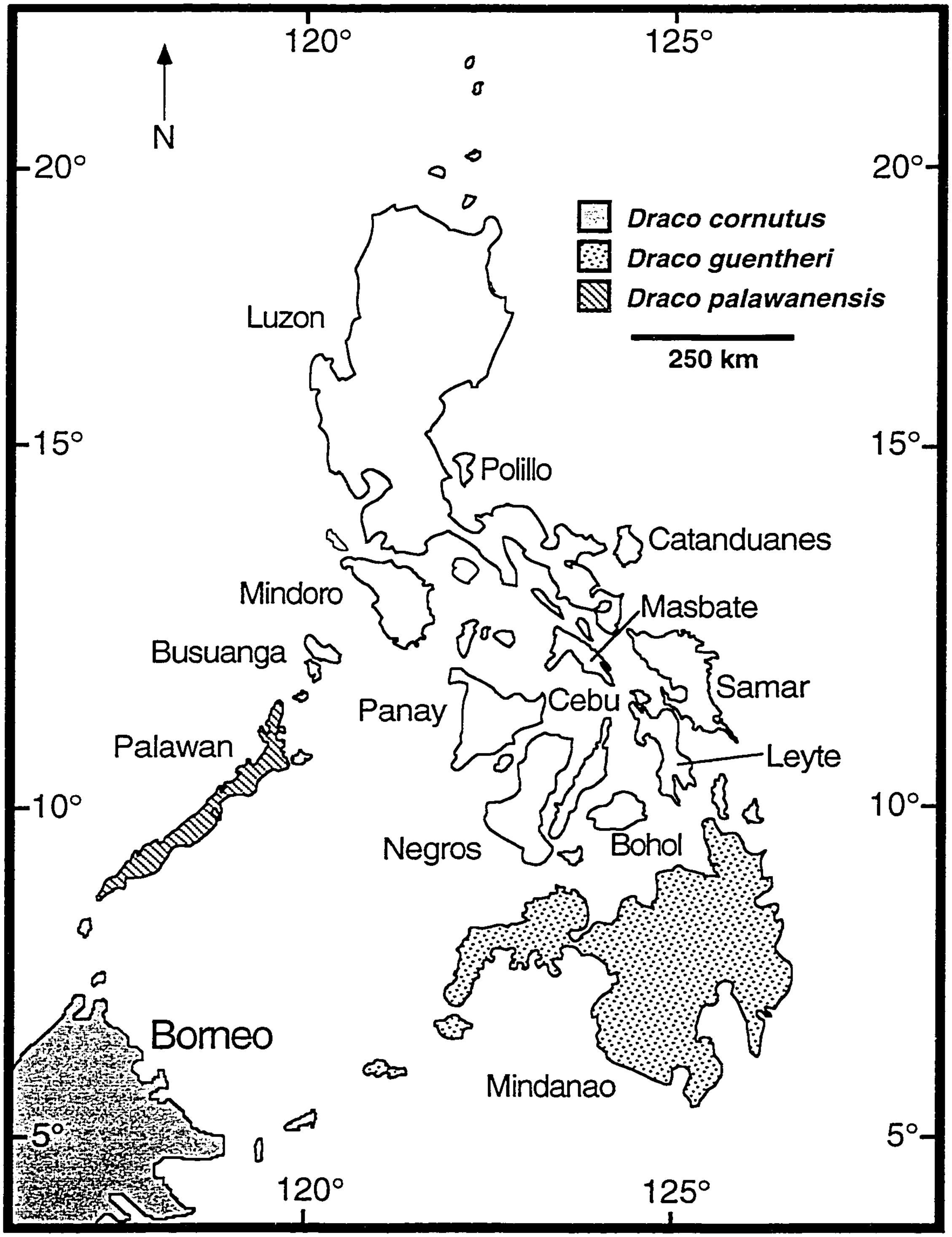
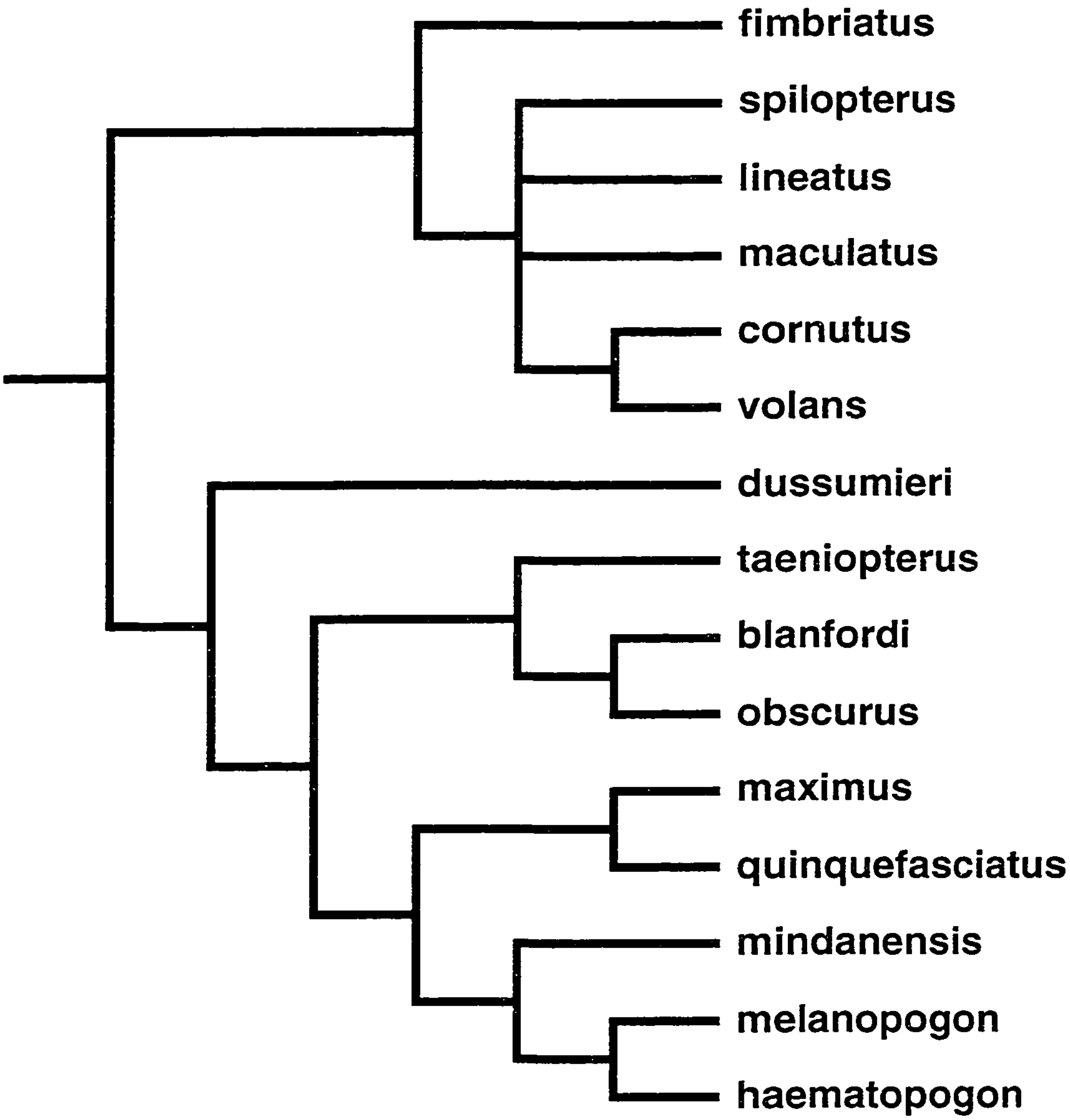

120°
125°
N
20°
20°
15°
15°
10°
10°
5°
5°
120°
125°
Draco cornutus
Draco guentheri
Draco palawanensis
250 km
Luzon
Polillo
Catanduanes
Mindoro
Masbate
Busuanga
Samar
Panay
Cebu
Palawan
Leyte
Negros
Bohol
Borneo
Mindanao

Figure 2.14. The phylogenetic hypothesis of Musters (1983).


fimbriatus
spilopterus
lineatus
maculatus
cornutus
volans
dussumieri
taeniopterus
blanfordi
obscurus
maximus
quinquefasciatus
mindanensis
melanopogon
haematopogon

CHAPTER 3

BODY SIZE EVOLUTION IN SOUTHEAST ASIAN FLYING LIZARDS (GENUS *DRACO*): IMPLICATIONS FOR THE EVOLUTION OF GLIDING PERFORMANCE

Body size has a tremendous impact on virtually every aspect of an organism's biology (Calder, 1984; Schmidt-Nielsen, 1984; Pennycuick, 1992). Locomotor performance, a behavior with direct fitness consequences, is no exception. However, with respect to most forms of locomotion, the impact that changes in body size have on performance can be exceedingly complex such that developing an understanding of the direct consequences of size change is difficult. For example, in a study of the effects of ontogenetic changes in size and shape on lizard sprinting performance, Garland (1985) found that data on scaling relationships of body proportions were inadequate to predict scaling relationships of performance measures such as maximum speed. Garland (1985) further argued that direct measurement of stride length, stride frequency, lengths of limb segments, hindlimb span, forelimb span, muscle contractile properties, and muscle contractile speed would all be necessary to determine the scaling of maximal running speed. This level of complexity is likely to apply to any locomotor mode, or for that matter any biomechanical function, that derives from the interaction between morphology and physiological processes such as muscle contraction. Therefore, if one wishes to develop a better understanding of the direct consequences that size–dependent changes in morphology have on locomotor performance, an ideal performance variable would allow for the decoupling of morphological and physiological factors. Gliding locomotion satisfies this requirement in that the power required to generate aerodynamic forces during gliding flight are derived exclusively from potential energy of the animal's body mass; no flapping of wings is involved. Therefore, variation in gliding performance associated with changes in overall body size is likely to be associated with changes in morphology because physiological processes are not an available substrate upon which selection may act to modify performance (although behavioral modifications remain a possibility). Given this advantage, the flying lizards (genus *Draco*) of Southeast Asia represent an excellent model system with which to investigate the role that body size evolution has played in the evolution of locomotor performance.

The flying lizards are remarkable in their ability to glide long distances using an airfoil formed by wing-like patagial membranes supported by elongate thoracic ribs. Although these lizards are famous for their gliding ability, little is known about the gliding performance of any one species, let alone interspecific variation in performance (but see Klingel, 1965). Flying lizards exhibit substantial body size variation, with maximum body mass spanning roughly an order of magnitude, and this size variation may have important consequences with respect to gliding performance. The purpose of this paper is to describe interspecific body size variation in flying lizards, and then to explore the implications that this size variation has for the evolution of gliding performance. In particular, I am interested in ascertaining whether evolutionary changes in body size have imposed constraints on aerodynamic performance. To address this question, I will analyze interspecific scaling relationships in *Draco* and then apply aerodynamic theory to determine whether larger species incur performance constraints associated with increased body size.

Allometric Variation in Body Size

The effect that body size variation is expected to have on gliding performance can be predicted by allometric scaling relationships (McMahon and Bonner, 1984; Schmidt-Nielsen, 1984). We know from simple geometric principles that under conditions of isometry (the condition in which individuals are essentially scale-replicas of one another, identical in shape), area varies with the square of the linear dimension, and volume (together with mass under constant density) varies with the cube of the linear dimension (Thompson, 1961; Sweet, 1980). Therefore, if *Draco* species of different sizes vary isometrically, we expect larger species to have relatively less wing area available for lift-generation on a per-unit mass basis than will smaller species, and we would further expect that the evolution of large size would compromise gliding locomotor performance. However, if *Draco* vary allometrically such that the relationship between area and mass is unaffected by overall changes in body size, then the evolution of large body size might have little or no impact on gliding performance. This condition is sometimes referred to as functional equivalence or functional similarity in the scaling/allometry literature (e.g. Sweet, 1980; LaBarbera, 1989). In this paper, I analyze allometric scaling relationships in flying lizards and formulate a general model predicting the consequences of size evolution for the evolution of gliding performance.

MATERIALS AND METHODS

Body Size Data

Body size data were obtained from 886 specimens representing 29 species of flying lizard. I measured body mass to the nearest 0.1g using either a 10g, 20g, 30g, or 50g spring-loaded pesola scale immediately after specimens were sacrificed for preparation in the field. The specimens were then preserved with 10 percent buffered formalin with their patagia fully extended, a procedure which allowed area measurements to be obtained in the laboratory. Measurements of total ventral surface area, wing area, and wing span (see Figure 3.1 for definitions) were obtained by using a digital scanner and importing the images into NIH Image 1.55 (U.S. National Institutes of Health; available at http://rsb.info.nih.gov/nih-image/). Because a primary objective of this study is to assess the role that large size has on gliding performance, and because there is substantial ontogenetic variation in wing loading (McGuire, unpublished data), I have only considered large adult representatives of each species in the calculation of species area and mass values. I calculated species values by taking the mean score of all individuals with a snout-vent length (SVL) within 10 percent of the largest individual in my sample (see Tables 3.1–3.2). I identified the largest individual on the basis of SVL rather than body mass because body mass exhibits substantial individual variation, particularly in females (gravid female body mass may be 50% or more greater than that of a nongravid female of the same SVL), and I did not want to bias the scaling analyses by using only particularly bulky individuals.

To analyze the relationship between surface area and body mass, I am focusing on wing loading, which is defined as follows:

$$\text{Wing loading} = Mg/S \qquad (1)$$

where M = body mass, g = acceleration due to gravity, and S is surface area of the lift-generating structures (Norberg, 1985, 1990). Wing loading is an important parameter for flight performance analyses because it is expected to be proportional to the square of the equilibrium flight or glide velocity (McMahon and Bonner, 1983; Norberg, 1985, 1990). Therefore, individuals with higher wing loading are expected to achieve their equilibrium glide at higher velocities. Traditionally, the area term in the wing loading equation describes the area measurement for the wing proper (Norberg, 1985, 1990). However, if other parts of the body are also contributing to the generation of lift, then area measurements for these parts of the body should also be included in the area term. This appears to be the case for *Draco*. All species of *Draco* expand their lateral throat lappets when gliding, which increases ventral surface area. Furthermore, the cross-sectional shape of the limbs suggests that each limb also may serve as an airfoil. Because it is possible that the arbitrary selection of a single area measure may have a substantial affect on the associated scaling relationships, I performed separate regression analyses using both total ventral area and wing area proper. Wing loading was evaluated across species by regressing surface area (S) on body mass (M).

Scaling Relationships

There has been some debate in the literature regarding the appropriate null hypothesis to be used in scaling analyses. Emerson and Bramble (1993) argued that isometry is the appropriate null model because isometry makes no *a priori* assumptions regarding function or performance. However, others have suggested that functional similarity is the appropriate null model because it is "the norm rather than the exception" in allometry studies (Sweet, 1980; see also Gould, 1966). Indeed, Rayner (1981) suggested that gliding animals in general exhibit functional equivalence. In this analysis, I treat isometry and functional similarity as alternative hypotheses and test them simultaneously. To test these hypotheses, I applied the power function (Huxley, 1932):

$$Y = aM^{b} \qquad (2)$$

This generally is log–transformed such that the equation takes the form

$$\mathrm{Log}\, Y = \mathrm{Log}\, a + b\, \mathrm{Log}\, M \qquad (3)$$

This equation explains how Y, in this case area, varies with respect to a size variable, in this case body mass M. When considering area/mass relationships, the expected slope under isometry, represented by the regression coefficient b, is 0.67 because area is expected to vary with the square of the linear dimension and mass with the cube. Under functional similarity, the expected slope is 1.0 because area and mass are expected to change at the same rate due to allometry.

Independent Contrasts

This study is focused primarily on the comparative analysis of interspecific data, and the nature of the analysis requires an explicitly phylogenetic framework. Felsenstein (1985) showed convincingly that data points representing species values should not be treated as independent observations in statistical analyses because of the potentially confounding effects of phylogenetic history (but see Price, 1997). However, a number of data transformation procedures can account for phylogenetic nonindependence if a phylogenetic estimate is available. The approach that I employed here was the calculation of standardized independent contrasts (Felsenstein, 1985) using the program CAIC version 2.02 (Purvis and Rambout, 1995). The phylogenetic estimates of *Draco* relationships that served as the historical framework for calculation of independent contrasts were generated by the author (Figures 3.2–3.6; Chapter 2). In Chapter 2, I analyzed 1165 base pairs of mitochondrial ND2 and tRNA sequence data for 51 species/populations of *Draco* and four outgroup species under maximum likelihood and maximum parsimony optimality criteria. The maximum likelihood analyses employed four alternative models of sequence evolution, and likelihood ratio tests showed that the estimate obtained under the general–time–reversible model with rate heterogeneity (GTR+G) explained the data significantly better than did the less parameter–rich Jukes–Cantor, Felsenstein, and Hasegawa–Kishino–Yano (with rate heterogeneity) models. Therefore, the GTR+G tree (Figure 3.2) is the only maximum likelihood estimate that will be employed here in the calculation of independent contrasts. Parsimony analyses were conducted under four alternative weighting procedures (all characters equally weighted, transversions weighted three times greater than transitions, 2nd codon positions weighted two times greater than first and third positions, and a combination of the latter two). In contrast to the likelihood analyses, it is not clear which of the parsimony weighting procedures has produced a significantly superior phylogenetic estimate. Therefore, independent contrast scores were calculated using the estimates derived from each of the parsimony analyses (see Figures 3.3–3.6). Branch length estimates for the parsimony trees were obtained by optimizing the GTR+G model parameters (including branch lengths) on the parsimony topology. In three of the four sets of parsimony analyses, multiple equally parsimonious trees were recovered. Rather than recalculating branch lengths for all of the equally parsimonious trees, I used only the 50% majority-rule consensus trees recovered in nonparametric bootstrap analyses under each of the four weighting criteria. To avoid heteroscedasticity of the residuals in the regression analyses, the branch lengths were log–transformed. After log-transformation, all branch lengths were multiplied by a constant to satisfy format requirements of CAIC. Purvis and Rambout (1995) also recommended regressing the standardized independent contrast scores on the reconstructed values at the adjacent node to assess whether the contrasts were appropriately standardized. I performed these analyses and found that the data appear to be understandardized. However, several branch length transformation procedures were attempted (including the log, square, square root, and reciprocal of the branch lengths). None of these transformations solved the problem and I therefore settled on the log transformation (which corrected problems of heteroscedasticity of the residuals). This may result in lack of independence of the variables of interest.

Price (1997) discussed situations in which applying independent contrasts in lieu of species values might be misleading. For example, species values should be independent data points when the traits of interest are under selection and there is sufficient additive genetic variance to allow the characters in question to be held at their contemporary mean values by selection. If these conditions hold true, then use of independent contrasts will inflate type II error, as well as require a variety of assumptions (such as a particular phylogenetic estimate) that, if violated, could compromise the results. Price (1997) also argued that use of independent contrasts may be inappropriate if there is one or more unobserved variables that are correlated with the variables of interest. In this situation, independent contrasts can control for some, but not all, of the confounding effects of unobserved variables and, for the reasons listed above, the limited beneficial effects of independent contrasts may not outweigh the cost of inflated type II error. Following the recommendations of Price (1997), I performed regression analyses on the untransformed species values, as well as on standardized independent contrasts.

Regression Model

Choosing the appropriate regression model for use in scaling analyses is a complex issue (Gould, 1966; Rayner, 1985; La Barbera, 1989; Harvey and Pagel, 1991). It has been argued that the most commonly used regression model, ordinary least squares (OLS), is inappropriate because it does not account for measurement error in the independent variable (Rayner, 1985; La Barbera, 1989; Harvey and Pagel, 1991). Several authors have suggested that one model within the general structural relations family of models, the reduced major axis (RMA), is the appropriate model for scaling studies (Ricker, 1973; Rayner, 1985) because it accounts for error in the independent variable. The RMA slope is simply the OLS regression coefficient divided by the correlation coefficient (Ricker, 1973; Rayner, 1985). I present both the OLS and RMA regression coefficients and 95% confidence intervals. The confidence intervals for OLS and RMA are identical (Kermack and Haldane, 1950), although they will be asymmetrical about the RMA regression line if the correlation coefficient is less than 1.0 (Ricker, 1973) and proper care should thus be taken when interpreting the confidence intervals with respect to RMA. All regression analyses based on independent contrasts scores were regressed through the origin and the independent variables were positivized (Garland et al., 1992).

RESULTS

The body size data by species are summarized in Tables 3.1 and 3.2. *Draco* exhibit substantial interspecific size variation, and it is clear that there has been substantial size evolution during the history of this group. In the context of the phylogenetic estimates presented here, large shifts in size have occurred on multiple occasions and neither the four largest species of *Draco* (*D. blanfordi*, *D. fimbriatus*, *D. indochinensis*, *D. maximus*; each with a maximum SVL > 130 mm), nor any subset of these four species, forms a monophyletic group.

Draco exhibit significant intersexual variation in the area–mass relationship. In regression analyses based on untransformed species values, an *F* test of adjusted means indicated that the slopes obtained both for the regression of total area and wing area on mass differ significantly between the sexes ($p<0.01$). Therefore, males and females were treated separately in all subsequent analyses.

The results of the regression analyses are presented in Figures 3.7–3.8 and in Tables 3.3–3.4. The observed regression coefficients are very close to the expected value under isometry (0.67), with 0.67 falling well within the 95% confidence intervals in all cases. The expected slope under functional similarity (1.0) falls well outside of the 95% confidence intervals in all cases. The use of RMA regression results in a slightly greater estimated slopes than those estimated using OLS, but the high correlation coefficients minimize the effect that choice of regression model has on this analysis. The use of untransformed species values versus standardized independent contrasts also has minimal effect on the results (Tables 3.3–3.4).

DISCUSSION

The analyses presented here indicate that isometry cannot be rejected for *Draco* species, whereas functional similarity can be rejected with confidence. This finding indicates that larger species generally have less surface area available on a per unit mass basis for the generation of lift forces than do smaller species. In other words, larger species have relatively higher wing loading. Wing loading is a parameter that has received much attention in the aerodynamics literature (it was first used in aeronautics), and the expected effects of relative wing loading variation are well understood (Norberg, 1990). Thus, we can make predictions regarding expected relative gliding performance in *Draco* species of different sizes. For example, aerodynamic theory tells us that wing loading is expected to be proportional to the square of the equilibrium glide velocity. The equilibrium glide velocity is a theoretical expectation under steady–state aerodynamics that maximizes the lift–to–drag ratio and minimizes the glide angle. Consider a theoretical *Draco* glide trajectory: the glide begins with a ballistic phase in which the lizard is accelerating under gravity to build the velocity that it requires in order to obtain sufficient lift to support its body mass. Once the lizard has reached the velocity that will maximize its lift–to–drag ratio, it should level out into the equilibrium phase of the glide. The equilibrium glide velocity should maximize the potential horizontal distance traveled during the glide (this is equivalent to the maximum range speed of powered aircraft; Alexander, 1992).

Another way to think about the relationship between size and glide velocity is in the context of lift generation. Aerodynamic theory tells us that lift is proportional to the square of velocity in many steady–state circumstances (McMahon and Bonner, 1983; Norberg, 1985, 1990; Alexander, 1992). Because larger species do not offset their greater relative body mass with a corresponding increase in area, they will not be able to generate sufficient lift to support their body mass when gliding at the same velocity as a smaller species with lower wing loading. Therefore, a larger species is expected to require a greater glide velocity than will a smaller species in order to perform an equivalent glide. We may expect that *Draco* will generally choose the glide speed that maximizes the glide distance (the equilibrium or maximum range glide speed), although the lizard may also choose a nonsteady–state glide speed (if, for example, it is more important to get to the landing point as rapidly as possible). Although the analysis of wing loading certainly suggests that the evolution of large body size should constrain gliding performance, this hypothesis requires further evaluation. It is possible that large size has evolved in *Draco* without compromising gliding performance via behavioral modifications that maximize gliding efficiency. Although the presence of such modifications seem unlikely, their presence clearly is testable in an experimental framework. The crucial test will come in the form of a comparative gliding performance study, as this will allow us to test the prediction that larger species are relatively poor gliders compared to their smaller congeners (McGuire, in progress).

The finding that *Draco* species essentially are isometric may have important ecological consequences for flying lizards. In nature, *Draco* frequently utilize their gliding ability. They glide from tree to tree when searching for food, searching for mates, chasing intruder males from their territories, and as a means of avoiding predators (Hairston, 1957; Alcala, 1967; John, 1967; Mori and Hikida, 1994; McGuire, personal observation). Indeed, with the exception of gravid females, which must leave the trees to oviposit, flying lizards may never come to the ground voluntarily. When they find themselves on the ground, they may be at great risk. Alcala (1967) found that the mortality rate in *Draco spilopterus* females was substantially greater than in males, despite the fact that males appear to be more conspicuous (males are territorial, spend much time displaying their vibrantly colored dewlaps and patagia, actively defend their territories from rival males, and glide more frequently). Alcala (1967) attributed the greater mortality rate in females to their need to come to the ground to deposit eggs. In contrast, males usually have greater mortality rates in lizards that exhibit territoriality (Trivers, 1972; Stamps, 1983).

Predictions

While the prior discussion was necessarily somewhat speculative, it cannot be disputed that gliding ability is important in the lives of flying lizards. The finding that *Draco* species are isometric, such that larger species have greater wing loading, strongly implies that larger species are relatively poor gliders when compared to smaller species. Thus, the evolution of large size may come with a cost in gliding performance, which presumably has ecological consequences for flying lizards. For example, larger species may not be able to avoid predators as successfully as smaller species. Larger species may also be constrained with respect to available habitat in the forest. If smaller species require lesser glide velocities in order to maximize their lift to drag ratio, then they should be able to achieve this velocity after a shorter ballistic dive. If smaller species require a shorter ballistic dive in order to glide a given distance, then they should be able to utilize lower heights on the trunks without sacrificing their ability to complete a glide to nearby trees. Thus, smaller species may be able to utilize a larger proportion of the available forest habitat, or occupy an otherwise unfilled habitat niche, by specializing in lower forest strata.

Inger (1983) investigated the stratification hypothesis by considering six sympatric Bornean species. He found that two species, *D. melanopogon* and *D. quinquefasciatus*, were captured at significantly lower tree heights than were the remaining four species (*D. haematopogon*, *D. maximus*, *D. obscurus*, and *D. sumatranus*). Although males of these two species do have lower wing loading than the remaining four (Table 3.1), the differences in wing loading between *D. quinquefasciatus*, *D. haematopogon*, and *D. sumatranus* are slight. A study of

Draco tree-height preferences is problematic for several reasons, and these may or may not apply to Inger (1983). First of all, the tree height observations will almost certainly be biased toward lower heights, especially if the data are based on capture records (the higher the lizard, the more difficult it is to capture). Secondly, the data should be limited to adult specimens because there is substantial ontogenetic variation in wing loading. Inger's (1983) data were based on capture records, and the sample was not limited to adults. Thus, although Inger's (1983) results did not reject the hypothesis that tree height is correlated with wing loading, a more compelling test would be based on a large sample of tree height observations (not limited to capture data), and would be based only on adults. Realistically, even if species with lower wing loading spend more time at lower heights than do species with high wing loading, such a relationship may be very difficult to show because species with lower wing loading clearly utilize the upper portions of the trees as do species with high wing loading (Bacon, 1970).

The finding that *Draco* are isometric predicts that *Draco* patagial area and shape may be morphologically constrained. Indeed, the size of the patagium appears to be limited by the linear distance between the fore and hind limb insertions. When the patagia are not being used, they are folded against the side of the body. When folded, the ribs supporting the patagia do not extend beyond the hind limb. If this is indeed a design constraint, then we might expect that the only way that relative wing area could be increased would be via an increase in the length of the trunk between the fore and hind limbs. A quick perusal of the regression plots presented in Figures 3.7–3.8 (as well as Tables 3.1–3.2) indicates that *Draco* species are not perfectly isometric and some relatively large species, such as *D.*

quinquefasciatus, have relatively low wing loading for their body mass. These species do appear to have relatively long trunks, but this observation requires empirical evaluation.

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Table 3.1. Mean values (± 1 SE) for six morphometric variables for male flying lizards. Sample sizes are in parentheses following taxon names. SVL and Wing Span in millimeters, Ventral Area and Wing Area in centimeters squared, Body Mass in grams, Wing Loading in Newtons per meter squared (N/m^2).

Species	SVL	Body Mass	Ventral Area	Wing Area	Wing Loading
beccarii (17)	68.79 ± 0.54	3.61 ± 0.11	29.09 ± 0.46	20.80 ± 0.43	12.17 ± 0.38
biaro (5)	73.50 ± 0.67	4.23 ± 0.04	33.16 ± 0.71	23.43 ± 0.55	12.52 ± 0.22
bimaculatus (26)	66.71 ± 0.39	3.03 ± 0.07	26.77 ± 0.74	18.33 ± 0.46	11.22 ± 0.31
blanfordi (20)	122.40 ± 0.81	14.18 ± 0.33	90.63 ± 1.57	68.70 ± 1.36	15.35 ± 0.28
bourouniensis (20)	77.75 ± 0.50	5.20 ± 0.13	36.91 ± 0.49	25.67 ± 0.35	13.81 ± 0.29
caerhulians (6)	71.25 ± 0.60	3.57 ± 0.11	29.98 ± 0.55	21.25 ± 0.53	11.66 ± 0.28
cornutus (4)	76.25 ± 1.03	4.23 ± 0.24	36.87 ± 1.86	28.32 ± 1.67	11.32 ± 0.89
cyanopterus (3)	87.83 ± 1.17	8.27 ± 0.49	43.96 ± 2.13	32.00 ± 1.91	18.41 ± 0.29
fimbriatus (3)	110.33 ± 1.86	16.90 ± 0.57	68.67 ± 2.99	47.18 ± 2.63	24.22 ± 1.49
formosus (11)	106.77 ± 1.01	10.42 ± 0.21	66.26 ± 1.26	48.86 ± 1.27	15.45 ± 0.36
guentheri (2)	71.50 ± 3.50	4.40 ± 0.50	30.81 ± 4.74	21.55 ± 3.68	14.09 ± 0.58
haematopogon (14)	80.25 ± 0.58	4.89 ± 0.11	40.52 ± 0.61	28.80 ± 0.57	11.83 ± 0.24
maculatus (12)	78.83 ± 0.73	5.59 ± 0.20	35.92 ± 1.11	24.96 ± 1.04	15.31 ± 0.50
maximus (8)	139.63 ± 1.43	22.00 ± 0.78	113.96 ± 3.66	86.77 ± 3.35	18.94 ± 0.50
melanopogon (43)	79.79 ± 0.28	3.66 ± 0.06	40.30 ± 0.38	30.54 ± 0.36	8.93 ± 0.16
mindanensis (4)	96.50 ± 1.32	7.28 ± 0.74	54.31 ± 2.91	39.44 ± 1.84	13.05 ± 0.68
obscurus (4)	96.00 ± 1.47	8.10 ± 0.25	54.53 ± 1.61	38.39 ± 1.38	14.58 ± 0.50
ornatus (6)	75.58 ± 0.66	4.66 ± 0.16	34.39 ± 1.03	24.39 ± 0.91	13.31 ± 0.45
palawanensis (8)	77.69 ± 1.07	4.61 ± 0.15	35.25 ± 0.79	26.45 ± 0.67	12.81 ± 0.21
quadrasi (2)	69.75 ± 0.35	3.50 ± 0.40	26.35 ± 0.23	18.10 ± 0.16	13.01 ± 1.38
quinquefasciatus (7)	101.50 ± 0.96	7.82 ± 0.25	67.77 ± 2.28	54.35 ± 2.07	11.35 ± 0.38
reticulatus (10)	85.05 ± 1.00	6.54 ± 0.18	45.52 ± 1.21	33.65 ± 0.97	14.14 ± 0.24
spilonotus (7)	63.21 ± 0.71	2.97 ± 0.08	24.66 ± 0.37	17.40 ± 0.36	11.81 ± 0.26

Table 3.1. Continued.

Species	SVL	Body Mass	Ventral Area	Wing Area	Wing Loading
spilopterus/Bicol (4)	73.00 ± 1.58	3.85 ± 0.17	29.32 ± 0.84	20.29 ± 0.64	12.87 ± 0.42
spilopterus/Polillo (4)	80.13 ± 1.48	4.58 ± 0.28	35.56 ± 2.38	25.66 ± 2.03	12.63 ± 0.29
spilopterus/Cebu (5)	77.80 ± 1.02	4.54 ± 0.14	35.47 ± 1.04	25.35 ± 0.97	12.55 ± 0.21
spilopterus/Siquijor (14)	78.64 ± 0.60	5.02 ± 0.11	35.65 ± 0.57	26.17 ± 0.47	13.81 ± 0.26
spilopterus/PN (8)	83.31 ± 0.99	6.09 ± 0.18	40.13 ± 1.31	29.44 ± 1.16	14.91 ± 0.38
sumatranus (11)	77.36 ± 0.72	4.70 ± 0.12	38.12 ± 1.10	29.10 ± 0.94	12.11 ± 0.19
taeniopterus (16)	73.47 ± 0.54	3.78 ± 0.10	32.18 ± 0.78	22.91 ± 0.66	11.60 ± 0.42
Tahulandang (16)	69.53 ± 0.44	3.75 ± 0.07	28.56 ± 0.37	19.34 ± 0.29	12.86 ± 0.20
volans (5)	70.00 ± 0.63	3.50 ± 0.16	29.88 ± 0.92	22.09 ± 0.89	11.52 ± 0.64

Table 3.2. Mean values (± 1 SE) for six morphometric variables for female flying lizards. Sample sizes are in parentheses following taxon names. SVL and Wing Span in millimeters, Ventral Area and Wing Area in centimeters squared, Body Mass in grams, Wing Loading in Newtons per meter squared (N/m^2).

Species	SVL	Body Mass	Ventral Area	Wing Area	Wing Loading
beccarii (8)	71.88 ± 1.00	5.63 ± 0.34	31.80 ± 1.06	22.63 ± 0.86	17.32 ± 0.83
bimaculatus (21)	68.00 ± 0.37	3.90 ± 0.12	27.62 ± 0.74	18.59 ± 0.49	13.96 ± 0.45
blanfordi (10)	107.80 ± 1.03	12.38 ± 0.81	75.05 ± 1.92	56.85 ± 1.83	16.19 ± 0.97
bourouniensis (11)	81.95 ± 0.87	7.33 ± 0.40	41.44 ± 1.06	28.90 ± 0.99	17.31 ± 0.83
caerhulians (3)	76.17 ± 0.44	6.42 ± 0.22	36.04 ± 1.33	25.89 ± 1.20	17.47 ± 0.56
cornutus (3)	83.33 ± 0.17	8.02 ± 0.39	41.01 ± 0.56	30.39 ± 0.57	19.14 ± 0.79
cristatellus (1)	85.00	9.90	44.97	32.90	21.57
cyanopterus (3)	91.33 ± 2.73	12.58 ± 1.18	49.05 ± 2.92	36.34 ± 2.55	25.10 ± 1.68
fimbriatus (5)	113.30 ± 1.66	20.52 ± 1.25	79.21 ± 3.44	58.94 ± 3.19	25.36 ± 1.01
formosus (7)	89.43 ± 1.09	8.84 ± 0.28	48.06 ± 2.17	34.66 ± 1.78	18.15 ± 0.67
haematopogon (9)	82.83 ± 0.90	6.88 ± 0.35	47.08 ± 1.94	34.29 ± 1.57	14.30 ± 0.36
maculatus (5)	77.00 ± 1.64	6.60 ± 0.47	34.46 ± 1.65	24.75 ± 1.56	18.80 ± 1.18
maximus (2)	142.50 ± 1.00	32.75 ± 0.75	128.52 ± 10.06	98.55 ± 10.94	25.17 ± 2.54
melanopogon (34)	83.76 ± 0.45	5.28 ± 0.13	46.12 ± 0.66	35.59 ± 0.58	11.23 ± 0.24
mindanensis (2)	82.50 ± 1.50	6.30 ± 1.00	42.61 ± 4.16	30.32 ± 2.84	14.40 ± 0.89
obscurus (4)	93.25 ± 1.18	9.69 ± 0.36	54.27 ± 1.19	39.74 ± 0.97	17.49 ± 0.53
ornatus (12)	83.58 ± 0.80	8.22 ± 0.31	42.88 ± 1.07	30.76 ± 0.95	18.82 ± 0.63
palawanensis (8)	81.50 ± 0.78	7.22 ± 0.28	37.54 ± 0.88	27.95 ± 0.76	18.92 ± 0.83
quadrasi (1)	73.50	4.70	30.06	19.81	15.32
quinquefasciatus (6)	107.83 ± 1.05	11.62 ± 0.25	73.46 ± 2.76	58.85 ± 2.38	15.48 ± 0.44
reticulatus (3)	88.17 ± 1.48	10.22 ± 0.74	50.88 ± 0.62	37.87 ± 0.57	19.65 ± 1.20
spilonotus (4)	66.63 ± 1.07	4.58 ± 0.38	27.60 ± 1.42	19.29 ± 1.08	16.21 ± 0.83
spilopterus/Bicol (1)	81.00	6.40	39.61	28.19	15.83

Table 3.2. Continued.

Species	SVL	Body Mass	Ventral Area	Wing Area	Wing Loading
spilopterus/Polillo (1)	91.00	9.30	47.87	35.81	19.04
spilopterus/Cebu (4)	85.13 ± 1.30	7.93 ± 0.76	43.03 ± 1.94	30.87 ± 1.54	17.93 ± 0.91
spilopterus/Siquijor (5)	82.70 ± 1.43	7.43 ± 0.41	40.44 ± 1.76	30.01 ± 1.51	18.11 ± 1.15
spilopterus/PN (3)	97.33 ± 2.96	13.73 ± 1.09	55.70 ± 4.18	40.30 ± 2.92	24.17 ± 0.89
sumatranus (8)	81.56 ± 0.92	6.63 ± 0.38	42.06 ± 1.53	32.52 ± 1.37	15.63 ± 1.17
taeniopterus (5)	72.70 ± 1.10	4.82 ± 0.51	32.85 ± 1.40	23.59 ± 1.27	14.50 ± 1.74
Tahulandang (10)	73.85 ± 0.61	5.94 ± 0.20	33.17 ± 0.43	22.96 ± 0.37	17.52 ± 0.47
volans (5)	75.60 ± 0.68	5.38 ± 0.23	34.67 ± 0.86	26.57 ± 0.89	15.19 ± 0.44

Table 3.3. Results of the ordinary least squares (OLS) and reduced major axis (RMA) regression analyses of total ventral surface area on body mass for males and females. Analyses were conducted on nontransformed species values (no phylogenetic correction) as well as on standardized independent contrasts calculated in the context of five alternative phylogenetic estimates and their corresponding branch length estimates. 95% confidence intervals are applicable to both OLS and RMA regression models.

Phylogenetic Estimate	OLS	Correlation Coefficient	RMA	95% Confidence Intervals
Males:				
Species values	0.70	0.95	0.74	0.62 – 0.79
GTR+G	0.67	0.96	0.70	0.59 – 0.74
Equal weight	0.66	0.95	0.69	0.57 – 0.74
Tv:Ti	0.65	0.95	0.69	0.57 – 0.73
2nd codon position	0.66	0.95	0.70	0.58 – 0.74
Tv:Ti/2nd codon position	0.67	0.95	0.70	0.59 – 0.75
Females:				
Species values	0.68	0.93	0.73	0.57 – 0.78
GTR+G	0.66	0.96	0.68	0.59 – 0.73
Equal weight	0.65	0.96	0.68	0.57 – 0.72
Tv:Ti	0.65	0.96	0.67	0.57 – 0.72
2nd codon position	0.65	0.96	0.68	0.58 – 0.72
Tv:Ti/2nd codon position	0.65	0.96	0.68	0.58 – 0.72

Table 3.4. Results of the ordinary least squares (OLS) and reduced major axis (RMA) regression analyses of wing area proper on body mass for males and females. See Table 3.3 for details.

Phylogenetic Estimate	OLS	Correlation Coefficient	RMA	95% Confidence Intervals
Males:				
Species values	0.73	0.93	0.79	0.62 – 0.84
GTR+G	0.70	0.94	0.75	0.60 – 0.80
Equal weight	0.68	0.92	0.74	0.57 – 0.79
Tv:Ti	0.68	0.92	0.73	0.57 – 0.78
2nd codon position	0.69	0.92	0.75	0.58 – 0.80
Tv:Ti/2nd codon position	0.70	0.93	0.76	0.59 – 0.81
Females:				
Species values	0.72	0.92	0.78	0.60 – 0.83
GTR+G	0.70	0.95	0.73	0.61 – 0.78
Equal weight	0.68	0.95	0.72	0.59 – 0.77
Tv:Ti	0.68	0.94	0.72	0.59 – 0.77
2nd codon position	0.69	0.95	0.72	0.60 – 0.77
Tv:Ti/2nd codon position	0.69	0.95	0.72	0.60 – 0.77

Figure 3.1. Ventral view of a *Draco* specimen defining total ventral area (the entire specimen), wing area proper (stippled area), and wing span.

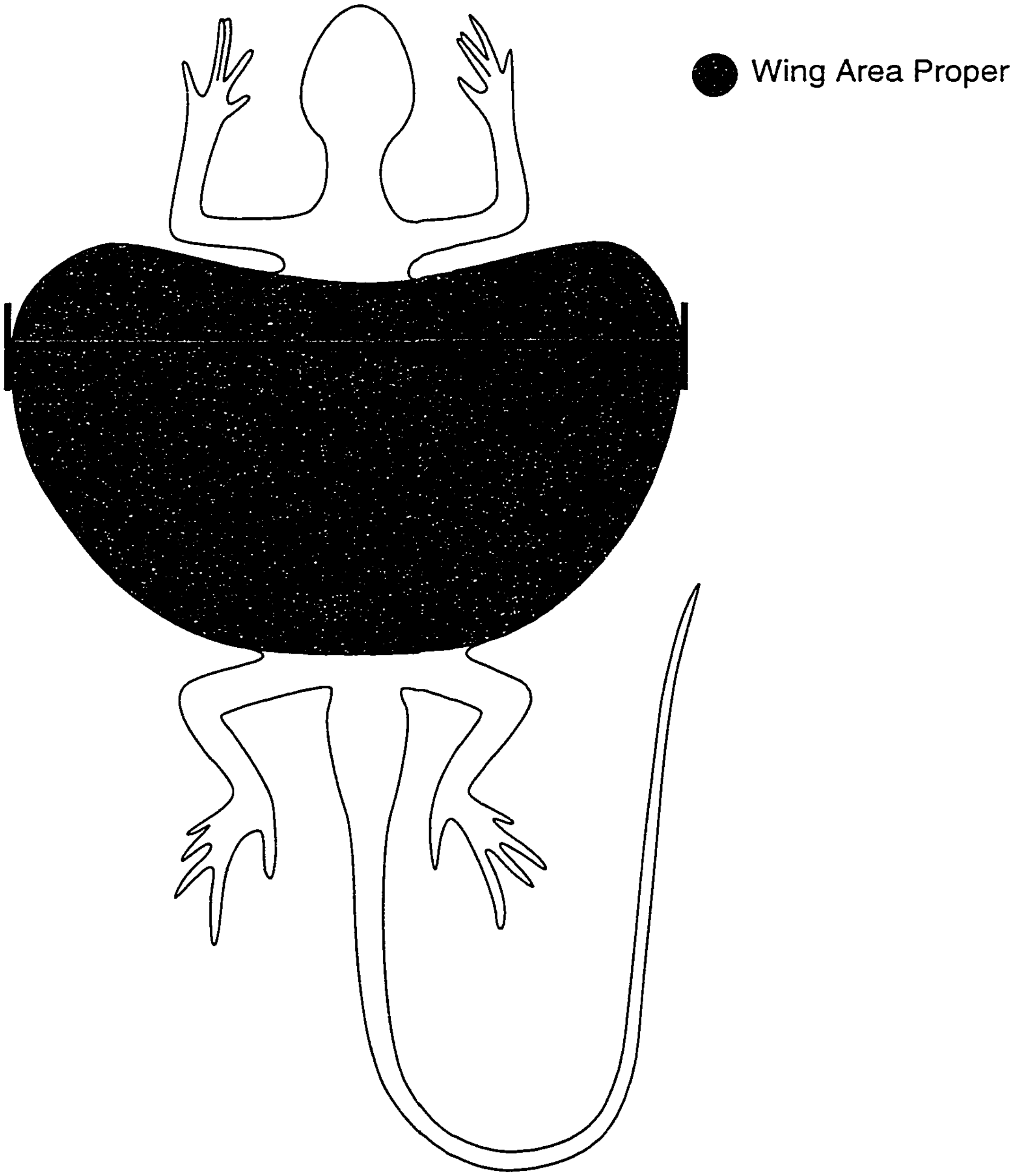

● Wing Area Proper

Figure 3.2. Phylogenetic estimate resulting from the maximum likelihood analysis under the GTR+G model (–ln likelihood = 21,498.24).

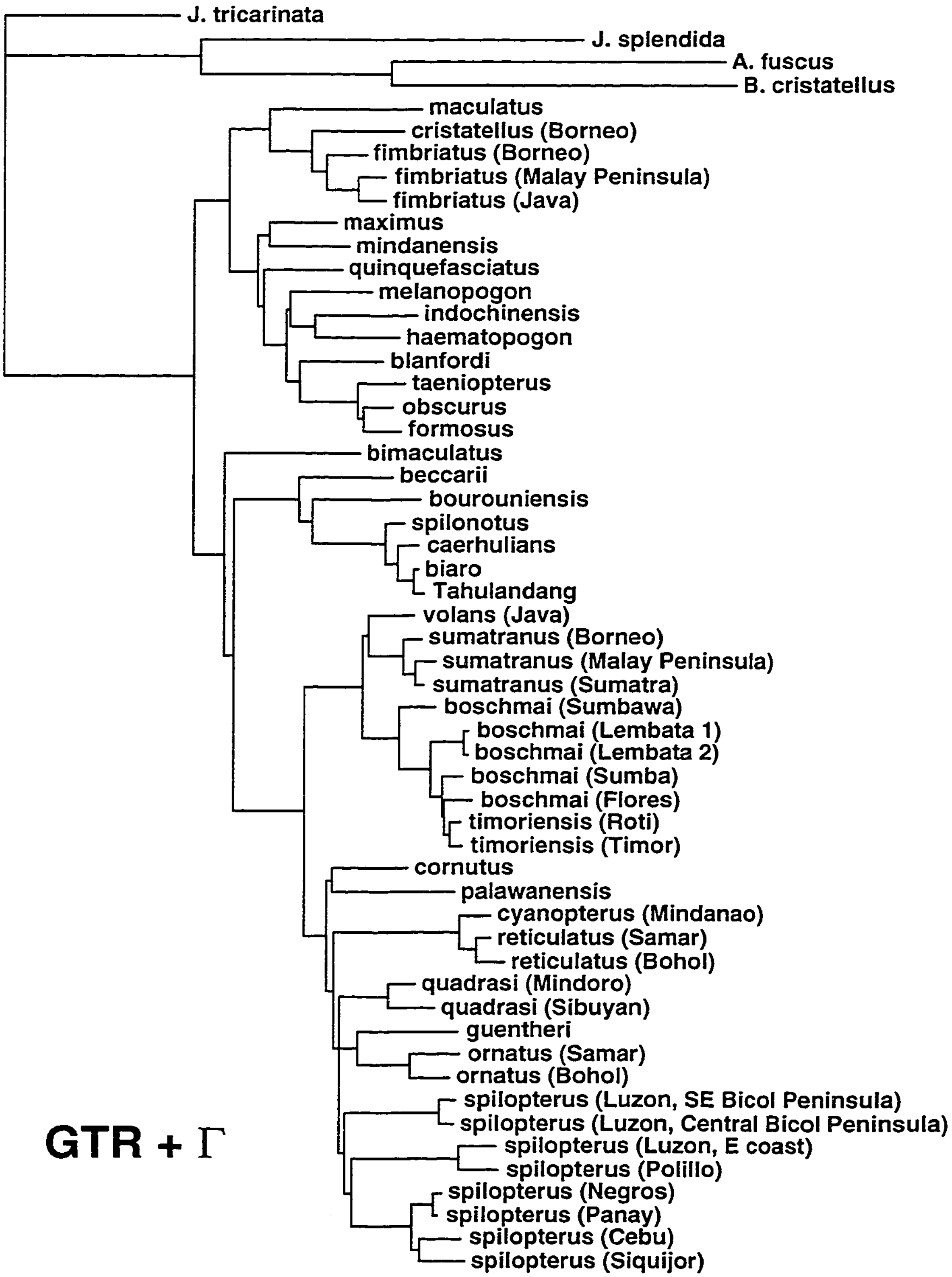

J. tricarinata
J. splendida
A. fuscus
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
maximus
mindanensis
quinquefasciatus
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Sumba)
boschmai (Flores)
timoriensis (Roti)
timoriensis (Timor)
cornutus
palawanensis
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
guentheri
ornatus (Samar)
ornatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, Central Bicol Peninsula)
spilopterus (Luzon, E coast)
spilopterus (Polillo)
spilopterus (Negros)
spilopterus (Panay)
spilopterus (Cebu)
spilopterus (Siquijor)
GTR + Γ

Figure 3.3. 50% majority–rule bootstrap consensus tree obtained with all nucleotide positions and gaps weighted equivalently. Branch lengths employed in the calculation of independent contrasts were estimated by optimizing the GTR+G model parameters on this topology.

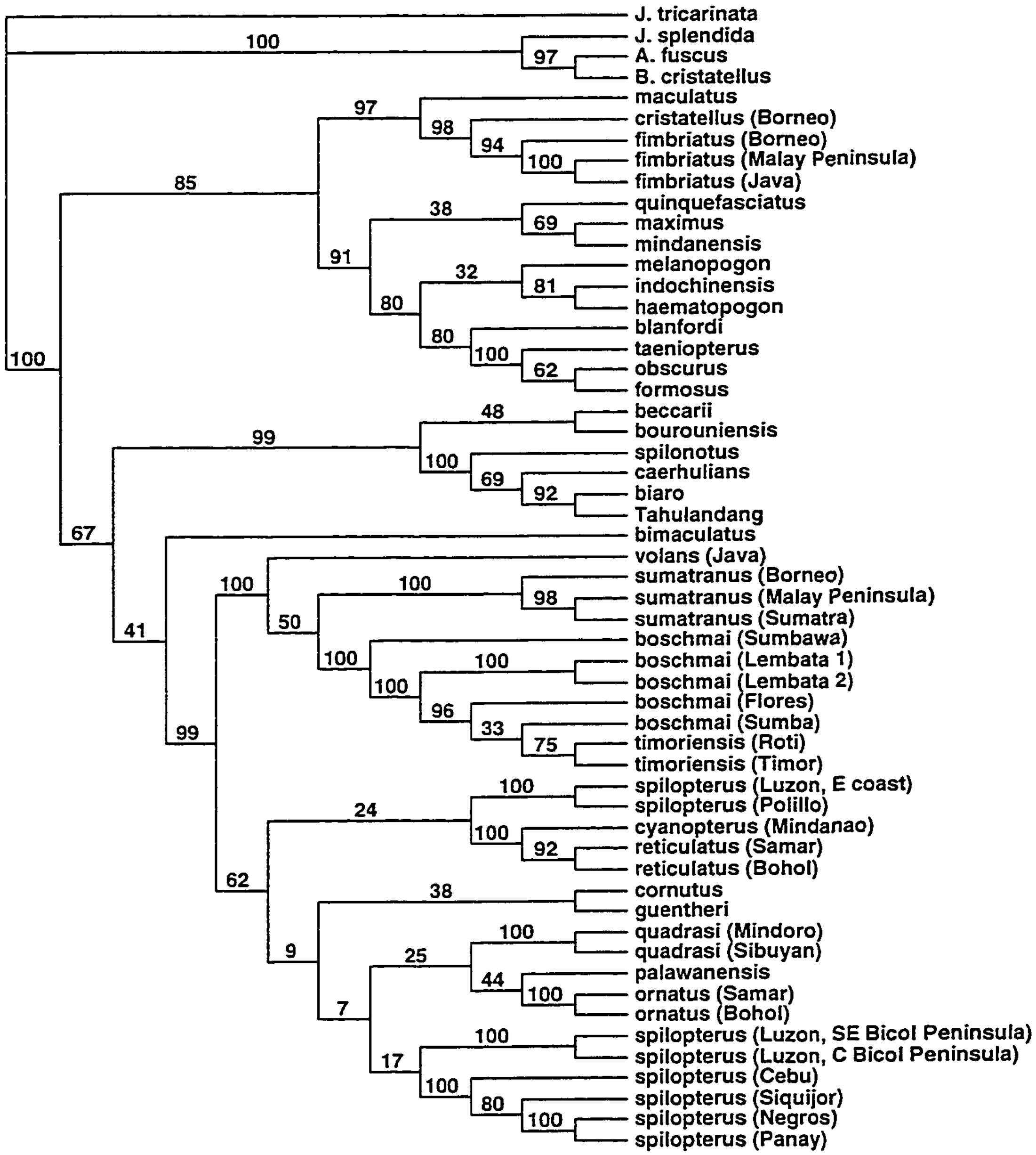

J. tricarinata
100
J. splendida
97
A. fuscus
B. cristatellus
maculatus
97
cristatellus (Borneo)
98
fimbriatus (Borneo)
94
fimbriatus (Malay Peninsula)
100
fimbriatus (Java)
85
quinquefasciatus
38
maximus
69
mindanensis
91
melanopogon
32
indochinensis
81
haematopogon
80
blanfordi
80
taeniopterus
100
obscurus
62
formosus
100
beccarii
48
bourouniensis
99
spilonotus
100
caerhulians
69
biaro
92
Tahulandang
67
bimaculatus
volans (Java)
100
sumatranus (Borneo)
100
sumatranus (Malay Peninsula)
98
sumatranus (Sumatra)
50
41
boschmai (Sumbawa)
100
boschmai (Lembata 1)
100
boschmai (Lembata 2)
100
boschmai (Flores)
96
boschmai (Sumba)
33
timoriensis (Roti)
75
timoriensis (Timor)
99
spilopterus (Luzon, E coast)
100
spilopterus (Polillo)
24
cyanopterus (Mindanao)
100
reticulatus (Samar)
92
reticulatus (Bohol)
62
cornutus
38
guentheri
quadrasi (Mindoro)
100
quadrasi (Sibuyan)
9
palawanensis
25
ornatus (Samar)
44
100
ornatus (Bohol)
7
spilopterus (Luzon, SE Bicol Peninsula)
100
spilopterus (Luzon, C Bicol Peninsula)
17
spilopterus (Cebu)
100
spilopterus (Siquijor)
80
spilopterus (Negros)
100
spilopterus (Panay)

Figure 3.4. 50% majority–rule bootstrap consensus tree obtained with transversions weighted three times greater than transitions and gaps weighted as transitions. Branch lengths employed in the calculation of independent contrasts were estimated by optimizing the GTR+G model parameters on this topology.

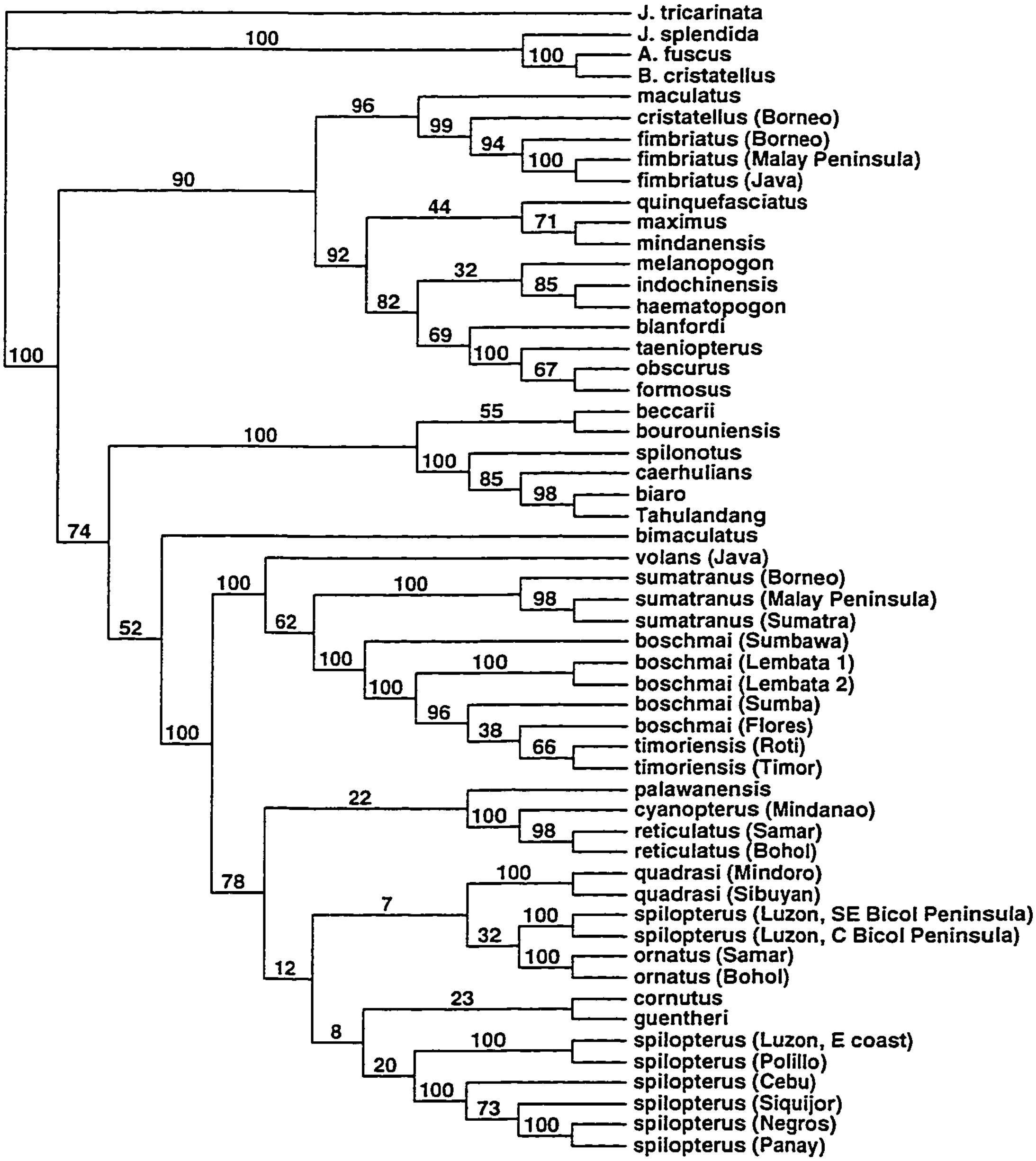

J. tricarinata
100
J. splendida
100
A. fuscus
B. cristatellus
96
maculatus
99
cristatellus (Borneo)
94
fimbriatus (Borneo)
90
100
fimbriatus (Malay Peninsula)
fimbriatus (Java)
44
quinquefasciatus
71
maximus
mindanensis
92
32
melanopogon
85
indochinensis
82
haematopogon
blanfordi
69
100
taeniopterus
100
67
obscurus
formosus
55
beccarii
bourouniensis
100
spilonotus
100
caerhulians
85
98
biaro
Tahulandang
74
bimaculatus
volans (Java)
100
100
sumatranus (Borneo)
98
sumatranus (Malay Peninsula)
52
62
sumatranus (Sumatra)
boschmai (Sumbawa)
100
100
boschmai (Lembata 1)
100
boschmai (Lembata 2)
boschmai (Sumba)
96
100
38
boschmai (Flores)
66
timoriensis (Roti)
timoriensis (Timor)
22
palawanensis
100
cyanopterus (Mindanao)
98
reticulatus (Samar)
reticulatus (Bohol)
100
78
quadrasi (Mindoro)
quadrasi (Sibuyan)
7
100
spilopterus (Luzon, SE Bicol Peninsula)
32
spilopterus (Luzon, C Bicol Peninsula)
100
ornatus (Samar)
12
ornatus (Bohol)
23
cornutus
guentheri
8
100
spilopterus (Luzon, E coast)
20
spilopterus (Polillo)
spilopterus (Cebu)
100
73
spilopterus (Siquijor)
100
spilopterus (Negros)
spilopterus (Panay)

Figure 3.5. 50% majority–rule bootstrap consensus tree obtained with nucleotides at second codon positions weighted two times greater than nucleotides at first and third positions; gaps weighted equivalently with first and third positions. Branch lengths employed in the calculation of independent contrasts were estimated by optimizing the GTR+G model parameters on this topology.

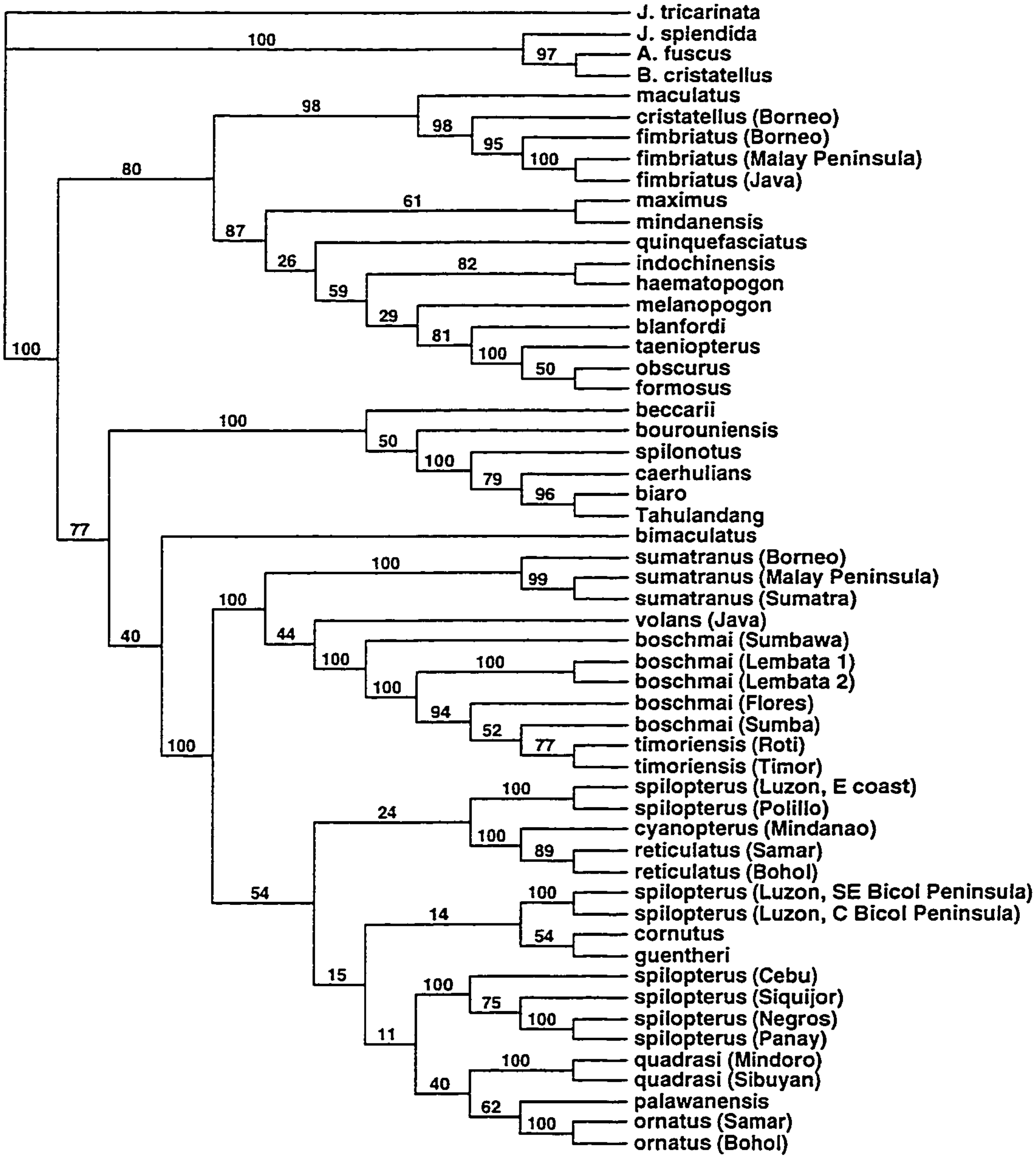

J. tricarinata
J. splendida
A. fuscus
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
maximus
mindanensis
quinquefasciatus
indochinensis
haematopogon
melanopogon
blanfordi
taeniopterus
obscurus
formosus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
bimaculatus
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
volans (Java)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Flores)
boschmai (Sumba)
timoriensis (Roti)
timoriensis (Timor)
spilopterus (Luzon, E coast)
spilopterus (Polillo)
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
cornutus
guentheri
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros)
spilopterus (Panay)
quadrasi (Mindoro)
quadrasi (Sibuyan)
palawanensis
ornatus (Samar)
ornatus (Bohol)
100
97
98
98
95
100
80
61
87
26
82
59
29
81
100
100
50
100
50
100
79
96
77
100
99
100
40
44
100
100
100
94
52
77
100
100
24
100
89
54
100
14
54
15
100
75
100
11
100
40
62
100

Figure 3.6. 50% majority–rule bootstrap consensus tree obtained with second codon positions weighted two times greater than first and third positions and transversions weighted three times greater than transitions. Branch lengths employed in the calculation of independent contrasts were estimated by optimizing the GTR+G model parameters on this topology.

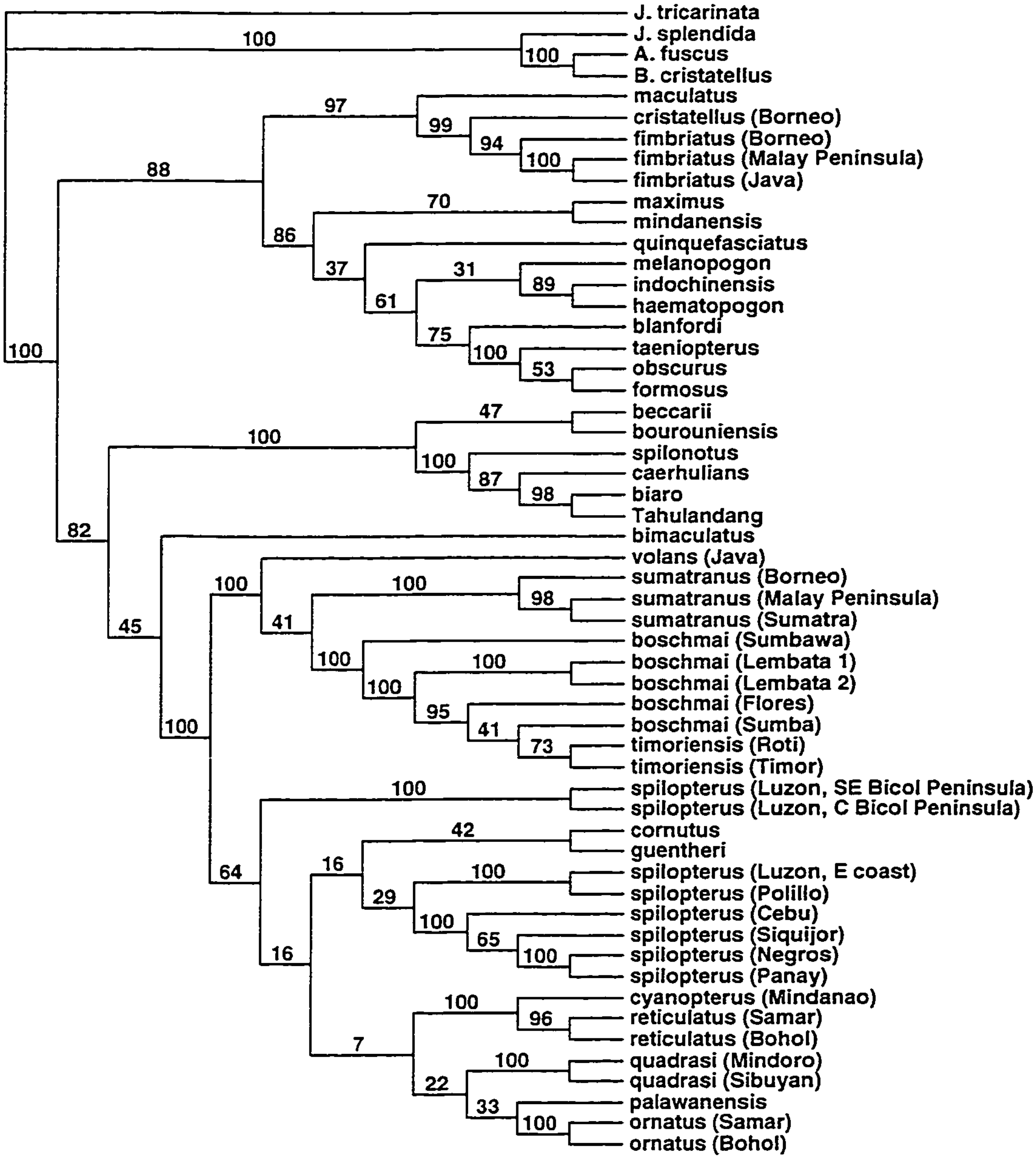
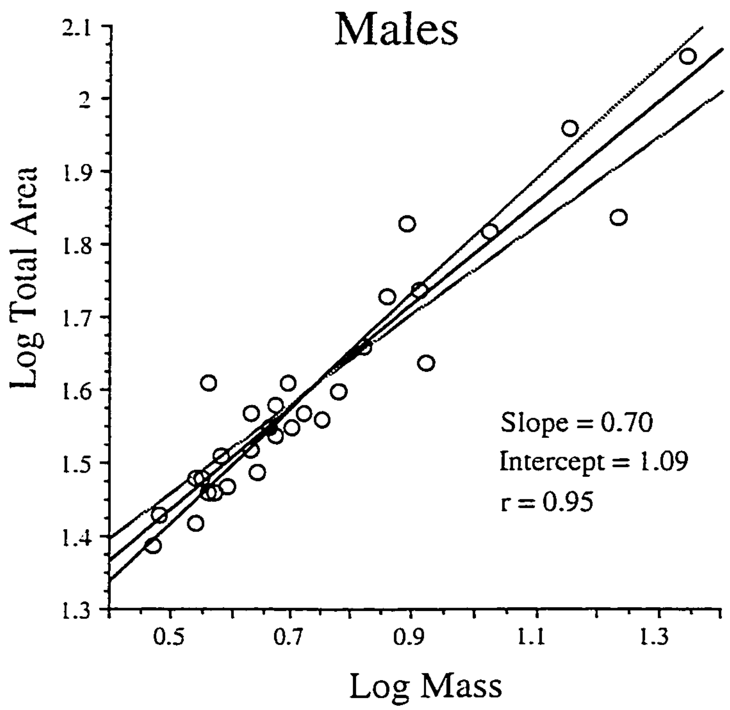

J. tricarinata
100
J. splendida
100
A. fuscus
B. cristatellus
97
maculatus
99
cristatellus (Borneo)
94
fimbriatus (Borneo)
88
100
fimbriatus (Malay Peninsula)
fimbriatus (Java)
70
maximus
mindanensis
86
quinquefasciatus
37
31
melanopogon
89
indochinensis
61
haematopogon
blanfordi
75
taeniopterus
100
100
53
obscurus
formosus
47
beccarii
100
bourouniensis
spilonotus
100
caerhulians
87
98
biaro
Tahulandang
82
bimaculatus
volans (Java)
100
sumatranus (Borneo)
100
98
sumatranus (Malay Peninsula)
45
41
sumatranus (Sumatra)
boschmai (Sumbawa)
100
100
boschmai (Lembata 1)
100
boschmai (Lembata 2)
boschmai (Flores)
95
boschmai (Sumba)
100
41
timoriensis (Roti)
73
timoriensis (Timor)
100
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, C Bicol Peninsula)
42
cornutus
16
guentheri
64
100
spilopterus (Luzon, E coast)
29
spilopterus (Polillo)
spilopterus (Cebu)
100
spilopterus (Siquijor)
65
100
spilopterus (Negros)
16
spilopterus (Panay)
100
cyanopterus (Mindanao)
96
reticulatus (Samar)
7
reticulatus (Bohol)
100
quadrasi (Mindoro)
22
quadrasi (Sibuyan)
33
palawanensis
100
ornatus (Samar)
ornatus (Bohol)

Figure 3.7. Ordinary least squares regression plots with total area on body mass (see Table 3.3 for RMA regression coefficient). The data are untransformed species values. The partially shaded lines are 95% confidence intervals.


Males
Log Total Area
2.1
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
0.5
0.7
0.9
1.1
1.3
Log Mass
Slope = 0.70
Intercept = 1.09
r = 0.95

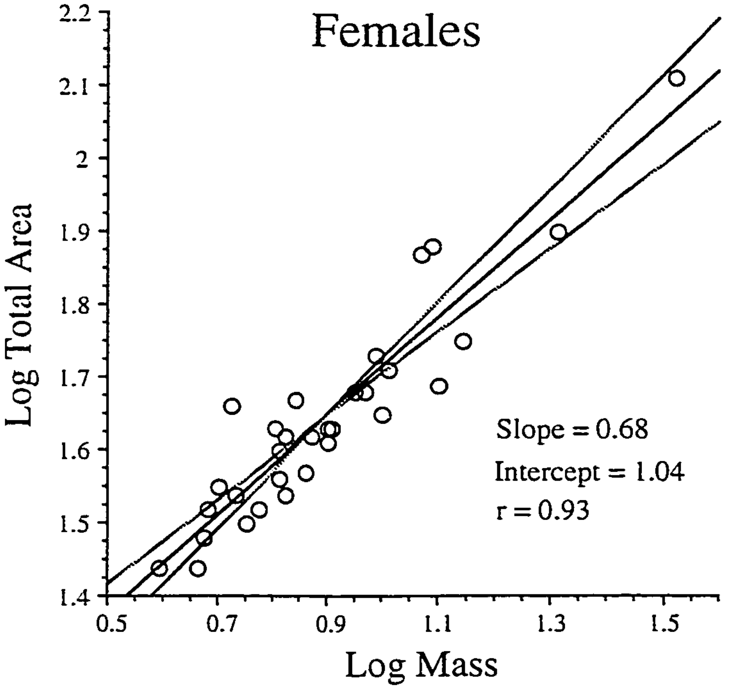
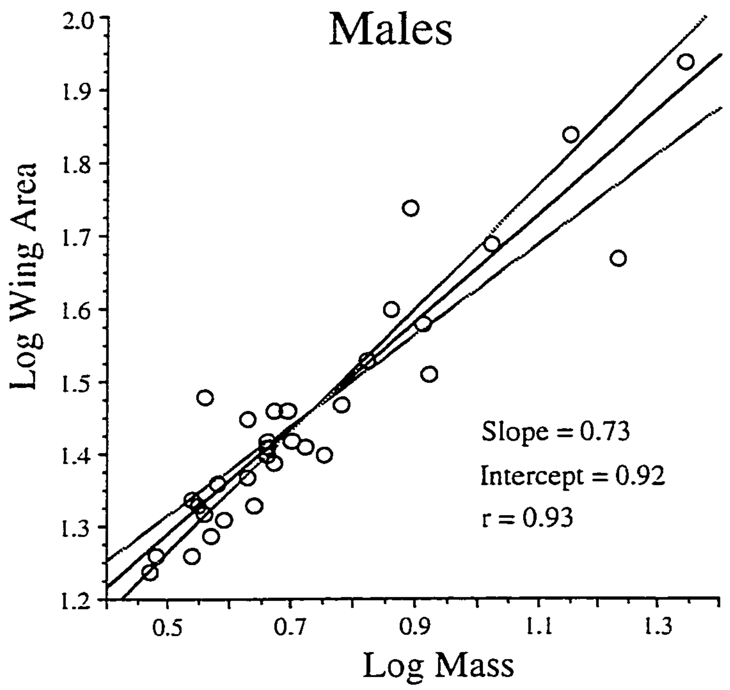
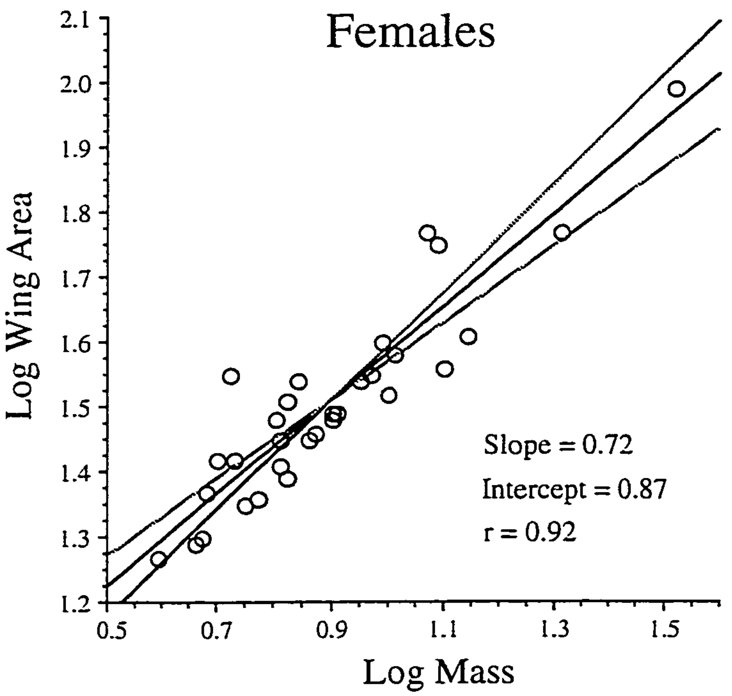

Females
Log Total Area
2.2
2.1
2
1.9
1.8
1.7
1.6
1.5
1.4
0.5
0.7
0.9
1.1
1.3
1.5
Log Mass
Slope = 0.68
Intercept = 1.04
r = 0.93

Figure 3.8. Ordinary least squares regression plots with wing area on body mass (see Table 3.4 for RMA regression coefficient). The data are untransformed species values. The partially shaded lines are 95% confidence intervals.


Males
Log Wing Area
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
0.5
0.7
0.9
1.1
1.3
Log Mass
Slope = 0.73
Intercept = 0.92
r = 0.93


Females
Log Wing Area
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
0.5
0.7
0.9
1.1
1.3
1.5
Log Mass
Slope = 0.72
Intercept = 0.87
r = 0.92

CHAPTER 4

THE EFFECTS OF BODY SIZE EVOLUTION ON GLIDING PERFORMANCE IN FLYING LIZARDS (GENUS *DRACO*)

Body size affects virtually every aspect of an organism's biology and therefore may be the single most important organismal characteristic (Calder, 1984; Schmidt-Nielsen, 1984; Pennycuick, 1992). Locomotor performance is among the most important of those features likely to be affected by body size variation because locomotor ability often is associated with foraging and reproductive success, as well as with predator avoidance. Understanding the effect that size variation has on locomotor performance can be problematic because, for most forms of locomotion, performance results from a complex interplay between morphology and physiology (e.g., Garland, 1985). I (Chapter 3) suggested that the Southeast Asian flying lizards represent an excellent model system with which to investigate size effects on locomotor performance because their locomotor mode of gliding is relatively independent of potentially confounding physiological processes. The purpose of the present paper is to assess the role that body size evolution has played in the evolution of gliding performance in Southeast Asian flying lizards.

The flying lizards are remarkable in their ability to glide long distances using an airfoil formed by wing-like patagial membranes supported by elongate thoracic ribs. Although these lizards are famous for their gliding ability, little is known about the gliding performance of any one species, let alone interspecific variation in performance (but see Klingel, 1965). Flying lizards exhibit substantial body size variation, ranging between 70 and 150 mm in snout-vent length (SVL) and spanning an order of magnitude (3–35 g) in body mass (McGuire, Chapter 3). Not only is there substantial size variation, but the area/mass relationship has been shown to vary isometrically in *Draco* (McGuire, Chapter 3), indicating that larger species do not compensate for their greater mass with a corresponding relative increase in the area of the lift–generating structures. This finding led me to hypothesize that larger species of flying lizards should be relatively poor gliders when compared with their smaller relatives. To test this hypothesis, we measured gliding performance in the field for 11 species of flying lizards spanning the entire size distribution of the genus. Before proceeding to the analysis of the performance data, we will first summarize the results of the scaling study to put the present study in proper context.

Scaling in Flying Lizards

The effect that body size variation is expected to have on gliding performance is directly influenced by allometric scaling relationships (McMahon and Bonner, 1984; Schmidt-Nielsen, 1984). We know from simple geometric principles that under conditions of isometry (the condition in which individuals are essentially scale-replicas of one another, identical in shape), area varies with the square of the linear dimension and volume (and therefore mass if we assume constant density) varies with the cube of the linear dimension (Thompson, 1961; Sweet, 1980). Therefore, if *Draco* species of different sizes vary isometrically, we expect larger species to have relatively less area available for lift-generation on a per-unit mass basis than will smaller species and we would further expect that the evolution of large size would compromise gliding locomotor performance. However, if *Draco* vary allometrically such that the relationship between area and mass is unaffected by overall changes in body size, then the evolution of large body size might have little or no impact on gliding performance. This condition is sometimes referred to as functional equivalence or functional similarity in the scaling/allometry literature (e.g. Sweet, 1980; LaBarbera, 1989). In a study comparing 29 species of flying lizards, McGuire (Chapter 3) tested the alternative hypotheses of isometry and functional equivalence and found that functional equivalence was strongly rejected by the data, whereas isometry could not be rejected. Indeed, the observed slopes when two alternative area measurements were regressed on body mass were very close to the exact slope predicted under isometry (0.67), and the expected slope under isometry fell well within the 95% confidence intervals in all cases. This morphological result strongly suggests size–dependent gliding performance in *Draco*.

MATERIALS AND METHODS

Gliding Trials

Gliding trials were conducted at three sites in Malaysia, two of which were on the Malay Peninsula (Ulu Gombak Field Studies Centre, Selangor, and Wang Kelian, Perlis) and one on the island of Borneo (Poring Hot Springs, Sabah). Live flying lizards were collected in nearby forest by stunning them with a plasticene projectile fired from a blowpipe. The lizards were then maintained in captivity for

2–5 days, during which period gliding trials were conducted. The lizards were not fed during this period. The gliding trials required a relatively large gliding arena such that the study animals could not easily escape into nearby vegetation. At each of our gliding arenas (large level fields), we erected two large poles, one of which served as a take-off pole and the other as a landing pole (Figure 4.1). We matched the dimensions of each of our arenas as closely as possible. Each take-off pole was approximately 6 meters in height, and the landing pole was 4–5 meters in height. The poles were placed 9.3 meters apart. A video camera (Sony Video8 Handycam) on a tripod was oriented orthogonally to a line drawn between the two poles at such a distance (and magnification) as to allow for the recording of complete glides between the two poles. With this camera arrangement, a known filming speed (60 fields/s), and a known distance between the bases of the two poles, performance data could be obtained from the video footage following image capture in the lab.

Lizards were placed on the take-off pole, encouraged to climb to the top of the pole (if necessary) by tapping on the pole or by prodding them with a long bamboo rod, and, following a 1–2 minute acclimation period, were coerced to jump from the take-off pole after further prodding with the bamboo rod. Either during the glide or immediately following the glide, horizontal wind velocity and direction (at a height of 3 meters) together with air temperature were measured with a digital anemometer (TSI VelociCalc Plus). When a lizard performed a straight glide to the left or right of the landing pole such that the deviation was approximately 30 degrees or less, the distance between the landing pole and the point in the lizard's trajectory between the pole and the camera was measured. Glide distances and velocities were obtained for these latter glides following appropriate trigonometric correction.

Glides in which the lizard banked left or right were excluded from consideration. Study lizards were sacrificed after they had either provided five suitable glides or after five days had passed since capture, whichever came first. Body mass was measured using a 10, 20, 30, or 50g spring-loaded pesola scale immediately prior to preservation in 10% formalin. Lizards were preserved with patagia fully spread in order to facilitate area measurements once the specimens were returned to the lab. Measurement protocols are described in Chapter 3.

Data Recovery

Raw video footage was processed in the lab with a Panasonic VCR (AG–1750) linked to a Macintosh Quadra 700 computer. Glides were plotted by viewing the video footage of the glide frame–by–frame while using the program QuickImage^{TM} to capture desired frames from which (*x*,*y*) coordinates were subsequently obtained. We attempted to record the coordinates documenting the position of the lizard every fifth field (= every 1/12 second). When the lizard could not be detected on the fifth field, we attempted to obtain its coordinates on a nearby frame. The coordinates were recorded in a spreadsheet into which the appropriate formulae were entered for the calculation of horizontal, vertical, and absolute velocities, as well glide duration. Because *Draco* are quite small relative to the area captured in each video frame, it is difficult to obtain the coordinates of the lizard with precision. Thus, we expect that the velocity measure taken between any two points will exhibit measurement error, but this variation should not exhibit systematic bias. We attempted to reduce this variation by applying a three–point smoothing algorithm to the raw positional data. The smoothing algorithm is simply the average of the reference velocity value and the uncorrected velocity values immediately before and after the reference value. Velocity corrections for glides in which the lizard deviated away from or toward the camera at a known angle were incorporated at this time. Angular deviations of the camera from horizontal were incorporated based on a known horizon (roof line) filmed for each camera orientation. A scatterplot depicting the glide trajectory was produced for each glide (see Figure 4.2 for a pair of representative glide trajectories).

Performance Parameters

The primary performance parameters measured in this study are maximum observed velocity during a glide, adjusted maximum velocity (the prior value correcting for wind velocity), height lost over a standard distance, and total glide angle. These parameters were chosen because there are clear predictions that can be made for each given the results of the scaling analysis. We did not attempt to evaluate maneuverability primarily because of difficulties in establishing a tractable experimental protocol, although our field observations suggest that smaller species are substantially more maneuverable than are the large species. Because our primary thesis is that body size evolution constrains gliding performance primarily through effects on wing loading, our statistical tests involve regression of performance parameters on wing loading. The relevant performance parameters are defined below.

Maximum velocity and adjusted maximum velocity.—Maximum velocity and adjusted maximum velocity differ only in that the latter includes a correction for the wind velocity measured at the time of the glide. When wind was perceptible, it was almost always in the form of a tailwind or headwind. We generally arranged the poles relative to the predominant wind direction such that glides directly toward the landing pole would be accompanied by a tailwind, as this seemed to increase the likelihood that the lizard would glide in the desired direction. Thus, most of our glides were accompanied by a tailwind. When there was a tailwind, the wind velocity was subtracted from the lizard's calculated horizontal component of velocity to produce the adjusted maximum velocity. In cases in which a headwind was observed, the wind velocity was added to the lizard's unadjusted horizontal velocity component.

Height lost.—We measured total height lost over a standard horizontal distance of 9.3 meters (Figure 4.3). Based on our observations, we expected to see differences in the values of the observed height lost when the lizard lands on the landing pole versus when it glides past the landing pole. We expected to see less height lost when lizards land on the pole because they generally finish the glide with a braking maneuver, which includes a terminal upswing (see Figures 4.2 and 4.3).

Total glide angle.—Total glide angle is simply the angle between the take-off position of the lizard and landing position of the lizard or, in the case of glides past the landing pole, the position at which the lizard passed the landing pole (Figure 4.3). Because we could not see the lizard's exact position on the landing pole for many glides, but could nevertheless interpolate the lizard's final position, we obtained the glide angle from the glide plot using a protractor rather than calculating a more precise glide angle from the actual coordinate data on the spreadsheet. As with height lost, we expect that the total glide angle will differ between glides to the landing pole and glides that extended beyond the landing pole because lizards that land on the pole generally initiate a braking maneuver with a terminal upswing in the trajectory, whereas lizards that glide past the pole usually exhibited no such braking maneuver.

Regression Models

Determining the appropriate regression model for use in biological studies is a complex issue (Gould, 1966; Rayner, 1985; La Barbera, 1989; Harvey and Pagel, 1991). The most commonly used model, ordinary least squares (OLS), may be inappropriate because it does not account for measurement error in the independent variable (Rayner, 1985; La Barbera, 1989; Harvey and Pagel, 1991). As an alternative, several authors have suggested the reduced major axis (RMA) model (Ricker, 1973; Rayner, 1985) because it incorporates error in the independent variable. Given that our independent variable (wing loading) almost certainly include some measurement error, we employed the reduced major axis (RMA) in this study. We have calculated our RMA slopes by dividing the OLS slope by its correlation coefficient (Ricker, 1973; Rayner, 1985). However, interpretation of 95% confidence intervals with RMA regression is problematic and care must be taken when attempting to use RMA confidence intervals for hypothesis testing (Ricker, 1973; Sokal and Rohlf, 1995). Because OLS will underestimate the regression coefficient when there is error in the independent variable, we present OLS 95% confidence intervals, which provide a conservative view of the lower bound (the critical confidence interval given that we are primarily concerned with testing for nonzero regression coefficients). All of the data employed in the regression analyses were log–transformed.

Data Partitions

Because the data are rather complex and there are several alternative ways that the data might be justifiably partitioned, multiple data sets were compiled for analysis. This analysis required two major sets of assumptions. The first set of assumptions relate to which observations can be treated as independent data points for statistical analysis. For example, we performed separate analyses in which all glides are treated as independent data points, including multiple glides per individual and multiple glides per species. We performed additional analyses which included only the best observed value per individual (based on minimum total glide angle), but still retained multiple glides per species. Finally, a third set of analyses included a single summary performance score per species. Twelve separate species–level analyses were conducted because the summary score was calculated under two alternative protocols (the mean score for all adults within a species, and the best observed value for the species), and because separate analyses were conducted three ways: pooling all glides, using only glides to the landing pole, and using only glides past the landing pole. All of the species–level data partitions were limited to single best glides per individual lizard. Species–level analyses were performed with and without transforming the data by calculating independent contrasts (Felsenstein, 1985).

Independent Contrasts

The analyses outlined above were conducted without accounting for statistical nonindependence due to phylogeny. Phylogenetic history can be disregarded if there is additive genetic variance for the variables in question and if they are presently under selection (Burt and Bell, 1987; Ridley, 1989; Price, 1997). Although this may very well be the case for performance variables that have important fitness consequences, we have nevertheless conducted independent contrasts analyses (Felsenstein, 1985) to remove phylogenetic effects. These analyses were conducted using the program CAIC version 2.02 (Purvis and Rambaut, 1995). The phylogenetic estimates of *Draco* relationships that served as the historical framework for calculation of independent contrasts were generated by the author (Chapter 2). In Chapter 2, we analyzed 1165 base pairs of mitochondrial ND2 and tRNA sequence data for 51 species/populations of *Draco* and four outgroup species under maximum likelihood and maximum parsimony optimality criteria. The maximum likelihood analyses employed four alternative models of sequence evolution, and likelihood ratio tests showed that the estimate obtained under the general–time–reversible model with rate heterogeneity (GTR+G) explained the data significantly better than did the less parameter–rich Jukes–Cantor, Felsenstein, and Hasegawa–Kishino–Yano (with rate heterogeneity) models. Therefore, we employed the GTR+G likelihood estimate (Figure 4.4), including branch lengths, in the calculation of independent contrasts. After log-transformation, all branch lengths were multiplied by a constant to satisfy format requirements of CAIC.

Equilibrium Glide

In addition to our analysis of comparative gliding performance, we were also interested in determining whether the glides obtained here included an equilibrium component. By definition, the equilibrium portion of a glide is characterized by a zero–change in velocity (Norberg, 1990). Under experimental conditions, this theoretical expectation is unlikely to be observed empirically given instantaneous variation in wind velocity during the glide and measurement error imposed by the digitizing process (Walker, 1998). We first attempted to quantify portions of the glide that were approaching equilibrium by calculating an arbitrary threshold value for percentage change in velocity, and then identifying those sections of the glide over which the observed change in velocity did not exceed the threshold. We considered three potential threshold values (5%, 10%, and 15%). This approach was deemed unsatisfactory because it is critically dependent on the amount of time separating the observed data points (two positional observations separated by a small enough duration will always exhibit less than the threshold change in velocity) and because a steady increase or decrease in velocity at increments less than the threshold value will result in the erroneous identification of an equilibrium region.

Given the difficulties associated with the quantitative approach described above, we instead utilized a qualitative approach. We used the program Quicksand (Walker, 1997) to provide velocity and acceleration profiles for all of our complete glides (i.e., those that included data points throughout the glide trajectory). This program employs several alternative smoothing algorithms that attempt to alleviate some of the measurement errors common to digitized locomotor data (Walker, 1998). In particular, we relied on the Lanczos five–point moving regression

(Lanczos, 1956), which appeared to produce less extreme smoothing than did the Butterworth filter (Winter, 1990) and quintic spline approaches (Woltring, 1985). Glides with velocity profiles that demonstrated a clear plateau region, indicating relatively stable velocities over an extended duration, were considered to be in equilibrium over the corresponding time interval.

RESULTS

A total of 249 glides were obtained for 11 species of *Draco*. Of 249 glides, 158 were glides directly to the landing pole and 91 were glides past the landing pole. Table 4.1 provides a breakdown of the total number of glides, glides to the pole, and glides past the pole for each species included in the study. The average wind velocity across all 249 glides was 0.98 m/s, with a range of 0–3 m/s. Because high wind could adversely affect our results, we generally did not attempt gliding trials when wind velocity exceeded 2 m/s. As a result, only six of 249 glides were accompanied by winds in excess of 2 m/s.

Comparative Gliding Performance

Analysis of the complete data set (including glides to and past the landing pole) revealed highly significant positive correlations (based on ANOVA) between wing loading and each of the four performance variables (maximum velocity, adjusted maximum velocity, height lost, and total glide angle; each with $p<0.0001$; Figures 4.5–4.8; Tables 4.1–4.4). When only the best observed values per individual (based on minimum glide angle) were included in the analysis, significant correlations between wing loading and each of the performance variables were again revealed (Figures 4.5–4.8; Tables 4.1–4.4), although the p-value was substantially reduced for unadjusted maximum velocity (p=0.02).

As with the analyses of the complete data set, analyses including all of the glides in which the lizard landed on the landing pole revealed highly significant positive correlations between wing loading and the performance parameters (Figures 4.5–4.8; Tables 4.1–4.4). When the analysis was limited to the best glide to the pole per individual lizard, the results were again highly significant (Figures 4.5–4.8; Tables 4.2–4.5).

Analysis of the data partition including all glides past the landing pole revealed highly significant positive correlations between wing loading and all of the performance parameters except unadjusted maximum velocity (p=0.03 for maximum velocity, $p \leq 0.0001$ for the remaining variables; Figures 4.5–4.8; Tables 4.2–4.5). When the analysis is limited to the best glide past the pole per individual, significant correlations between wing loading and adjusted maximum velocity, height lost, and total glide angle are obtained, but a nonsignificant result (p=0.10) is obtained for unadjusted maximum velocity (Figures 4.5–4.8; Tables 4.2–4.5).

Results of the species–level analyses using untransformed data differed depending on the protocol for selecting the representative values for wing loading and the four performance parameters. When the representative species values were selected by taking mean scores for all adults (using only a single glide per individual lizard), no significant positive correlations were found between wing loading and the four performance parameters regardless of whether the data set was restricted to glides to the landing pole, glides past the landing pole, or the complete data set

(Figures 4.9–4.12; Tables 4.1–4.4). When the representative species values were based on the best observed glide for an adult individual (determined by minimum glide angle), significant positive correlations were observed for height lost and total glide angle for the complete data set and the data set composed only of glides to the landing pole (Figures 4.11–4.12; Tables 4.3–4.4). Regression of height lost and total glide angle were both nonsignificant when the data were restricted to glides past the landing pole (p=0.06 and p=0.07, respectively; Figures 4.11–4.12; Tables 4.3–4.4). Because data for glides past the landing pole were not obtained for *Draco fimbriatus* and *D. sumatranus*, the failure to identify a significant positive correlation between height lost and total glide angle with this data partition might be the result of two fewer data points in this partition. Regressions of the two velocity parameters on wing loading were nonsignificant with each of the three data partitions (Figures 4.9–4.10; Tables 4.1–4.2).

Results of the species–level analyses based on phylogenetically transformed data are similar to those obtained with nontransformed data in that all analyses based on the data set composed of mean species scores were again nonsignificant (except for adjusted maximum velocity in the data set composed of glides to the landing pole, p=0.036; Figure 4.14; Table 4.3). Height lost and total glide angle were found to be significantly and positively correlated with wing loading in some of the analyses based on the data set with best observed species values (Figures 4.15–4.16; Tables 4.4–4.5). With the complete data set, both height lost and total glide angle were found to be significantly and positively correlated with wing loading (Figures 4.15–4.16; Tables 4.4–4.5). Only height lost was significantly correlated with wing loading with the data set composed of glides to the landing pole, although total glide angle was again near-significant (p=0.08; Figure 4.15; Table 4.5). As with the untransformed data, analyses based on glides past the landing pole revealed no significant correlations between wing loading and the performance parameters (Figures 4.13–4.16; Tables 4.2–4.5). Neither velocity parameter was found to be significantly correlated with wing loading (Figures 4.13–4.14; Tables 4.2–4.3).

Equilibrium Glides

Examination of the velocity profiles for individual glides revealed three primary glide types in our data set, each characterized by a readily identifiable velocity profile (Figure 4.17). Velocity profiles characterized by a plateau (approximating zero–change in velocity) were identified as equilibrium glides. Of 150 glides for which complete velocity profiles were generated, 72 (48.0%) were found to include a substantial equilibrium component. A second type of glide was characterized by a velocity profile with a sharp peak (Figure 4.17). These glides were characterized by steady acceleration through the first 1/2 to 2/3 of the glide, followed by rapid deceleration as the lizard approached the landing pole. This glide type generally was associated with glides to the landing pole (39 of 50, 78.0%), although lizards that glided past the landing pole occasionally began to decelerate before reaching the pole. The third glide type was characterized by a velocity profile indicating steady acceleration throughout the glide (Figure 4.17). This glide type was nearly always associated with glides past the landing pole (25 of 28, 89.3%).

The percentage of all glides to the landing pole that were equilibrium glides was calculated for 8 wing-loading classes (Figure 4.18) as a means of assessing whether individuals with lower wing loading were more likely to perform an equilibrium glide. Among lizards with wing loading between 6 and 9.9 N/m2, more than 80% of all glides to the pole (n=22) were equilibrium glides. Among individuals with wing loading between 10 and 13.9 N/m2, 50% of all glides to the pole (n=40) were equilibrium glides. Among individuals with wing loading between 14 and 17.9 N/m2, 36% of all glides to the pole (n=25) were equilibrium glides. Among individuals with wing loading higher than 18 N/m2, 60% of all glides to the pole were equilibrium glides, although sample sizes were small for this wing loading category (n=5).

DISCUSSION

Comparative Gliding Performance

The results of the comparative gliding performance analyses are congruent with the predictions generated in the analysis of scaling relationships for *Draco* (McGuire, Chapter 3). That study indicated that *Draco* are essentially isometric, with larger species having relatively less area available on a per–unit–mass basis for lift generation. In other words, larger species (and larger individuals within species) generally have higher wing loadings than do smaller species. Wing loading is a critical parameter in aerodynamic studies, and knowledge of the wing loading relationships among *Draco* species allows clear predictions regarding relative performance. For example, wing loading is expected to be proportional to the square of the equilibrium glide velocity (Norberg, 1990). Therefore, individuals with higher wing loading should exhibit greater glide velocities, and should perform longer ballistic dives in order to achieve that velocity. As a result, we expect that individuals with higher wing loading will sustain a greater loss in height over a standard horizontal distance and will exhibit greater total glide angles over a standard horizontal distance. Thus, larger species, which generally have a higher wing loading, should incur a cost relative to smaller species in the form of reduced gliding performance, assuming that larger species cannot compensate for their greater wing loading via morphological or behavioral modifications.

The results of the present study are largely concordant with the predictions derived from aerodynamic theory. Analyses that treat all glides produced by different individual lizards as independent observations, even if they are the same species, suggest that wing loading is strongly and positively correlated with the four performance parameters measured here. However, these analyses require a major assumption that may not be statistically defensible – namely that the performance parameters under study are unaffected and unbiased by phylogenetic history.

Results of the interspecific analyses utilizing single wing loading and performance values for each species revealed that wing loading is significant correlated with height lost and with total glide angle in analyses of the complete data set, and of the data set composed of glides to the pole, provided that the representative species value is the best observed value for adults of the species and not the mean value among adults of the species. Similar results were obtained in species–level analyses with and without phylogenetic correction. The finding that the results are nearly always nonsignificant when mean species scores are employed (the one exception was adjusted maximum velocity in the data set composed of glides to the pole), but often significant when the best observed species scores are used is not particularly surprising because there is substantial variation in gliding performance evident in our data set, especially among individuals with lower wing loading. Thus, if a positive relationship does exist between height lost, total glide angle, and wing loading, we would expect that larger individuals would have less flexibility with respect to gliding performance than would individuals with lower wing loading. In other words, an individual with lower wing loading can perform glides spanning a diversity of glide angles ranging from shallow to steep, whereas an individual with higher wing loading cannot generate sufficient lift unless it performs a steep glide. Examination of the glide plots including all glides (Figures 4.7–4.8) suggest that this is indeed the case. For example, individuals at the lower end of the wing loading spectrum exhibit glide angles ranging from 15°–35°, whereas every glide angle produced by an individual with wing loading above 16N/m2 is greater than 25° (with a maximum observed glide angle of 34°). Therefore, the mean score for smaller species with lower wing loading may not approach maximum performance for the species, whereas the mean values for larger species are more likely to be nearer the species maximum performance limit. This relationship would tend to underestimate the regression coefficient if mean species values are employed rather than best observed values.

Support for the contention that smaller species with lower wing loading have greater flexibility with respect to glide angle can be seen by considering the range of glide angles generated by the same individual. Extreme examples include *Draco melanopogon* number 1702 (wing loading=8.72 N/m^2), which produced glide angles of 26.2°, 24.4°, and 16.25°; *D. melanopogon* number 1811 (wing loading=12.75 N/m^2), which produced glides of 32.75° and 19.75°; and *D. melanopogon* number 1740 (wing loading=8.01 N/m^2), which generated glide angles of 26.1° and 18°. If nothing else, these observations indicate that these smaller *Draco* can utilize very different gliding strategies when traversing equivalent horizontal distances. This observation also suggests that any single glide observation is unlikely to be true reflection of the performance limits of that individual.

Equilibrium Glides

The velocity profile analysis indicate that the flying lizards employed in this study performed three types of glides (Figure 4.17). About half of the glides exhibited an obvious velocity plateau, which we interpret as the portion of the glide in which the animal is in equilibrium. The two remaining velocity profile types are here treated as indicators of a nonequilibrium glide. One of these glide types was characterized by a distinct velocity peak, followed by deceleration. In these glides, it seems likely that the lizard could not or did not reach its equilibrium velocity before beginning the deceleration phase of the glide. Most of these glides (78%) were to the pole, suggesting that deceleration was in preparation for landing. The third glide type was characterized by continuous acceleration throughout the glide and was almost always associated with glides past the landing pole. This observation suggests that these lizards had not yet achieved their equilibrium glide velocity – assuming, of course, that flying lizards always select their theoretical equilibrium velocity during extended glides.

The distance separating the poles during our gliding trials are relatively similar to the spacing of trees utilized by *Draco* in Southeast Asian dipterocarp rainforest. Thus, our finding that more than half of the glides obtained in this study were nonequilibrium glides suggests that nonequilibrium gliding may be important to flying lizards in nature. The data further suggest that the larger species of *Draco* with higher wing loading are least likely to be in equilibrium over glides with a horizontal distance of approximately 10 m or less (Figure 4.18). This result appears consistent with the idea that larger species generally require either take-off heights greater than 6 meters or horizontal glide lengths of greater than 9 meters to achieve an equilibrium glide. However, the fact that *D. fimbriatus*, with the highest wing loading of any species included in the study, produced multiple equilibrium glides to the landing pole indicates that arena dimensions do not preclude equilibrium glides in species with high wing loading.

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Table 4.1. Results of the regression analyses of maximum velocity on wing loading. OLS refers to the ordinary least squares regression coefficient, r refers to correlation coefficient under OLS, RMA refers to the reduced major axis regression coefficient, p–value is from an ANOVA test for a nonzero regression coefficient.

Species	Total Number of Glides	Glides to Pole	Glides Past Pole
Draco blanfordi	36	15	21
Draco fimbriatus	8	8	0
Draco formosus	33	25	8
Draco haematopogon	22	9	13
Draco maculatus	25	20	5
Draco maximus	15	9	6
Draco melanopogon	70	45	25
Draco obscurus	9	7	2
Draco quinquefasciatus	8	6	2
Draco sumatranus	2	2	0
Draco taeniopterus	21	12	9
Total:	249	158	91

Table 4.2. Results of the regression analyses of maximum velocity on wing loading. OLS refers to the ordinary least squares regression coefficient, r refers to correlation coefficient under OLS, RMA refers to the reduced major axis regression coefficient, p value is from an ANOVA test for a nonzero regression coefficient.

Data Partition	OLS	r	RMA	n	p value
MULTIPLE GLIDES PER SPECIES					
Glides to and past pole:					
Multiple glides per individual	0.188	0.253	0.743	250	<0.0001
Best glide per individual	0.170	0.219	0.776	118	0.017
Glides to pole:					
Multiple glides per individual	0.204	0.293	0.696	159	0.0002
Best glide per individual	0.284	0.386	0.736	82	0.0003
Glides past pole:					
Multiple glides per individual	0.174	0.228	0.763	91	0.030
Best glide per individual	0.187	0.217	0.863	60	0.097
UNTRANSFORMED SPECIES VALUES					
Glides to and past pole:					
Mean score for adults	0.014	0.032	0.439	11	0.926
Best score for adults	0.138	0.333	0.414	11	0.317
Glides to pole:					
Mean score for adults	0.130	0.313	0.415	11	0.350
Best score for adults	0.143	0.295	0.485	11	0.378
Glides past pole:					
Mean score for adults	0.096	0.122	0.784	8	0.774
Best score for adults	0.271	0.310	0.875	8	0.455
INDEPENDENT CONTRASTS					
Glides to and past pole:					
Multiple glides per individual	-0.035	0.058	-0.606	10	0.866
Best glide per individual	0.210	0.346	0.606	10	0.296
Glides to pole:					
Multiple glides per individual	0.201	0.349	0.575	10	0.293
Best glide per individual	0.145	0.224	0.648	10	0.508
Glides past pole:					
Multiple glides per individual	0.070	0.092	0.759	7	0.828
Best glide per individual	0.309	0.383	0.806	7	0.348

Table 4.3. Results of the regression analyses of adjusted maximum velocity on wing loading. OLS refers to the ordinary least squares regression coefficient, r refers to correlation coefficient under OLS, RMA refers to the reduced major axis regression coefficient, p value is from an ANOVA test for a nonzero regression coefficient.

Data Partition	OLS	r	RMA	n	p value
MULTIPLE GLIDES PER SPECIES					
Glides to and past pole:					
Multiple glides per individual	0.250	0.375	0.666	250	<0.0001
Best glide per individual	0.206	0.321	0.642	118	0.004
Glides to pole:					
Multiple glides per individual	0.236	0.371	0.635	159	<0.0001
Best glide per individual	0.300	0.420	0.715	82	<0.0001
Glides past pole:					
Multiple glides per individual	0.283	0.390	0.726	91	0.0001
Best glide per individual	0.312	0.401	0.778	60	0.002
UNTRANSFORMED SPECIES VALUES					
Glides to and past pole:					
Mean score for adults	0.117	0.241	0.486	11	0.475
Best score for adults	0.098	0.161	0.608	11	0.634
Glides to pole:					
Mean score for adults	0.266	0.501	0.531	11	0.117
Best score for adults	0.074	0.158	0.46	11	0.644
Glides past pole:					
Mean score for adults	0.155	0.179	0.866	8	0.672
Best score for adults	0.403	0.405	0.995	8	0.319
INDEPENDENT CONTRASTS					
Glides to and past pole:					
Multiple glides per individual	0.068	0.130	0.522	10	0.705
Best glide per individual	0.130	0.192	0.676	10	0.574
Glides to pole:					
Multiple glides per individual	0.325	0.636	0.511	10	0.036
Best glide per individual	0.156	0.297	0.526	10	0.375
Glides past pole:					
Multiple glides per individual	0.143	0.167	0.855	7	0.694
Best glide per individual	0.352	0.394	0.894	7	0.335

Table 4.4. Results of the regression analyses of height lost on wing loading. OLS refers to the ordinary least squares regression coefficient, r refers to correlation coefficient under OLS, RMA refers to the reduced major axis regression coefficient, p value is from an ANOVA test for a nonzero regression coefficient.

Data Partition	OLS	r	RMA	n	p value
MULTIPLE GLIDES PER SPECIES					
Glides to and past pole:					
Multiple glides per individual	0.324	0.508	0.638	184	<0.0001
Best glide per individual	0.296	0.421	0.704	102	<0.0001
Glides to pole:					
Multiple glides per individual	0.317	0.516	0.615	122	<0.0001
Best glide per individual	0.307	0.474	0.647	82	<0.0001
Glides past pole:					
Multiple glides per individual	0.352	0.532	0.662	62	<0.0001
Best glide per individual	0.323	0.457	0.707	44	0.002
UNTRANSFORMED SPECIES VALUES					
Glides to and past pole:					
Mean score for adults	0.174	0.483	0.360	11	0.133
Best score for adults	0.521	0.856	0.609	11	0.0008
Glides to pole:					
Mean score for adults	0.233	0.504	0.462	11	0.114
Best score for adults	0.423	0.755	0.560	11	0.007
Glides past pole:					
Mean score for adults	0.244	0.559	0.437	8	0.150
Best score for adults	0.529	0.679	0.779	8	0.064
INDEPENDENT CONTRASTS					
Glides to and past pole:					
Multiple glides per individual	0.157	0.371	0.423	10	0.261
Best glide per individual	0.546	0.797	0.685	10	0.003
Glides to pole:					
Multiple glides per individual	0.270	0.467	0.578	10	0.148
Best glide per individual	0.407	0.639	0.637	10	0.035
Glides past pole:					
Multiple glides per individual	0.217	0.491	0.442	7	0.216
Best glide per individual	0.444	0.569	0.780	7	0.141

Table 4.5. Results of the regression analyses of total glide angle on wing loading. OLS refers to the ordinary least squares regression coefficient, r refers to correlation coefficient under OLS, RMA refers to the reduced major axis regression coefficient, p value is from an ANOVA test for a nonzero regression coefficient.

Data Partition	OLS	r	RMA	n	p value
MULTIPLE GLIDES PER SPECIES					
Glides to and past pole:					
Multiple glides per individual	0.278	0.477	0.582	184	<0.0001
Best glide per individual	0.263	0.414	0.636	102	<0.0001
Glides to pole:					
Multiple glides per individual	0.266	0.438	0.607	122	<0.0001
Best glide per individual	0.255	0.399	0.640	82	0.0002
Glides past pole:					
Multiple glides per individual	0.305	0.570	0.535	62	<0.0001
Best glide per individual	0.284	0.498	0.570	44	0.0006
UNTRANSFORMED SPECIES VALUES					
Glides to and past pole:					
Mean score for adults	0.201	0.503	0.400	11	0.115
Best score for adults	0.495	0.837	0.592	11	0.001
Glides to pole:					
Mean score for adults	0.187	0.470	0.398	11	0.145
Best score for adults	0.389	0.701	0.555	11	0.016
Glides past pole:					
Mean score for adults	0.232	0.464	0.500	8	0.247
Best score for adults	0.473	0.672	0.704	8	0.068
INDEPENDENT CONTRASTS					
Glides to and past pole:					
Multiple glides per individual	0.189	0.396	0.477	10	0.227
Best glide per individual	0.482	0.741	0.651	10	0.009
Glides to pole:					
Multiple glides per individual	0.211	0.436	0.484	10	0.180
Best glide per individual	0.360	0.556	0.648	10	0.076
Glides past pole:					
Multiple glides per individual	0.230	0.476	0.483	7	0.233
Best glide per individual	0.355	0.522	0.681	7	0.185

Figure 4.1. Dimensions of the glide arena employed in the field gliding trials.

Glide Arena

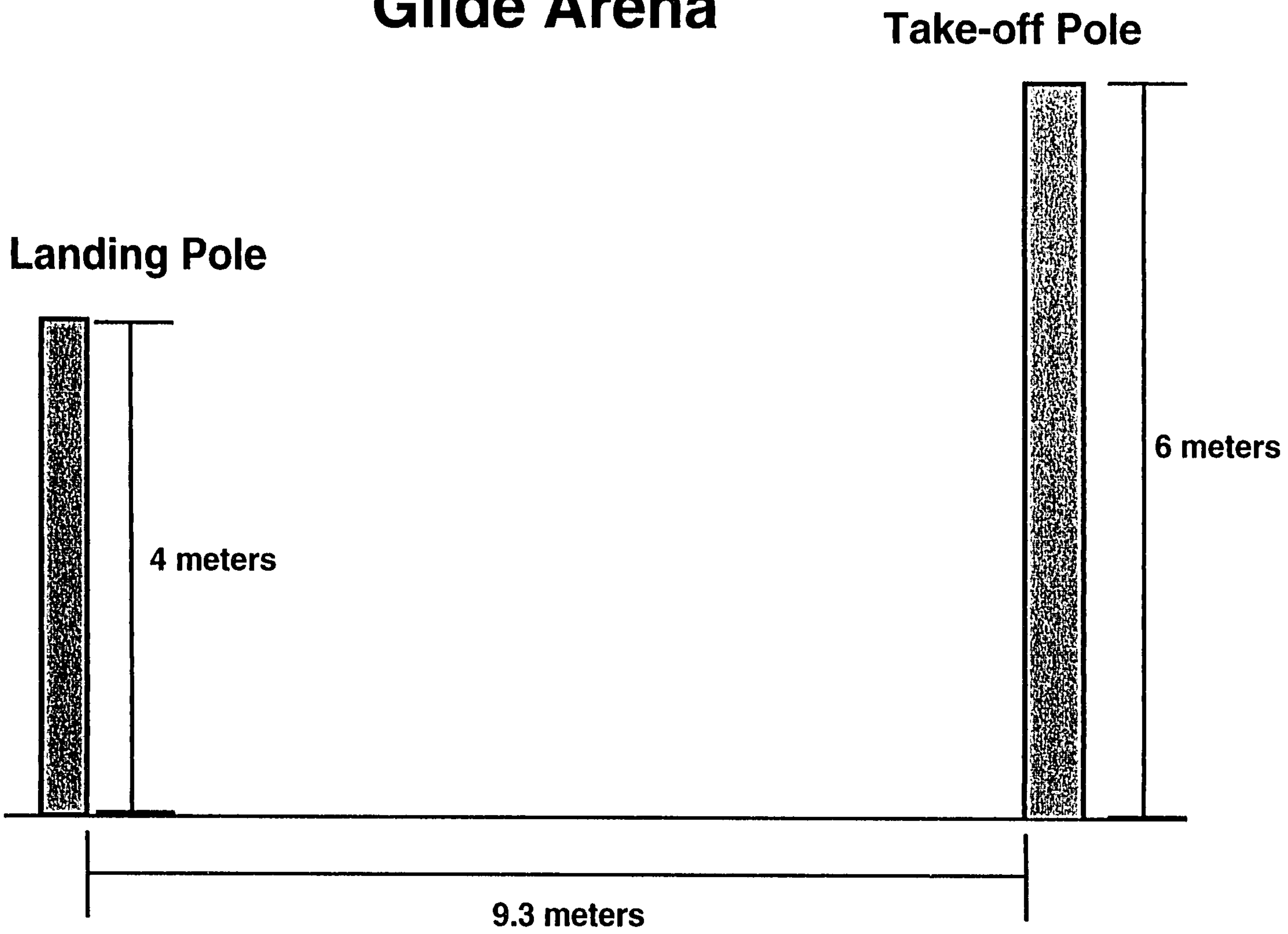


Figure 4.2. Representative glide trajectories for two species of *Draco*, *D. fimbriatus* (body mass = 21.6 g) and *D. melanopogon* (body mass = 2.95 g), near the ends of the size spectrum for the genus.

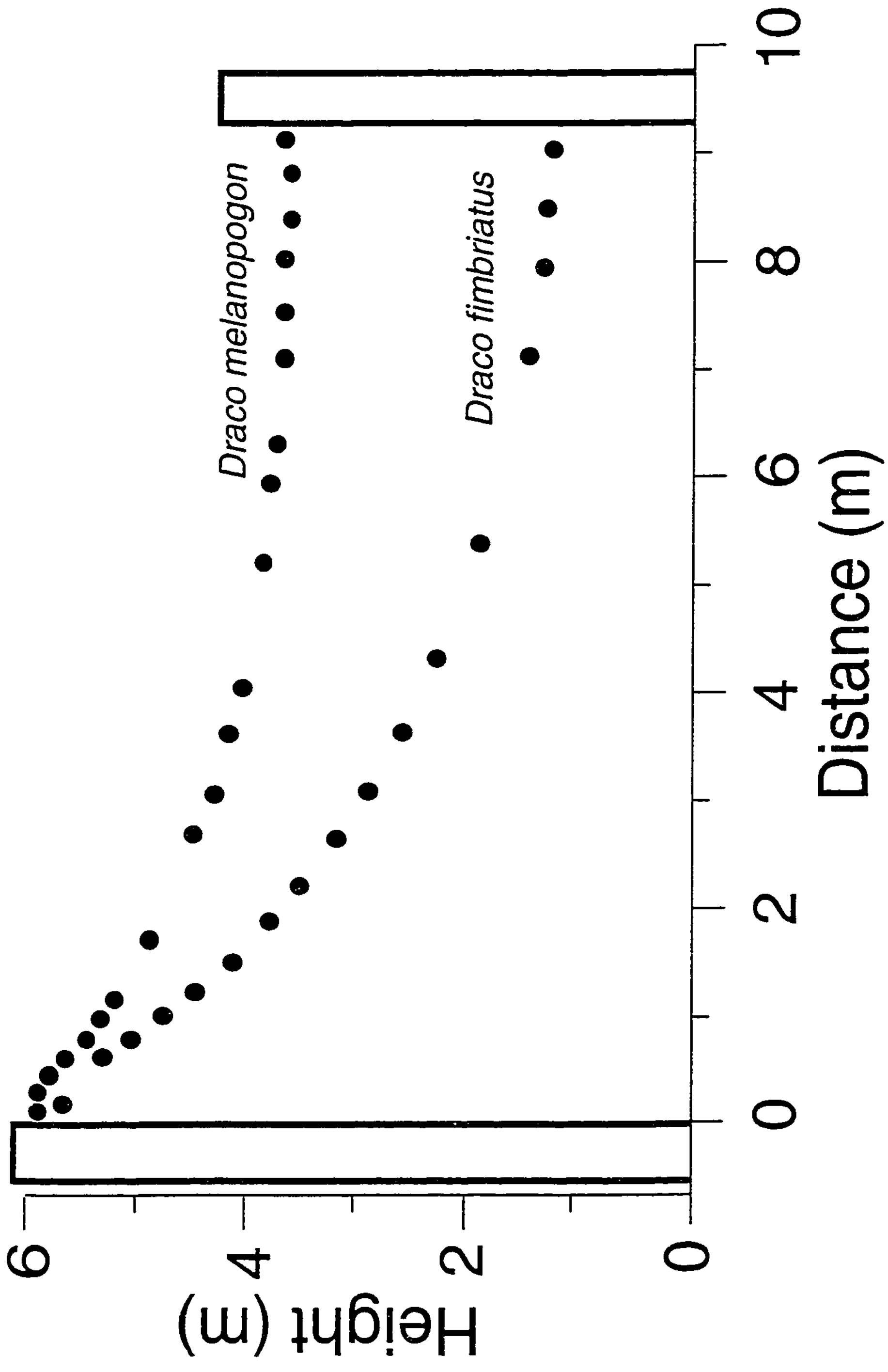

Height (m)
0
2
4
6
Distance (m)
0
2
4
6
8
10
Draco melanopogon
Draco fimbriatus

Figure 4.3. Definitions of height lost and total glide angle from a hypothetical *Draco* glide trajectory.

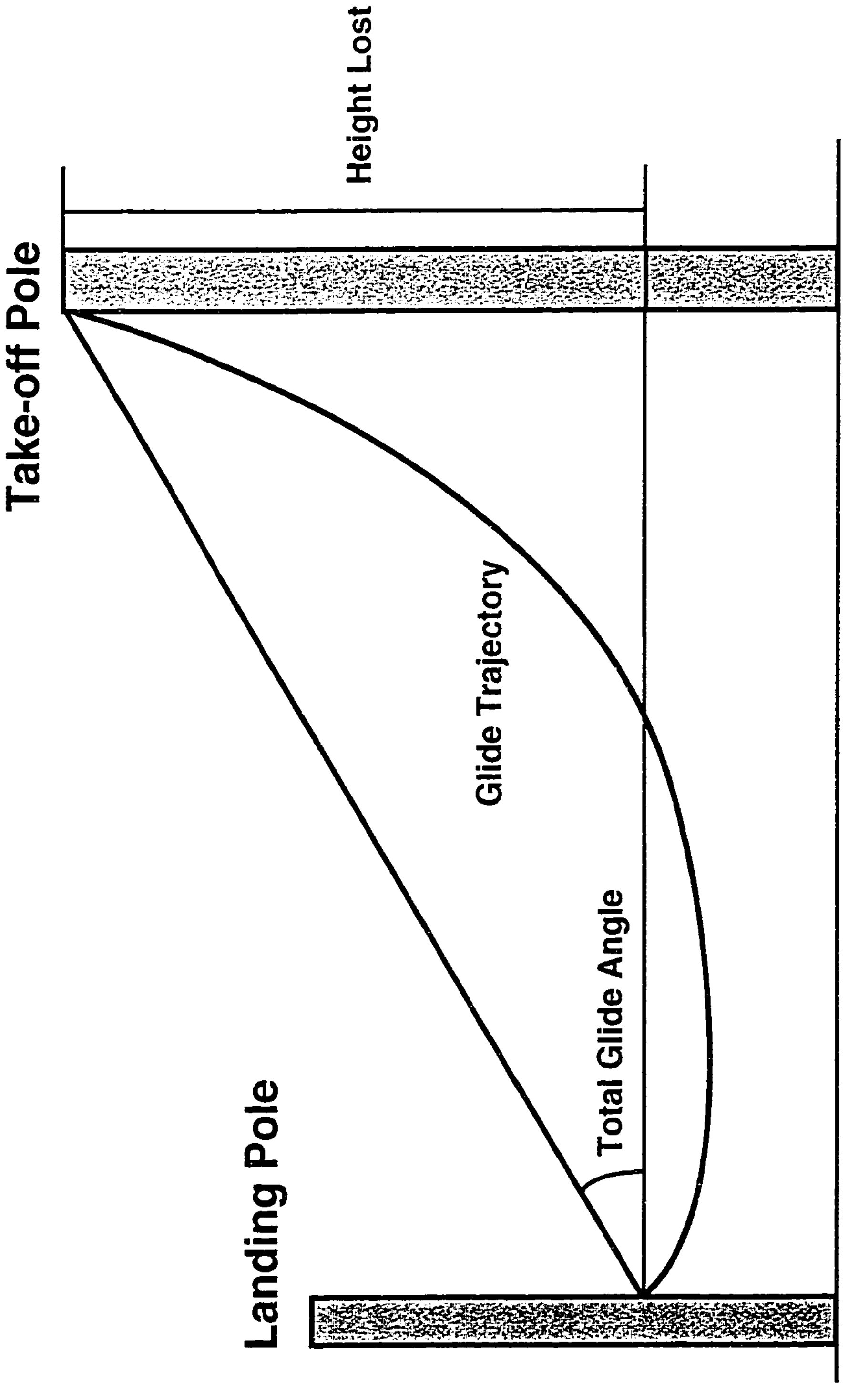

Take-off Pole
Landing Pole
Height Lost
Glide Trajectory
Total Glide Angle

Figure 4.4. Phylogram depicting the results of the GTR+G maximum likelihood analysis (McGuire, Chapter 2).

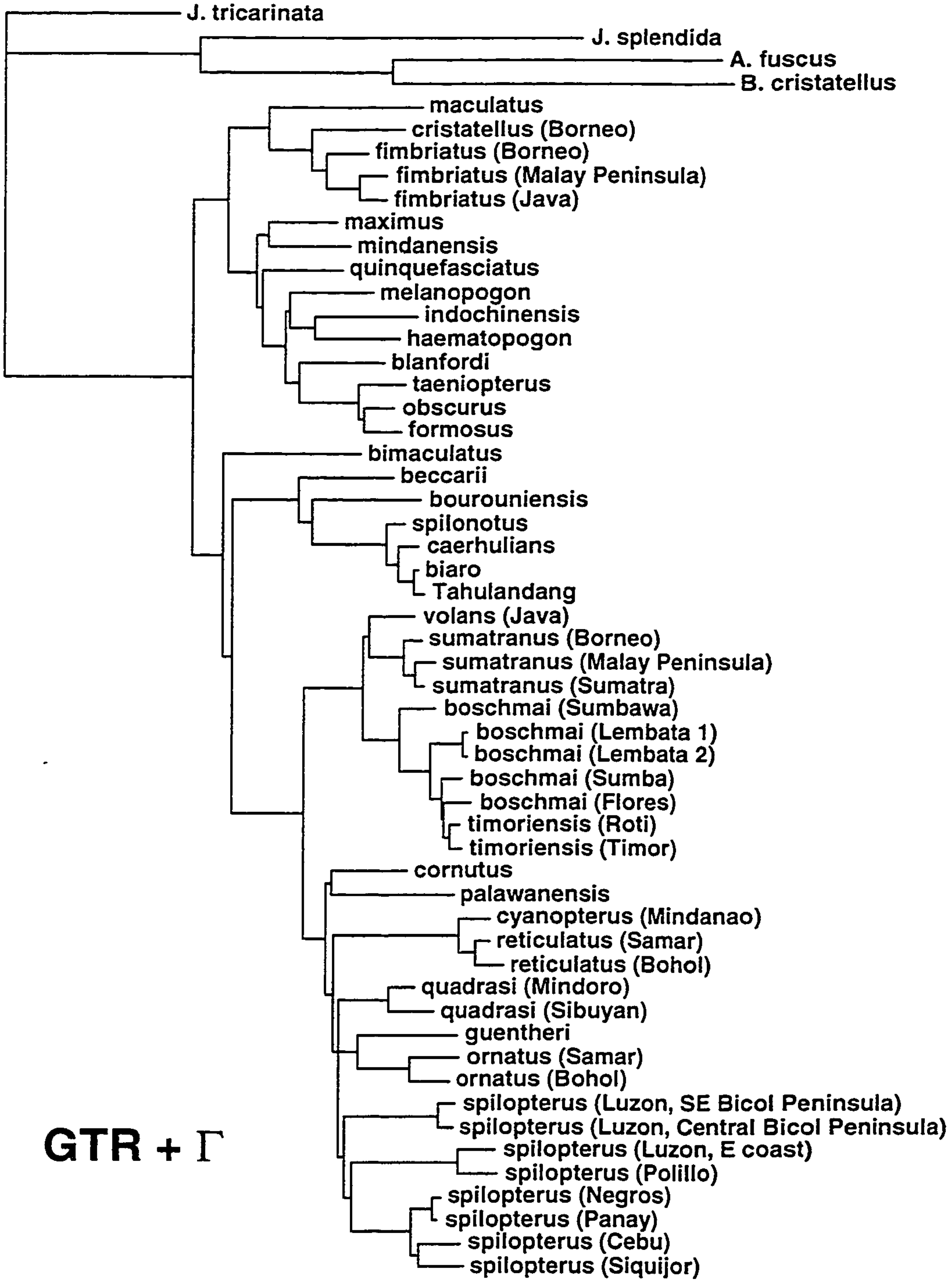

J. tricarinata
J. splendida
A. fuscus
B. cristatellus
maculatus
cristatellus (Borneo)
fimbriatus (Borneo)
fimbriatus (Malay Peninsula)
fimbriatus (Java)
maximus
mindanensis
quinquefasciatus
melanopogon
indochinensis
haematopogon
blanfordi
taeniopterus
obscurus
formosus
bimaculatus
beccarii
bourouniensis
spilonotus
caerhulians
biaro
Tahulandang
volans (Java)
sumatranus (Borneo)
sumatranus (Malay Peninsula)
sumatranus (Sumatra)
boschmai (Sumbawa)
boschmai (Lembata 1)
boschmai (Lembata 2)
boschmai (Sumba)
boschmai (Flores)
timoriensis (Roti)
timoriensis (Timor)
cornutus
palawanensis
cyanopterus (Mindanao)
reticulatus (Samar)
reticulatus (Bohol)
quadrasi (Mindoro)
quadrasi (Sibuyan)
guentheri
ornatus (Samar)
ornatus (Bohol)
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, Central Bicol Peninsula)
spilopterus (Luzon, E coast)
spilopterus (Polillo)
spilopterus (Negros)
spilopterus (Panay)
spilopterus (Cebu)
spilopterus (Siquijor)
GTR + Γ

Figure 4.5. Regression plots (ordinary least squares) illustrating results when maximum velocity is regressed on wing loading. The data set partitions include multiple glides per species. The data are log–transformed. The dashed lines represent 95% confidence intervals.

Maximum Velocity

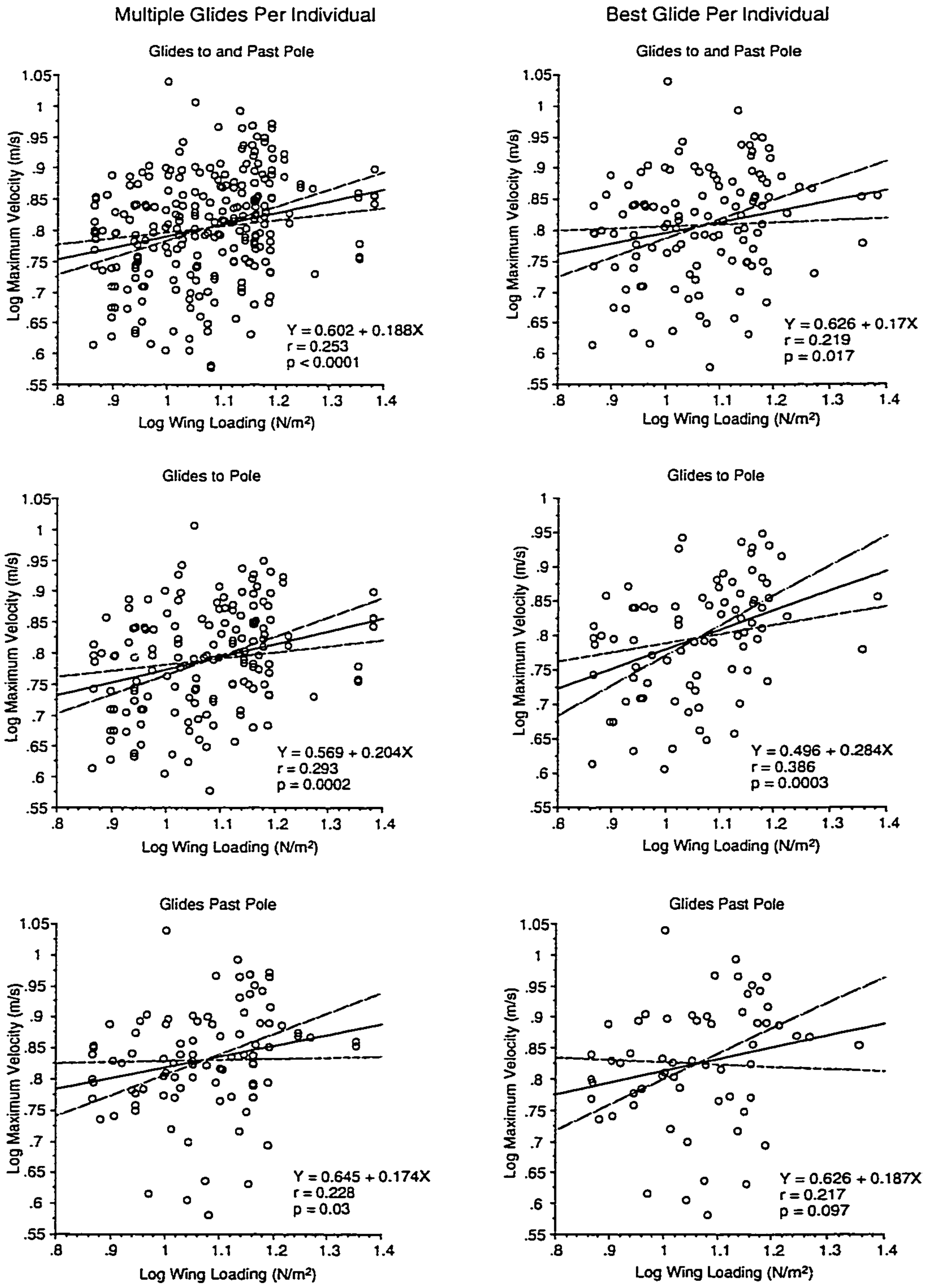


Figure 4.6. Regression plots (ordinary least squares) illustrating results when adjusted maximum velocity is regressed on wing loading. The data set partitions include multiple glides per species.

Adjusted Maximum Velocity

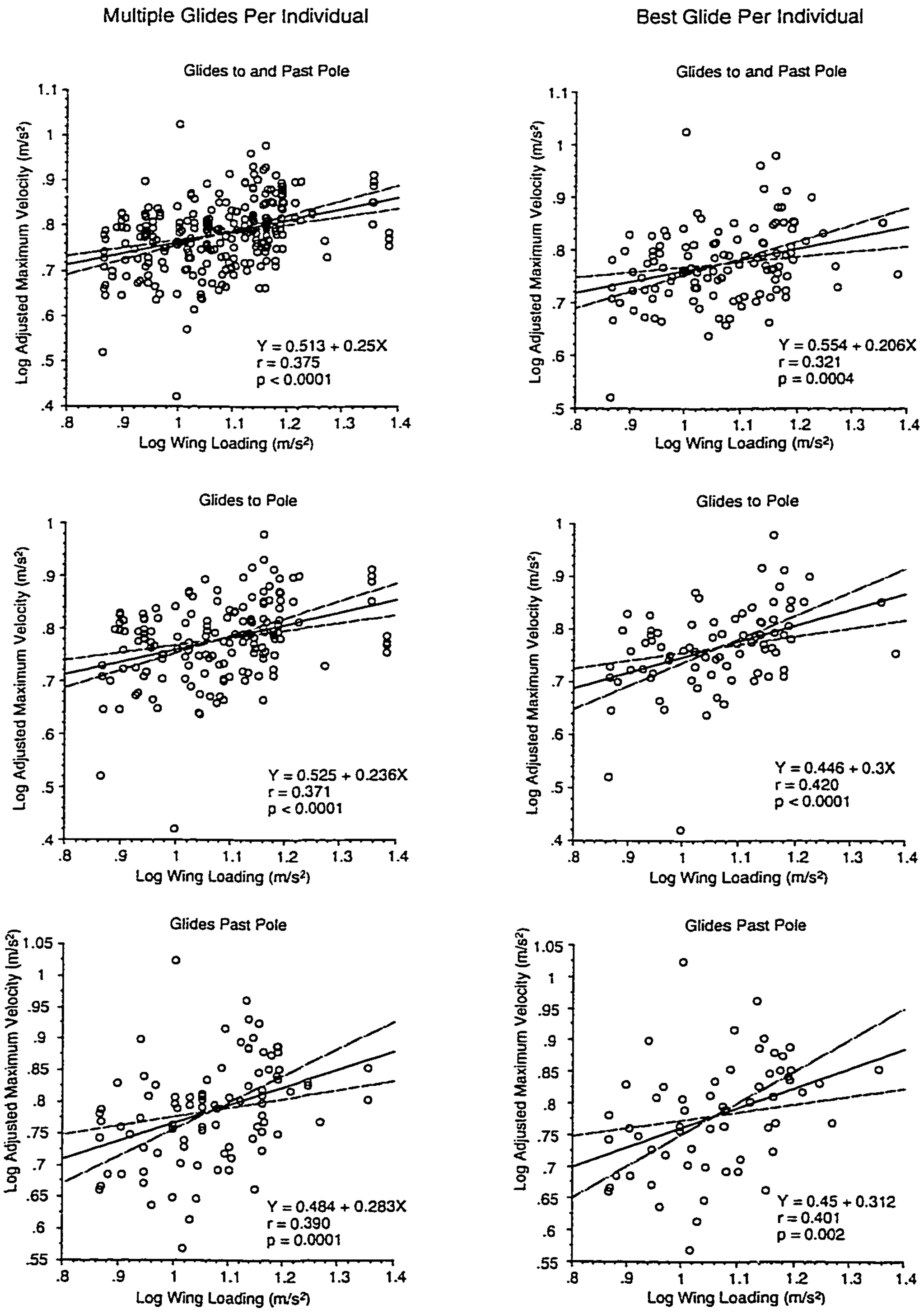


Figure 4.7. Regression plots (ordinary least squares) illustrating results when height lost is regressed on wing loading. The data set partitions include multiple glides per species.

Height Lost

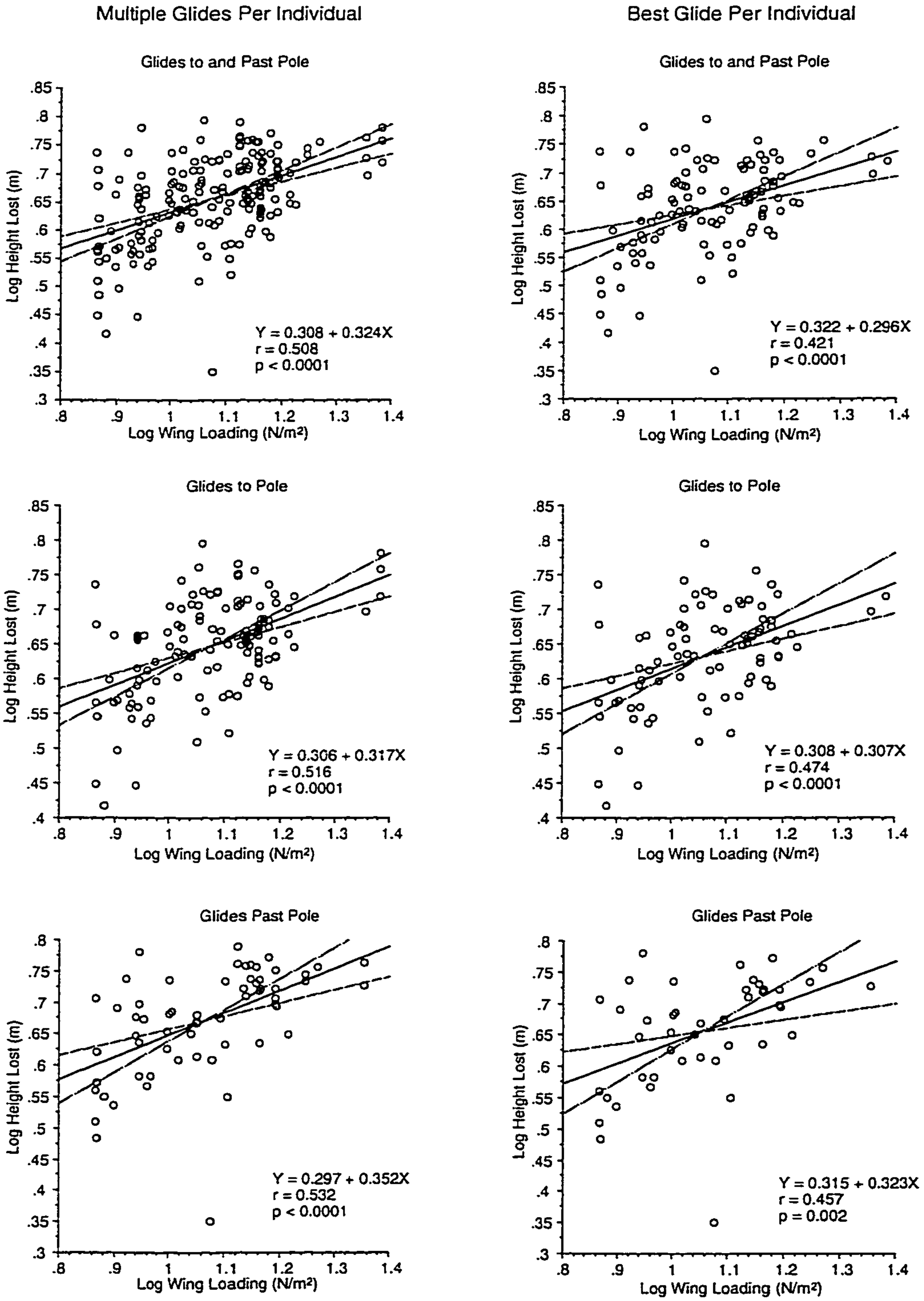

Multiple Glides Per Individual
Best Glide Per Individual
Glides to and Past Pole
Y = 0.308 + 0.324X
r = 0.508
p < 0.0001
Glides to and Past Pole
Y = 0.322 + 0.296X
r = 0.421
p < 0.0001
Glides to Pole
Y = 0.306 + 0.317X
r = 0.516
p < 0.0001
Glides to Pole
Y = 0.308 + 0.307X
r = 0.474
p < 0.0001
Glides Past Pole
Y = 0.297 + 0.352X
r = 0.532
p < 0.0001
Glides Past Pole
Y = 0.315 + 0.323X
r = 0.457
p = 0.002
Log Height Lost (m)
Log Wing Loading (N/m²)
.3
.35
.4
.45
.5
.55
.6
.65
.7
.75
.8
.85
.8
.9
1
1.1
1.2
1.3
1.4

Figure 4.8. Regression plots (ordinary least squares) illustrating results when total glide angle is regressed on wing loading. The data set partitions include multiple glides per species.

Height Lost

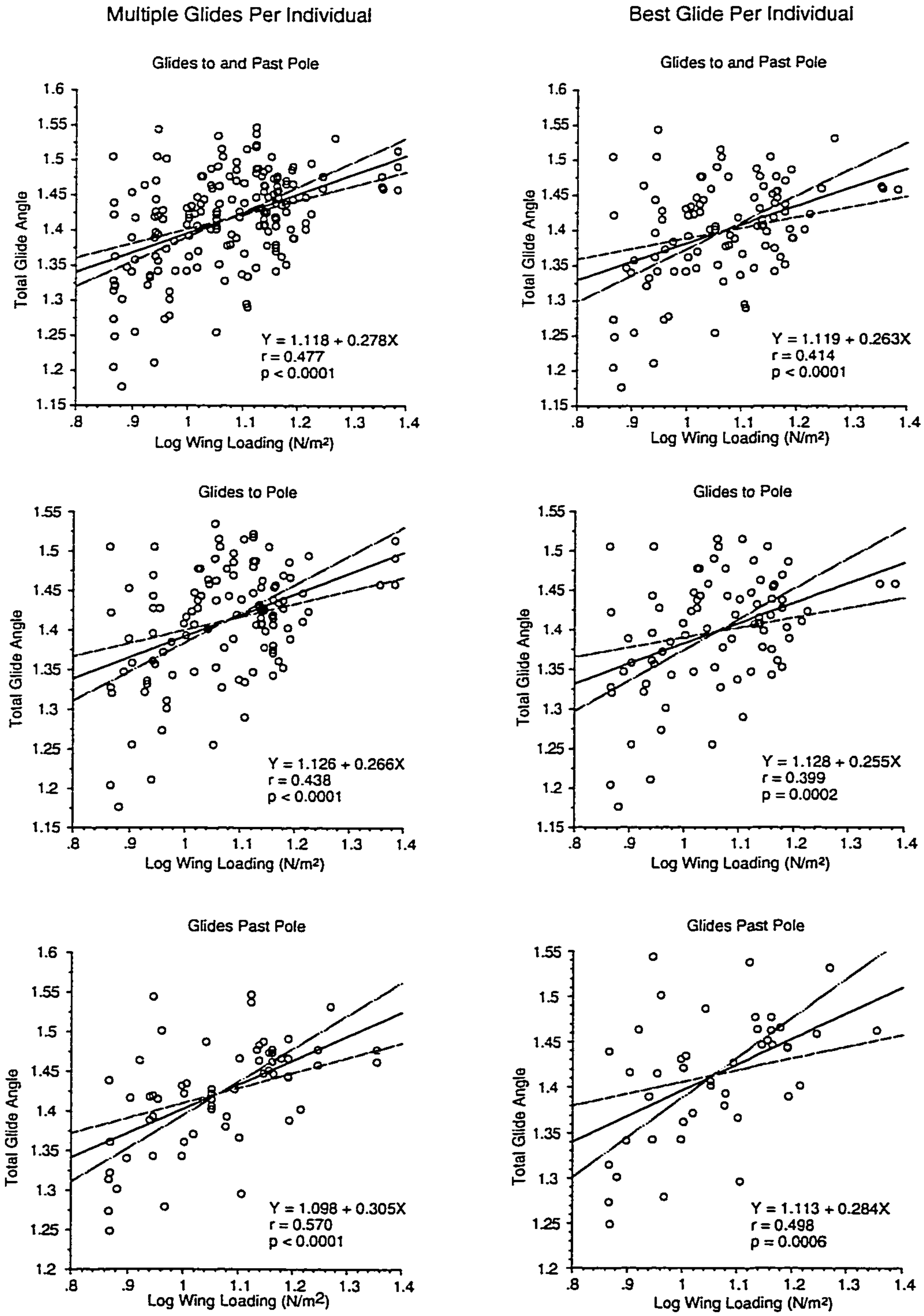

Multiple Glides Per Individual
Best Glide Per Individual
Glides to and Past Pole
Y = 1.118 + 0.278X
r = 0.477
p < 0.0001
Glides to and Past Pole
Y = 1.119 + 0.263X
r = 0.414
p < 0.0001
Glides to Pole
Y = 1.126 + 0.266X
r = 0.438
p < 0.0001
Glides to Pole
Y = 1.128 + 0.255X
r = 0.399
p = 0.0002
Glides Past Pole
Y = 1.098 + 0.305X
r = 0.570
p < 0.0001
Glides Past Pole
Y = 1.113 + 0.284X
r = 0.498
p = 0.0006
Total Glide Angle
Log Wing Loading (N/m2)
1.15
1.2
1.25
1.3
1.35
1.4
1.45
1.5
1.55
1.6
.8
.9
1
1.1
1.2
1.3
1.4

Figure 4.9. Regression plots (ordinary least squares) illustrating results when maximum velocity is regressed on wing loading. The data set partitions include uncorrected summary values for each species.

Maximum Velocity

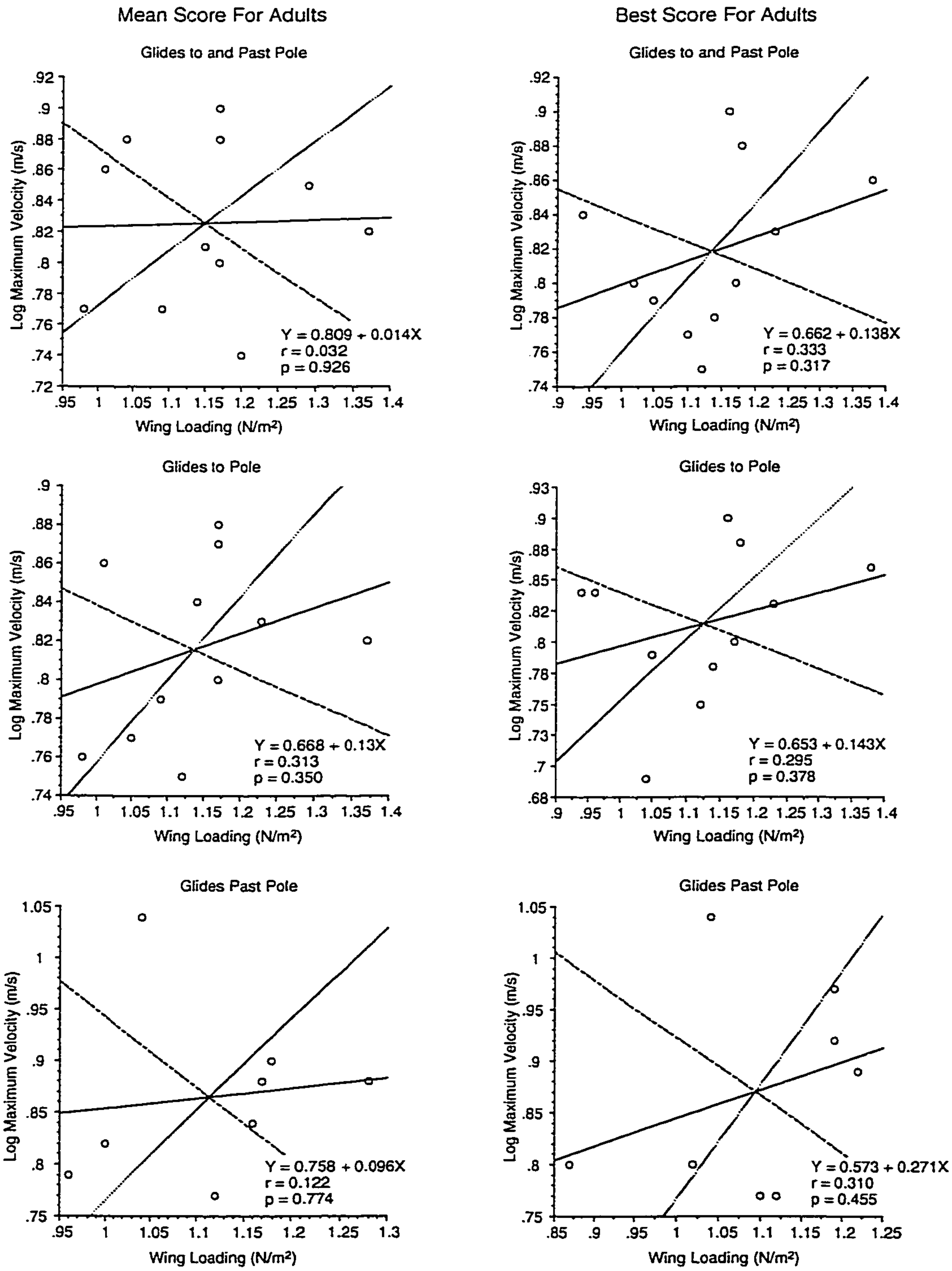


Figure 4.10. Regression plots (ordinary least squares) illustrating results when adjusted maximum velocity is regressed on wing loading. The data set partitions include uncorrected summary values for each species.

Adjusted Maximum Velocity

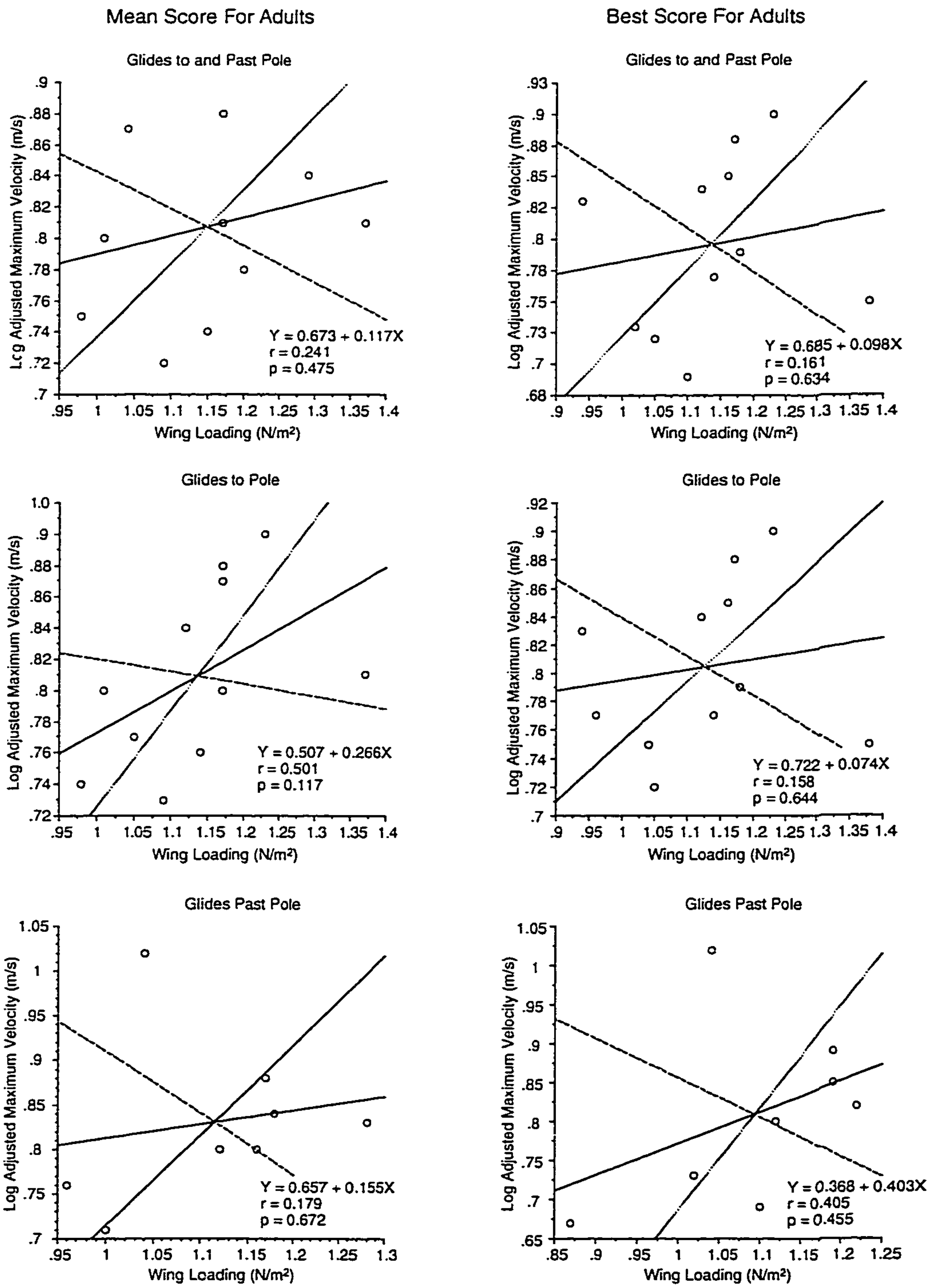


Figure 4.11. Regression plots (ordinary least squares) illustrating results when height lost is regressed on wing loading. The data set partitions include uncorrected summary values for each species.

Height Lost

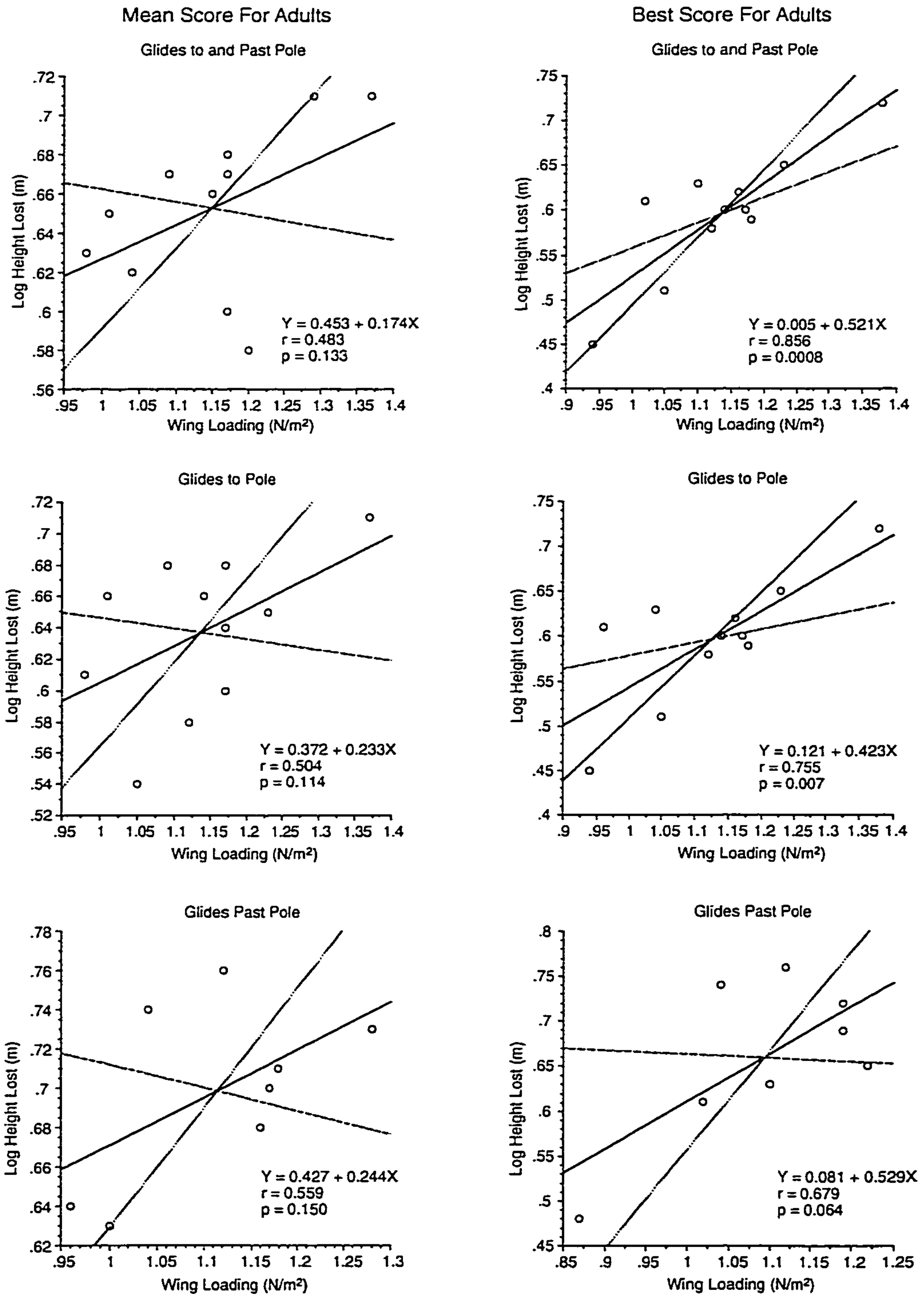

Mean Score For Adults
Best Score For Adults
Glides to and Past Pole
Log Height Lost (m)
.72
.7
.68
.66
.64
.62
.6
.58
.56
.95 1 1.05 1.1 1.15 1.2 1.25 1.3 1.35 1.4
Wing Loading (N/m²)
Y = 0.453 + 0.174X
r = 0.483
p = 0.133
Glides to and Past Pole
Log Height Lost (m)
.75
.7
.65
.6
.55
.5
.45
.4
.9 .95 1 1.05 1.1 1.15 1.2 1.25 1.3 1.35 1.4
Wing Loading (N/m²)
Y = 0.005 + 0.521X
r = 0.856
p = 0.0008
Glides to Pole
Log Height Lost (m)
.72
.7
.68
.66
.64
.62
.6
.58
.56
.54
.52
.95 1 1.05 1.1 1.15 1.2 1.25 1.3 1.35 1.4
Wing Loading (N/m²)
Y = 0.372 + 0.233X
r = 0.504
p = 0.114
Glides to Pole
Log Height Lost (m)
.75
.7
.65
.6
.55
.5
.45
.4
.9 .95 1 1.05 1.1 1.15 1.2 1.25 1.3 1.35 1.4
Wing Loading (N/m²)
Y = 0.121 + 0.423X
r = 0.755
p = 0.007
Glides Past Pole
Log Height Lost (m)
.78
.76
.74
.72
.7
.68
.66
.64
.62
.95 1 1.05 1.1 1.15 1.2 1.25 1.3
Wing Loading (N/m²)
Y = 0.427 + 0.244X
r = 0.559
p = 0.150
Glides Past Pole
Log Height Lost (m)
.8
.75
.7
.65
.6
.55
.5
.45
.85 .9 .95 1 1.05 1.1 1.15 1.2 1.25
Wing Loading (N/m²)
Y = 0.081 + 0.529X
r = 0.679
p = 0.064

Figure 4.12. Regression plots (ordinary least squares) illustrating results when total glide angle is regressed on wing loading. The data set partitions include uncorrected summary values for each species.

Total Glide Angle

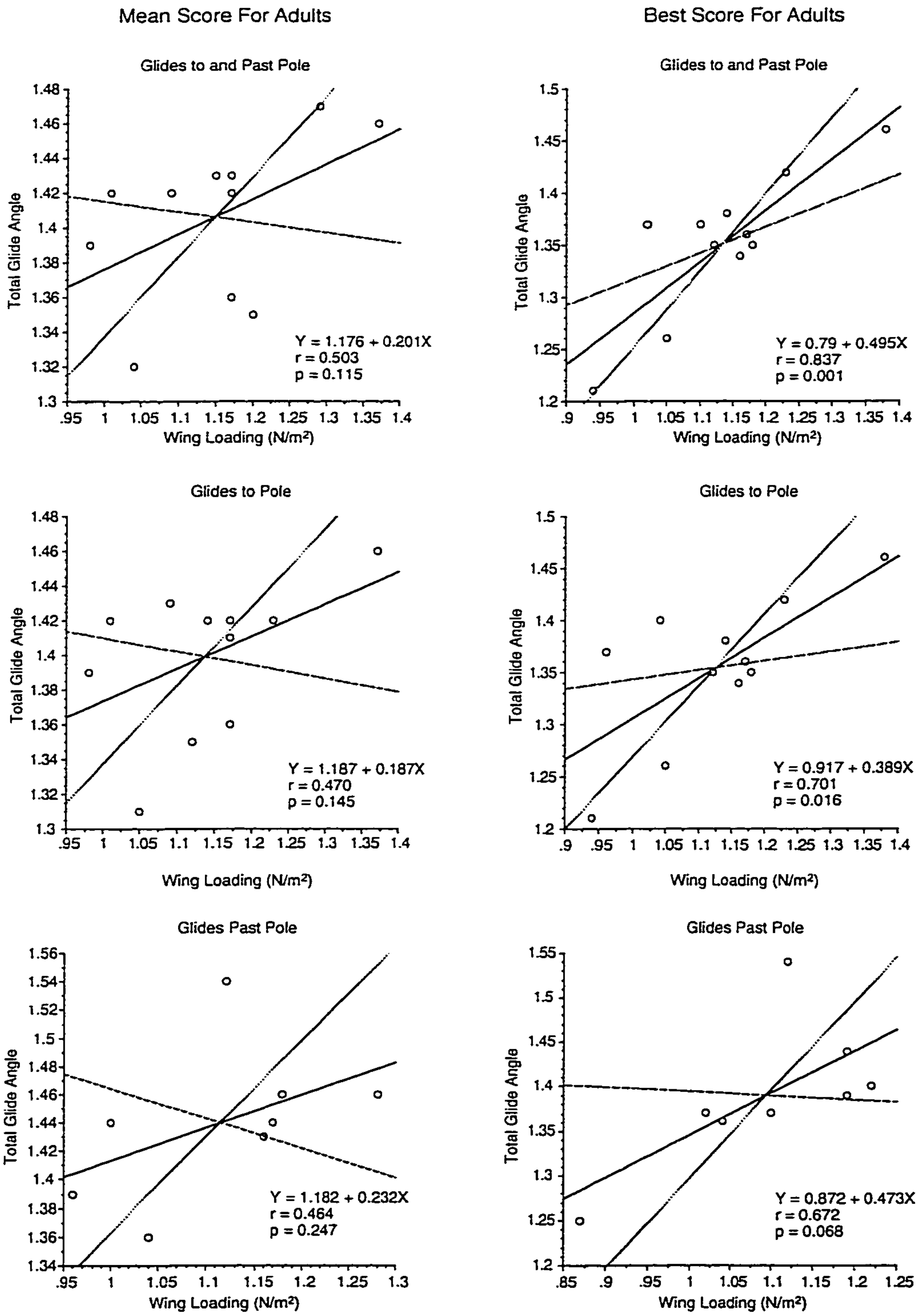
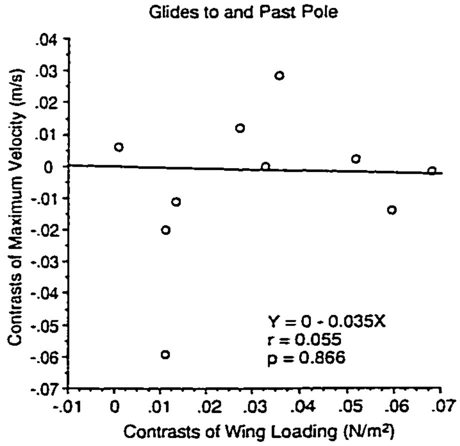
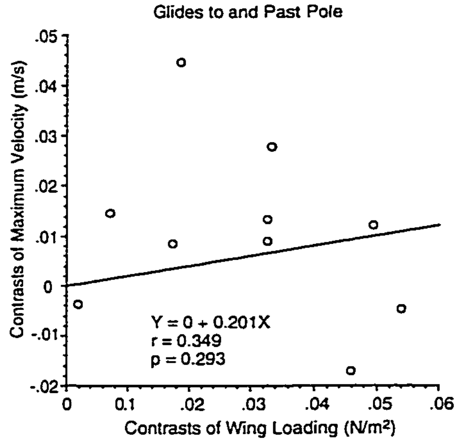


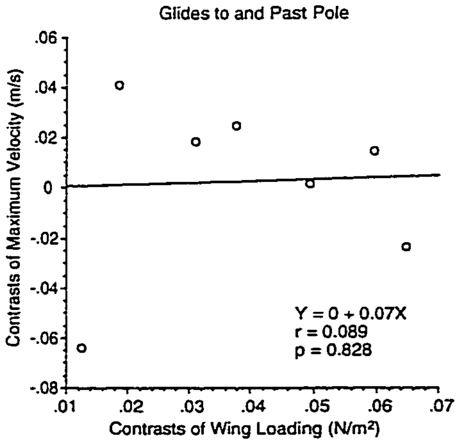
Figure 4.13. Regression plots (ordinary least squares) illustrating results when maximum velocity is regressed on wing loading. The data are independent contrasts summary values for each species.

Maximum Velocity

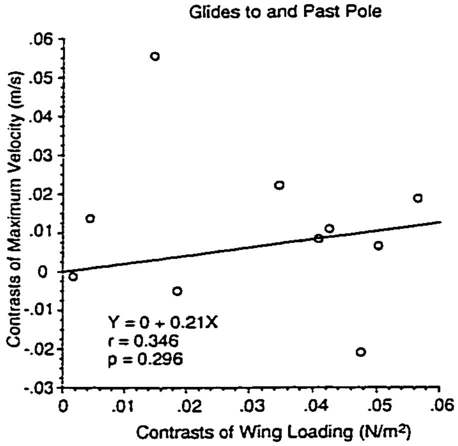
Mean Score For Adults

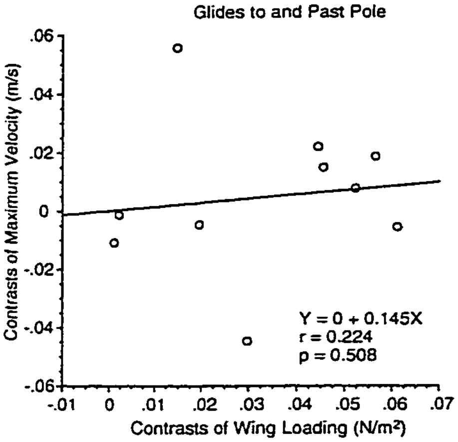






Best Score For Adults





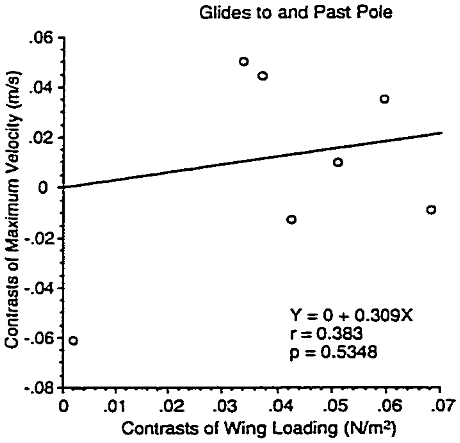
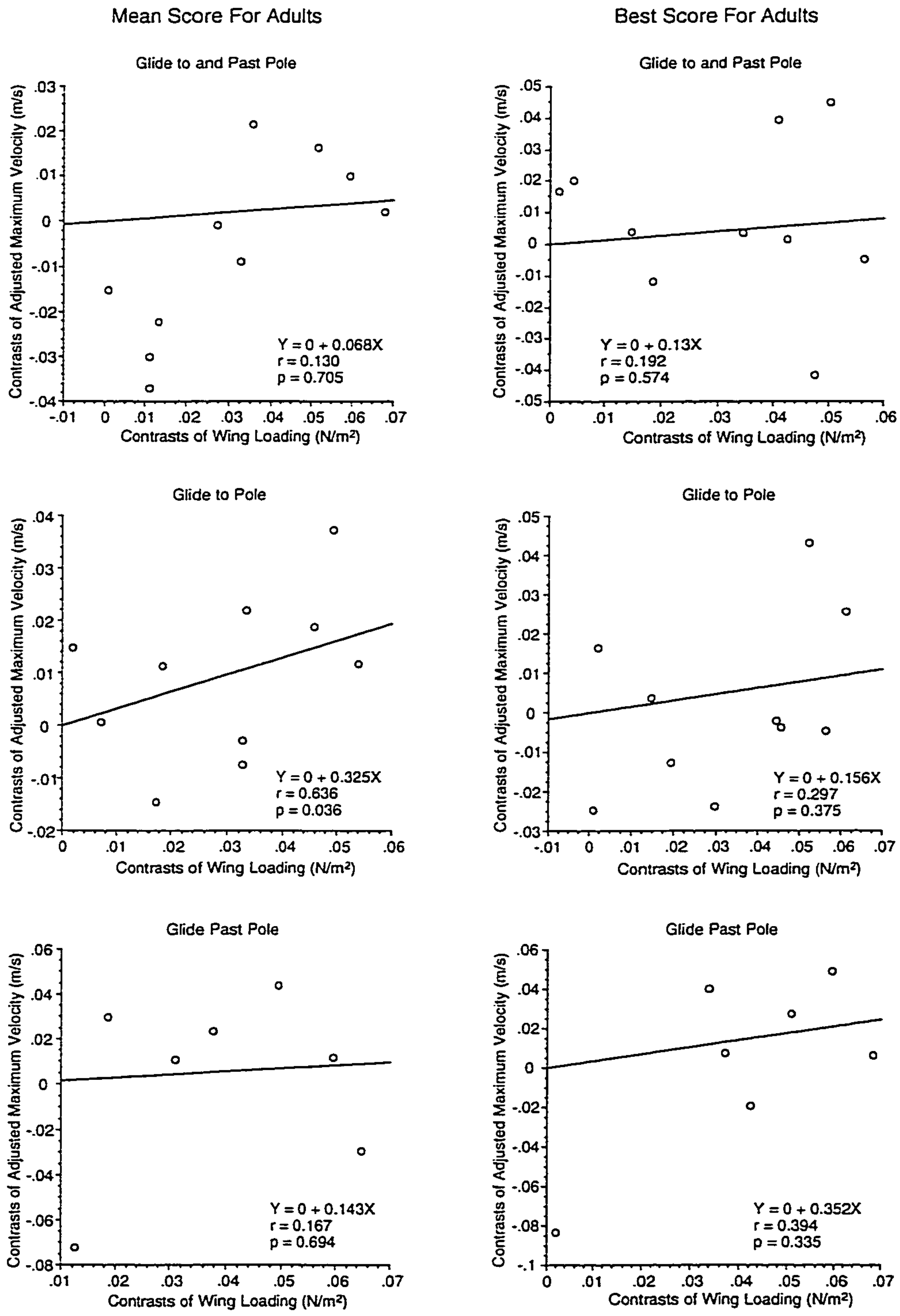


Figure 4.14. Regression plots (ordinary least squares) illustrating results when adjusted maximum velocity is regressed on wing loading. The data are independent contrasts summary values for each species.

Adjusted Maximum Velocity



Mean Score For Adults

Best Score For Adults

Figure 4.15. Regression plots (ordinary least squares) illustrating results when height lost is regressed on wing loading. The data are independent contrasts summary values for each species.

Height Lost

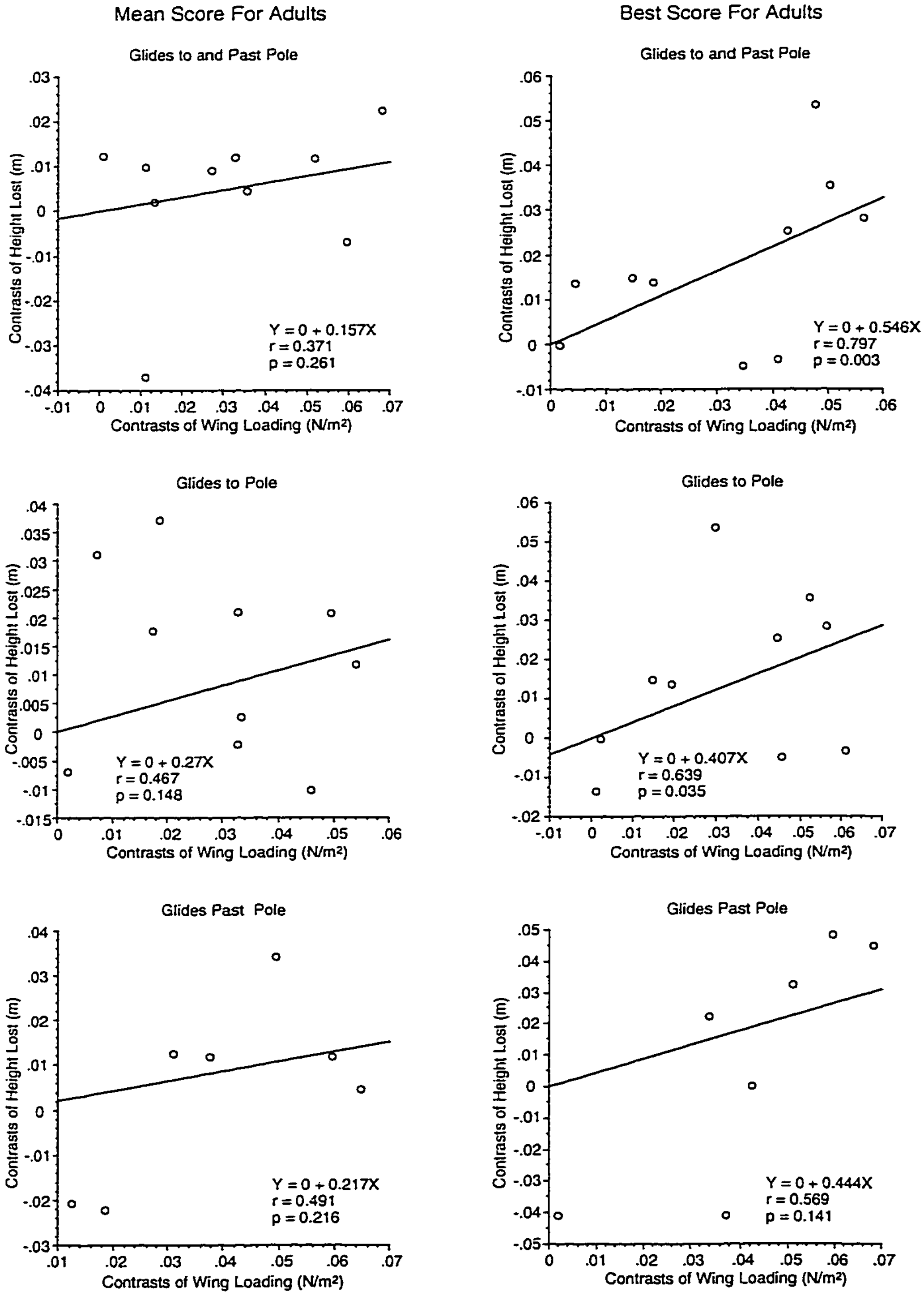

Mean Score For Adults
Best Score For Adults
Glides to and Past Pole
Contrasts of Height Lost (m)
Contrasts of Wing Loading (N/m²)
Y = 0 + 0.157X
r = 0.371
p = 0.261
.03
.02
.01
0
-.01
-.02
-.03
-.04
-.01
0
.01
.02
.03
.04
.05
.06
.07
Glides to and Past Pole
Y = 0 + 0.546X
r = 0.797
p = 0.003
.06
.05
.04
.03
.02
.01
0
-.01
0
.01
.02
.03
.04
.05
.06
Glides to Pole
Y = 0 + 0.27X
r = 0.467
p = 0.148
.04
.035
.03
.025
.02
.015
.01
.005
0
-.005
-.01
-.015
0
.01
.02
.03
.04
.05
.06
Glides to Pole
Y = 0 + 0.407X
r = 0.639
p = 0.035
.06
.05
.04
.03
.02
.01
0
-.01
-.02
-.01
0
.01
.02
.03
.04
.05
.06
.07
Glides Past Pole
Y = 0 + 0.217X
r = 0.491
p = 0.216
.04
.03
.02
.01
0
-.01
-.02
-.03
.01
.02
.03
.04
.05
.06
.07
Glides Past Pole
Y = 0 + 0.444X
r = 0.569
p = 0.141
.05
.04
.03
.02
.01
0
-.01
-.02
-.03
-.04
-.05
0
.01
.02
.03
.04
.05
.06
.07

Figure 4.16. Regression plots (ordinary least squares) illustrating results when total glide angle is regressed on wing loading. The data are independent contrasts summary values for each species.

Total Glide Angle

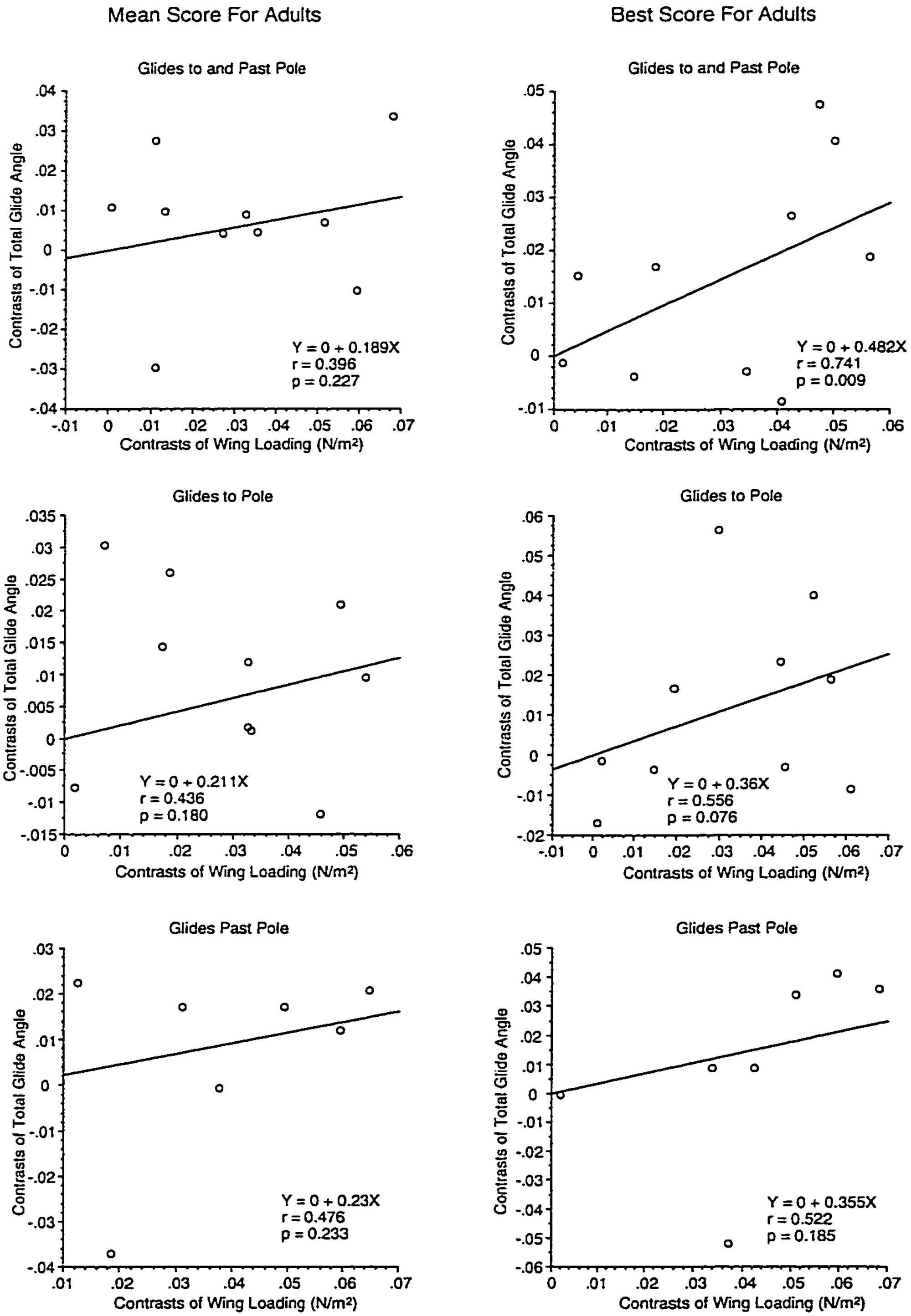
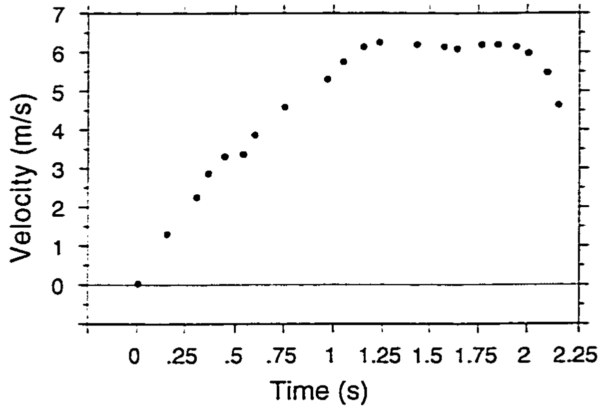
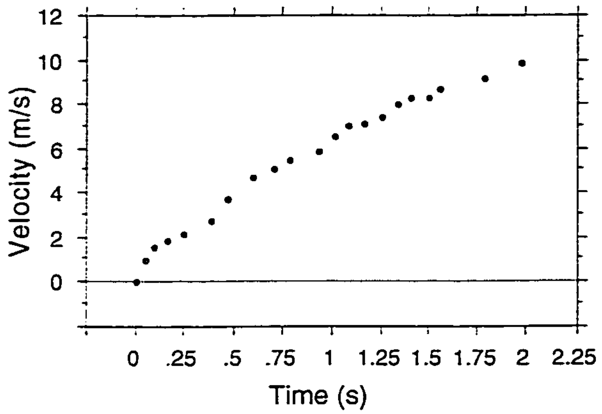


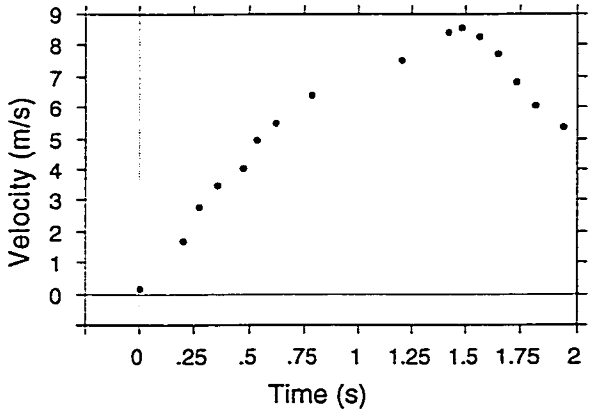
Figure 4.17. Velocity profiles illustrating the three patterns observed in this study. The velocity data were smoothed using the Lanczos 5–point moving regression (Lanczos, 1956). The equilibrium glide was obtained from a *Draco melanopogon* with wing loading of 7.37 N/m^2. The glide exhibiting steady acceleration was obtained from a *D. blanfordi* with wing loading of 14.32 N/m^2. The glide exhibiting the velocity peak was obtained from a *D. taeniopterus* with wing loading of 10.54 N/m^2.



Equilibrium Glide

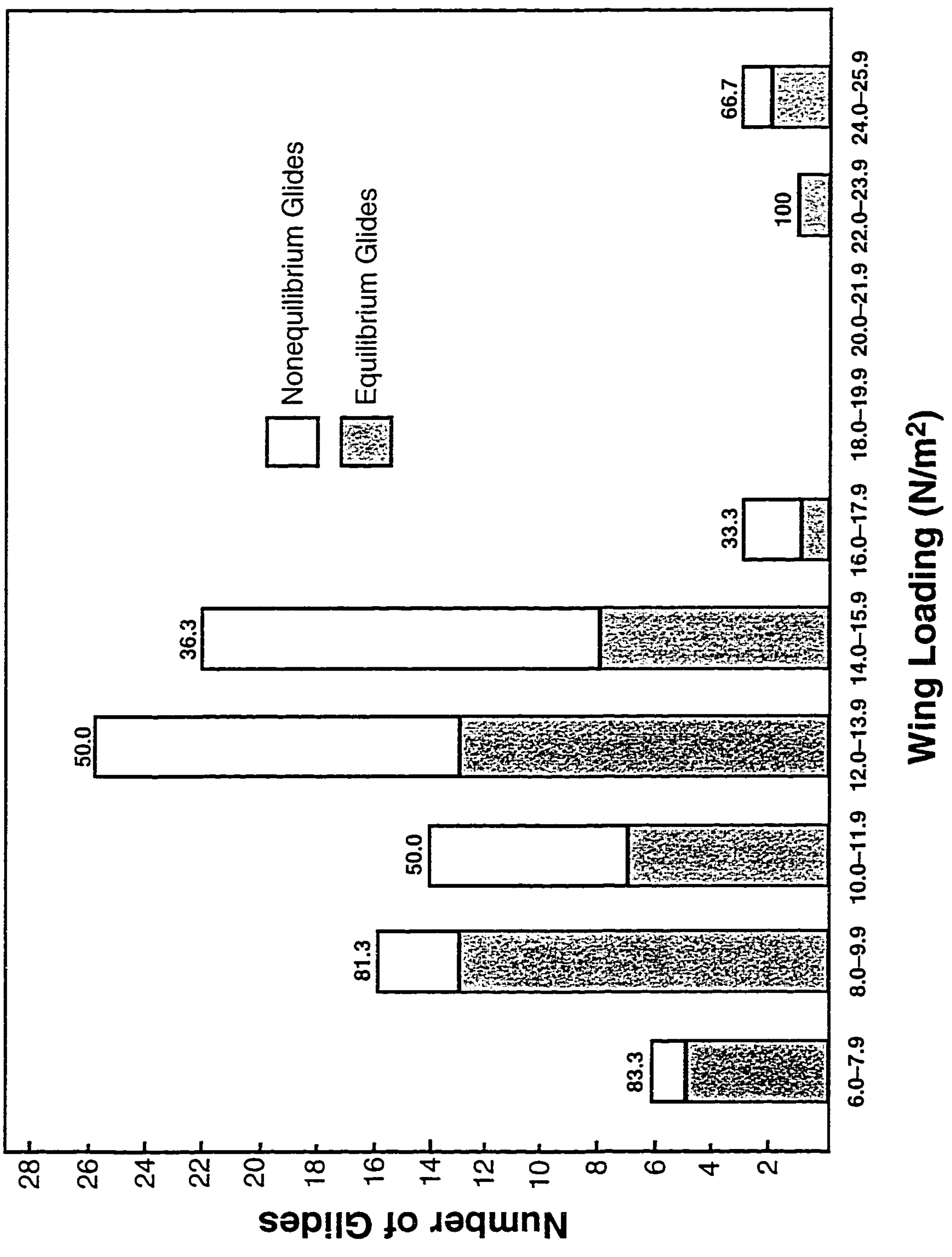


Steady Acceleration



Velocity Peak

Figure 4.18. Box plots illustrating the frequency of equilibrium glides by wing loading when the lizard performed a glide to the landing pole. The stippled portion of each column represents the number of equilibrium glides, the unstippled area represents number of nonequilibrium glides (representing either steady acceleration of a velocity peak).



Number of Glides
28
26
24
22
20
18
16
14
12
10
8
6
4
2
Wing Loading (N/m²)
6.0–7.9
8.0–9.9
10.0–11.9
12.0–13.9
14.0–15.9
16.0–17.9
18.0–19.9
20.0–21.9
22.0–23.9
24.0–25.9
83.3
81.3
50.0
50.0
36.3
33.3
100
66.7
Nonequilibrium Glides
Equilibrium Glides

APPENDIX 1

Specimens Examined

Holotypes are designated by "**H**" and paratypes by "**P**". CMNH refers to the Cincinnati Museum of Natural History herpetology collection. JAM refers to Jimmy A. McGuire field numbers. RSK refers to Robert S. Kennedy field numbers.

Draco bimaculatus—Philippines: Basilan Island (CAS 60193–94); Leyte Island (CAS 85649–50); Samar Island (TNHC 55082–84, 55086–90, 55092–95). *D. cyanopterus*—Philippines: Camiguin Sur Island (CAS 28200, 28349); Mindanao Island (BMNH 77.10.9.13, 77.12.13.16 [syntypes of *D. everetti*]; JAM 1287; CAS 15554–55; TNHC 56838–46; USNM 38394). *Draco guentheri*—"Philippines" (BMNH 79.4.16.4 **H**); Philippines: Basilan Island (CAS 60370–72); Jolo Island (CAS 18410–11, 60889–95); Mindanao Island (JAM 1268; CAS 10372, 10972–83; CMNH 5660, 5667, 5671–72; TNHC 56837); Siminor Island (CM 1856–57, 1859–65). *D. jareckii*—Philippines: Batan Island (CMNH 3782–84, 5657; MCZ 44141; PNM 5776–77; RSK 2027, 2063, 2108; USNM 266501, 266513). *D. mindanensis*—Philippines: Leyte Island (CAS 24600, 24639); Mindanao Island (JAM 1269; CAS 23561–62, 61974, 133566, 133684; CMNH 5673–75; FMNH 63157; LSU 41679; PNM 5777–78). *D. ornatus*—Philippines: Bohol Island (TNHC 58505–12, JAM 1561; USNM 228979, 228996); Leyte Island (CAS 24626, 24628); Mindanao Island (CAS 133151, 133254; CM 1919–20; CMNH 5676–77; PNM 5779); Samar Island (FMNH 96498–507; TNHC 55070–81;

USNM Field 222740–41). *D. palawanensis*—Philippines: Palawan Island (CAS 28612 **P**, 28614–16 **P**, 28649 **P**, 157297–98 **P**, 157328 **P**, 157350 **P**; CMNH 5636–42 **P**; PNM 5770 **H**, 5769 **P**, 5771–75 **P**; TNHC 56707–25 **P**; USNM 15262-63). *D. quadrasi*—Philippines: Mindoro Island (TNHC 55064–69); Romblon Island (USNM 38638); Semirara Island (CAS 127851–52); Sibuyan Island (CAS 62480–81, 73853–57, 139176–78; CM 2238–40, 2242–43, 236070; MCZ 20096). *D. reticulatus*—"Philippines" (BMNH 1946.8.27.28, type of *D. reticulatus*); Philippines: Bohol Island (FMNH 202747; TNHC 56700–07, 56862–69; USNM 228993); Lapinin Chico Island (CAS 27521); Leyte Island (CAS 60922–25, 85640; MCZ 26169); Samar Island (TNHC 55055–58, 55060–63). *D. spilopterus*—"Borneo?"—(BMNH 1947.8.27.25 **H**, holotype of *D.* rostratus, true locality unknown); Philippines: Bantayan Island (CAS 124483–84); Boracay Island (CAS 127886, 127916, 127961, 128031); Carabao Island (CAS 128151, 128162, 128169); Catanduanes Island (FMNH 247989; USNM 318703, 318706, 318721); Cebu Island (FMNH 96282–86, 96566–69; TNHC 58496–504, 59491–94); Guimaras Island (CAS 125277, 125280–81, 125295); Inampulugan Island (CAS 27966, 28027); Kalotkot Island (CAS 60554–55); Lubang Island (CM 1833–38, 1841–45, 1847–50); Luzon Island (CAS 61108; CM 1846, 1851–55; CMNH field number H304; CMNH 4387–89; TNHC 55005–13, 55097–06; USNM 56677, 180200, 291420, 306006); Marinduque Island (CM 65111–18, 65120); Masbate Island (CAS 144231, 144244); Mindoro Island (CAS 20339); Negros Island (AMNH 86604–07; CAS 17962–63, 17967–71, 92865, 92868, 92873; ROM 17455–71; TNHC 58540–51, 58553–55, 58557–58; USNM 305937); Panay Island (TNHC 58471–80, 58482–89; JAM 1506; USNM 38991–92); Polillo Island

(TNHC 55014–22, 55098, 55107–11); Siquijor Island (CAS 26333–36; TNHC 58513–15, 58516–38); Tablas Island (CAS 139188, 185499).

APPENDIX 2

ALIGNED DNA SEQUENCE

Base positions 1–12 represent tRNA methionine; positions 13–1040 represent the ND2 protein coding gene; positions 1041–1119 represent the tRNA tryptophan; positions 1120–1122 represent a nontranscribed spacer; positions 1123–1165 represent tRNA alanine. Positions 522–544 represent the internal primer sequence and were excluded from consideration in the phylogenetic analyses. Positions 1056–1067, 1101–1106, and 1120–1122 could not be aligned unambiguously and also were excluded from the phylogenetic analyses.

	10 20 30 40 50
Aphaniotis fuscus	ACCTCCTGATAATTCAAGTCCTAGTCACAGCCCTCACTTTCATAATAATC
Bronchocoela cristatella	ACCTCCTGATAATACGAACCACCGCCACAATCTACATACTAACAGGAATT
Japalura splendida	ACCCCCTGACAATACAAACCACAGCCACAACCGCAATCTTCATAGGGCTT
Japalura tricarinata	ACCCTCTAGTAATACCTTCCCTGACTACCGCTGTGTTATTCCTAGGCGTC
maximus	ACCTTCTAGAAATACCAATCACCGTTATTTTAATACTATCCCTAAGCATC
quinquefasciatus	ACCTTCTAGTAATACCAACCCCTGCTATCTTAATATTATCCCTAAGTATC
spilopterus (Luzon, SE Bicol Pen.)	ACCCTCTAGTAATACCAACAATTGCAACCCTAATCCTCTACCTTAGCATT
spilopterus (Luzon, C Bicol Pen.)	ACCCTCTAGTAATACCAACAATTGCAACCCTAATCCTCTACCTTAGCATC
spilopterus (Luzon, E coast)	ACCCTTTAGTAATACCAACAACTGCAACCCTACTTCTATATCTTAGTATC
spilopterus (Polillo)	ACCCTTTAGTAATATCAACAGCTACAACCCTAATTCTGTATCTTAGCATC
spilopterus (Negros)	ACCCTCTAGTAATACCAACAATTGCAACCTCAACCCTTTATCTTAGTATC
spilopterus (Panay)	ACCCTCTAGTAATACCAACAATTGCAACCTCAACCCTTTATCTTAGTATC
spilopterus (Cebu)	ACCCTCTAGTAATACCAACAATTGCAACCTCAATCCTTTACCTTAGCATC
spilopterus (Siquijor)	ACCCTCTAGTAATACCAACAATTGCAACCTCAATCCTCTATCTTAGCATC
bimaculatus	ACCTTCTAGTAATGCCAACAACCGCCACCCTGATACTATACCTCAGTATT
blanfordi	ACCTTCTAGTTATACCAACCCCTGCTATCTTGATATTATCTATTAGCGTT
indochinensis	ACCCTCTAGTTATGCCAGCTACCGCCACCCTAATACTTACCCTAAGCATT
cornutus	ACCTTCTAGTAATACCAACAACCGCAACCTTAATCCTTTACCTTAGCATT
cyanopterus (Mindanao)	ACCTTCTGGTTATACCGACAGTCGCAACCTTGATCCTTTTCCTTGGCATT
reticulatus (Samar)	ACCTTCTGGTTATACCGACAGCTGCAACCTTGATCCTTTTCCTTGGCATT
reticulatus (Bohol)	ACCCTCTGGTTATACCGACAGCTGCAACCCTGATCCTTTTCCTTGGCATT
maculatus	ACCTTCTAGCAATACCAACCCCTGCTATTCTAATATTATTCACAAGCGTC
mindanensis	GGCCTCTAGAAATACCAACCGCCGCTACATTAATACTATCTCTAAGCATC
obscurus	ACCTTCTAGTTATACCGGCCTCCGCCACCCTAATATTATCCGTAAGCATT
taeniopterus	ACCTTCTAGTTATACCAGCCACTGCCACCCTAATACTATCTATGAGCATT
ornatus (Samar)	ACCTTCTAGTAATACCAACAATTGCAACCTTAGTCCTTTACCTTAGCATC
ornatus (Bohol)	ACCCTCTAGTAATACCAACAATTGCAACCTTAACCCTCTACCTTAGCATC
fimbriatus (Borneo)	ACCTTCTAGCAATACCAACCCCGGCTATTTTTATGTTATCCCTGAGCATC
cristatellus (Borneo)	ACCCTCTAGCAATACCAACCCCTGCTATCTTCATACTACTAATAAGCATC
fimbriatus (Malay Pen.)	AGCCTCTAGCAATACCAACCCCCGCTATACTTGTACTACTCCTGAGCATC
fimbriatus (Java)	ACCCTCTAGCAATACCGACCCCCGCTATATTTGTACTACTCCTGAGCATC
melanopogon	GCCTTCTAGTAATACCAACCACTGCCACCTTAATATTACTACTAAGCATC
haematopogon	GACCTCTAGTAATACCAGTCCCCGCCACCTTAATACTTTTCCTGAGCATC
guentheri	ACCTTCTAGTAATACCAACAATCGCAACCTTAATTCTTTACCTTAGCATC
quadrasi (Mindoro)	ACCCTCTAGTAATACCAACAATTGCAACCTCAATCCTCTATCTTAGCATC
palawanensis	ACCTTCTGATAATGCCAACAATTGCAACTTTTATTCTTTACATTAGTATT
formosus	GCCTTCTAGCTATACCAGCCCCCGCCACCCTAATACTATCCATAAGCATT
sumatranus (Borneo)	ACCCTTTAGTAATACCAACAACTGCAACCCTAATATTTTACCTAAGCATT
sumatranus (Malay Pen.)	ACCCTTTAGTAATACCAACAACTGCAACCCTAATACTTTACCTAAGCATT
sumatranus (Sumatra)	ACCCTTTAGTAATACCAACAACTGCAACCCTAATACTTTACCTAAGCATT
volans (Java)	AACCTCTAGTAATACCAACACCTGCAACCCTAATACTCTACCTAAGCATT
quadrasi (Sibuyan)	ACCTTCTAGTAATACCAACAATTGCAACCTCAATTCTCTACCTTAGCATC
boschmai (Flores)	ACCCTCTAGTAATACCAACAACTGCAACCCTTATACTCTATCTAAGCATT

boschmai (Sumba)	ACCCTCTAGTAATACCAACAGCTGCAACCCTTATACTCTATCTAAGCATT
boschmai (Lembata 1)	ACCCTCTAGTAATACCAACAACTGCAACCCTAATACTCTACCTAAGCATT
boschmai (Lembata 2)	ACCCTCTAGTGATACCAACAACTGCAACCCTAATACTCTACCTAAGCATT
boschmai (Sumbawa)	ACCCTCTAGTAATACCAACAACTACAACCCTAATACTCTACCTAAGCATC
timoriensis (Roti)	ACCCTCTAGTAATACCAACAGCTGCAACCCTTATACTCTACCTAAGCATT
timoriensis (Timor)	ACCCTCTAGTAATACCAACAGCTGCAACCCTTATACTCTTCCTAAGCATT
beccarii	AGCCTCTGGTAATACCAATAGCTGCTACCACAATCCTATCTCTAAGTATT
biaro	AACCTCTAGTAATACCAACAGCTGCTACCATAATTTTATCCCTAAGCATT
"Tahulandang"	AACCTCTAGTAATACCAACAGCTGCTACCATAATCTTATCCCTAAGCATT
bourouniensis	AACCTCTAGTAATACCAGCCACCGCTACCACAATCCTATACCTAAGCATT
caerhulians	AACCCCTAGTAATACCAACAGCTGCTACCATAATTTTAGTCCTAAGCATT
spilonotus	AACCCCTAGTAATACCAACAGCTGCTACCACAATTTTATTCCTAAGCATT

	60 . 70 . 80 . 90 . 100 .
Aphaniotis fuscus	TTCATTGGAACACTCATTGTTTCCTCTAGTAACAGCCTACTAATAGCCTG
Bronchocoela cristatella	TCAATTGGAACAATTATAGTCACTTCAAGCAATAGCTGAATACTAGCCTG
Japalura splendida	ACCATAAGTAGTACTTTTGTTATAATAAGCAACAACTGGCTCCTGGCCTG
Japalura tricarinata	ACAACAGGCACAGCCATCGCAATATCTAGCCATCATTGACTGACCGCTTG
maximus	ATAATAGGCACAATTATTACAGTGTCCAGCCACCACTGACTGACAGCCTG
quinquefasciatus	GCAATAGGCACAATCATTACAATATCTAGCCACCACTGACTAACAGCCTG
spilopterus (Luzon, SE Bicol Pen.)	ACAATGGGCACAATCATCACAATATCAAGTCACCACTGACTGACCGCCTG
spilopterus (Luzon, C Bicol Pen.)	ACAATAGGCACAATCATCACAATATCAAGTCACCACTGACTGACCGCCTG
spilopterus (Luzon, E coast)	ACAACAGGCACAATCATCACAATATCGAGCCACCATTGACTGATGGCTTG
spilopterus (Polillo)	ATAACAGGCACAATCATCACAATATCAAGCCATCACTGACTTGCAGCTTG
spilopterus (Negros)	GCAACCGGCACAATCATTACAATATCTAGTCACCACTGACTCATGGCCTG
spilopterus (Panay)	GCAACCGGCACAATCATTACAATATCTAGTCACCACTGACTCATGGCCTG
spilopterus (Cebu)	GCAATCGGCACAATCATTACAATATCCAGTCACCATTGACTCATAGCCTG
spilopterus (Siquijor)	GCAGCCGGCACAATCATTACAATATCTAGTCACCACTGACTCATGGCCTG
bimaculatus	GCAATAGGCACAATCATTACAATATCGAGTCATCACTGATTAACAGCCTG
blanfordi	GCAATAGGCACAATTATTACAATCTCCAGCCACCACTGACTCACAGTGTG
indochinensis	ATAGCAGGCACAATTATCACTTTATCGAGCCACCACTGACTGATAGCCTG
cornutus	ATAACAGGCACAATCATCACAATATCCAGCCACCACTGACTAATGGCCTG
cyanopterus (Mindanao)	ATAATAGGCACTATCATCACAATATCTAGCCACCATTGACTAACCGCCTG
reticulatus (Samar)	ACAATAGGCACTATCATCACAATATCTAGCCATCATTGACTGACCGCCTG
reticulatus (Bohol)	ACAACAGGCACTATCATCACAATATCTAGCCATCATTGACTAACCGCCTG
maculatus	ATTCTGGGTACAATAGTCACCGTATCTAGCCACCACTGATTAACAGCCTG
mindanensis	ACAACAGGCACAATTATTACAATATCCAGCCACCACTGACTAACAGCCTG
obscurus	GCAATAGGCACAATTATTACAATTTCCAGCCACCACTGACTAACGGCCTG
taeniopterus	GCAATAGGCACAATTATTACAATTTCCAGCCACCACTGACTAACAACCTG
ornatus (Samar)	GCTACAGGCACAATCATCACCGTATCAAGTCATCACTGACTAACAGCCTG
ornatus (Bohol)	ACCATGGGCACAATCATCACCGTATCAAGTCACCATTGACTAACAGCCTG
fimbriatus (Borneo)	ACAATAGGCACAATTATTACCATCTCCAGCCACCACTGATTAACAGCCTG
cristatellus (Borneo)	ACGATAGGCACAATTATTACCATCTCCAGCCACCACTGGCTAACCGCTTG
fimbriatus (Malay Pen.)	ACAATGGGCACCATTATTACTATCTCCAGTCACCACTGACTAACAGCCTG
fimbriatus (Java)	ACAATGGGCACAATTATTACTATCTCCAGCCACCACTGACTAACAGCCTG
melanopogon	GCAATAGGCACAGTCATCACAATGTCTAGCCACCACTGGCTGACAGCCTG
haematopogon	ACAATGGGCACAATTATTACAATCTCTAGCCACCACTGACTAACAGCCTG
guentheri	ATACTGGGCACAATCATTACAATATCAAGTCACCACTGATTAATAGCCTG
quadrasi (Mindoro)	ACAATAGGCACCATCATTACAATATCAAGTCACCACTGACTTACAGCTTG
palawanensis	ACAATGGGCACAATCATCACAATATCCAGTCATCATTGACTAACAGCCTG
formosus	GCAATAGGCACAATTATTACAACCTCCAGCCACCACTGACTAACAGCCTG
sumatranus (Borneo)	ACAATAGGCACAATCATCACAATATCAAGCCATCATTGATTAACAGCCTG
sumatranus (Malay Pen.)	ACAATAGGCACAATCATCACGATGTCAAGCCATCATTGATTGACAGCCTG
sumatranus (Sumatra)	ACAATAGGCACAATCATCACGATGTCAAGCCATCATTGATTGACTGCCTG
volans (Java)	ACAATAGGCACAGTCATCACAATATCAAGCCATCACTGATTAACAGCCTG
quadrasi (Sibuyan)	ACAATAGGCACCATTATTACAATATCAAGTCACCACTGACTAACAGCCTG
boschmai (Flores)	ACAATAGGCACGACCATCACATTATCAAGCCACCATTGACTAACAGCCTG
boschmai (Sumba)	ACAATAGGCACGACCATCACATTATCAAGTCACCATTGACTAACAGCCTG
boschmai (Lembata 1)	ACAACAGGCACGACCATCACATTATCAAGCCACCACTGACTAACAGCCTG
boschmai (Lembata 2)	ACAACAGGCACGACCATCACATTATCAAGCCACCACTGACTGACAGCCTG
boschmai (Sumbawa)	ACAATAGGCACAGTCATCACATTATCAAGCCATCATTGACTCACAGCCTG
timoriensis (Roti)	ACAATAGGCACGGCAATCACACTATCAAGCCACCATTGACTAACAGCCTG
timoriensis (Timor)	ACAATAGGCACGGCCATCACATTATCAAGCCACCATTGACTAACAGCCTG
beccarii	ACAGCAGGCACAATCGTTACAATATCTAGCCACCACTGACTAACAGCCTG
biaro	GCAACCGGCACAATCATCACTATATCCAGCCACCACTGACTAACAGCCTG
"Tahulandang"	GCAACCGGCACAATCATCACTATATCCAGCCACCACTGACTAACAGCCTG
bourouniensis	GCAGCAGGAACAATCATTACAATATCTAGCCACCACTGATTAACAGCCTG
caerhulians	GCAACAGGCACAATCATCACTATATCCAGCCACCACTGACTAACAGCCTG
spilonotus	GCAACAGGCACAATCATCACTATATCCAGCCACCACTGACTAACAGCCTG

	110 120 130 140 150
Aphaniotis fuscus	ACTAGGACTAGAATTAAATACATTTGCAATCCTACCACTAATTTCAAAAA
Bronchocoela cristatella	ACTAGGACTAGAACTAAACTCATTCGCCATTTTACCACTAATCTCAAAAA
Japalura splendida	GCTCAACCTAGAAATAAACACACTGGCCATCCTACCAGTAATCTCAAAAA
Japalura tricarinata	AGTTGGATTAGAACTAAATACGCTAGCCCTACTACCAGTTATCTCAAAAA
maximus	AGCAGGCCTAGAACTAAATACACTAGCCATCCTACCAATCATTTCAAAAA
quinquefasciatus	AGCCGGATTAGAATTAAACACACTAGCCATCCTACCTATTATTTCAAAAA
spilopterus (Luzon, SE Bicol Pen.)	AATAGGCCTAGAACTAAACACATTGGCCACCCTACCAATCATTTCAAAAA
spilopterus (Luzon, C Bicol Pen.)	AATAGGACTAGAACTAAACACATTGGCCACCCTACCCATCATTTCAAAAA
spilopterus (Luzon, E coast)	AATGGGGTTAGAACTAAATGCCCTAGCCGTCCTACCAATTATCTCAAAAA
spilopterus (Polillo)	AATGGGGTTGGAGCTAAACACACTAGCCATCCTACCAATTATCTCAAAAA
spilopterus (Negros)	AATAGGGCTAGAACTAAACACCCTGGCTGTTTTACCAATCATTTCAAAAA
spilopterus (Panay)	AATAGGGCTAGAACTAAACACCCTGGCTGTTTTACCAATCATTTCAAAAA
spilopterus (Cebu)	AATGGGATTAGAACTAAACACATTAGCCATTTTACCAGTTATCTCAAAAA
spilopterus (Siquijor)	AATGGGATTAGAGCTAAATACCCTAGCTATTTTACCCATTATTTCAAAAA
bimaculatus	ATTAGGGCTAGAACTAAATATGCTAGCCATCCTTCCAATTATCTCAAAAA
blanfordi	AGCCGGATTAGAAATAAATACACTAGCCATCCTGCCCATTATCTCAAAAA
indochinensis	AGCCGGACTAGAAATAAATACGCTAGCCATTCTACCCGTTATTTCAAAAA
cornutus	AATGGGACTAGAACTAAACATATTGGCCACCCTGCCAATTATCTCAAAAA
cyanopterus (Mindanao)	AATAGGACTAGAACTAAACACGCTAGCCATGCTACCCATCATCTCAAAGA
reticulatus (Samar)	AATGGGGTTAGAACTAAACACACTAGCCATCCTACCCATCATCTCAAAGA
reticulatus (Bohol)	AATGGGGTTAGAACTAAACATACTAGCCATCCTACCCATCATCTCAAAGA
maculatus	GCTTGGGCTAGAAATTAACACGCTAGCCATTCTTCCAATTATTGCAAAAA
mindanensis	AGCCGGACTGGAATTAAATACCCTGGCTATCCTACCAATCATCTCAAAAA
obscurus	AGCCGGACTAGAATTAAATACACTTGCCATCCTGCCCTTTATTTCAAAGA
taeniopterus	AGCCGGACTAGAGTTAAATACACTGGCCATCCTACCCTTTATTTCAAAAA
ornatus (Samar)	AATAGGATTAGAATTAAACATGCTGGCCATTTTACCAGTTATTTCAAAAT
ornatus (Bohol)	AGTAGGATTAGAGTTGAACATACTGGCCATTTTGCCAGTCATCTCAAAAA
fimbriatus (Borneo)	AGCTGGATTAGAAATAAATGCACTGGCCATCCTCCCAATTATTTCGAAAA
cristatellus (Borneo)	AGCAGGGCTAGAGATAAACACACTAGCCATCCTCCCAATTATCTCAAAAA
fimbriatus (Malay Pen.)	AGCAGGTCTTGAAATAAACGCACTAGCCGTCCTTCCAATTATTTCAAAGA
fimbriatus (Java)	AGCAGGACTTGAAATAAACGCACTAGCCATCCTTCCAATTATCTCAAAGA
melanopogon	AGCCGGACTAGAATTAAATACCCTAGCCATACTACCCATTATTTCAAAAA
haematopogon	AGCTGGACTAGAACTTAACACCTTGGCCATCCTACCCGTCATCTCAAAAA
guentheri	AATAGGACTAGAACTAAACACACTAGCTGTCCTGCCAATTATCTCAAAAA
quadrasi (Mindoro)	AATAGGACTAGAATTAAACATACTAGCCATTTTACCAATTATCTCAAAAA
palawanensis	AATAGGATTAGAATTAAACATACTAGCCATTTTACCAATTATTTCAAAGA
formosus	AGCCGGACTAGAATTAAATACACTTGCCATCCTGCCCTTTATTTCAAAAA
sumatranus (Borneo)	AATAGGACTAGAAATAAACACATTAGCAATTTTACCAATTATTTCAAAGA
sumatranus (Malay Pen.)	AATAGGACTAGAAATAAACATATTAGCAATCTTACCAATTATCTCAAAGA
sumatranus (Sumatra)	AATAGGACTAGAAATAAACGCATTAGCAATTTTACCAATTATTTCAAAGA
volans (Java)	AATAGGACTTGAAATAAACACATTAGCAATTCTACCAATTATCTCAAAAA
quadrasi (Sibuyan)	AATAGGACTAGAACTAAATATGCTAGGCATTCTACCAATTATCTCAAAAA
boschmai (Flores)	AATAGGACTAGAAATAAACTCATTGGCAATCCTTCCCATCATTTCAAATA
boschmai (Sumba)	AATAGGACTAGAGATAAACTCATTGGCGATTCTTCCAATCATCTCAAATA
boschmai (Lembata 1)	AATAGGCCTAGAAATAAACTCATTGGCAATTCTTCCCATCATTTCAAATA
boschmai (Lembata 2)	AATAGGCCTAGAAATAAACTCATTGGCAATTCTTCCCATCATTTCAAATA
boschmai (Sumbawa)	AATGGGACTAGAAATAAACACATTGGCAATCCTACCAATTATCTCAAATA
timoriensis (Roti)	AATAGGACTAGAAATAAACTCATTGGCAATTCTTCCAATCATCTCAAACA
timoriensis (Timor)	AATAGGACTAGAAATAAACTCATTGGCAATTCTTCCAATCATCTCAAACA
beccarii	ATTGGGACTAGAGTTAAACACATTAGCCATCCTCCCCATTATCTCAAAAA
biaro	ACTAGGCCTAGAATTGAACACACTAGCCGTCCTCCCCATCATCTCAAAAA
"Tahulandang"	ACTAGGCCTAGAATTGAACACACTAGCCGTCCTCCCCATCATCTCAAAAA
bourouniensis	ACTGGGCCTAGAACTAAATACACTAGCCATCCTCCCCATCATCTCGAAAA
caerhulians	ACTAGGCCTAGAACTGAACACACTAGCCGTCCTCCCCATCATTTCAAAAA
spilonotus	ACTAGGCCTAGAGCTGAACACACTGGCCATCCTTCCCATCATCTCAAAAA

	160 170 180 190 200
Aphaniotis fuscus	CAAAACACCCACGATCTATTGAAGCAACAACAAAATACTTTATTACACAA
Bronchocoela cristatella	CAAAACACCCACGATCCATTGAAGCCGCAACAAAATACTTCTTAACACAA
Japalura splendida	CAAAACACCCGCGAGCAATCGAGGCCTCAACAAAATACTTTCTAACACAG
Japalura tricarinata	CTAAACACCCCCGATCAATTGAAGCCTCAACAAAATACTTCCTAACGCAA
maximus	CCAAGCACCCTCGTGCAATTGAAGCCGCAACAAAATATTTCCTAACACAA
quinquefasciatus	CCAAACACCCCCGCGCTATCGAAGCCGCAACAAAATACTTTCTAACACAG
spilopterus (Luzon, SE Bicol Pen.)	CGAAACACCCGCGAGCAAATGAAGCTGCAACAAAATATTTTTTAACACAA
spilopterus (Luzon, C Bicol Pen.)	CGAAACACCCACGAGCAAATGAAGCTGCAACAAAATATTTTCTAACACAA
spilopterus (Luzon, E coast)	CAAAACACCCACGAGCAAACGAGGCTGCTACTAAATACTTCTTAACGCAA
spilopterus (Polillo)	CAAAACACCCACGAGCAAACGAAGCTGCTACAAAGTACTTCCTAACGCAA
spilopterus (Negros)	CAAAACATCCACGAGCAAACGAAGCCGCAACAAAATATTTTCTAACACAA
spilopterus (Panay)	CAAAACATCCACGAGCAAACGAAGCCGCAACAAAATATTTTCTAACACAA
spilopterus (Cebu)	CAAAACATCCACGAGCAAACGAAGCCGCAACAAAGTATTTTCTAACACAA
spilopterus (Siquijor)	CAAAACATCCACGAGCAAGCGAAGCCGCAACAAAGTATTTTCTAACACAA
bimaculatus	CTAAACACCCGCGAGCAACAGAGGCCGCCACAAAGTACTTTCTAGCACAA
blanfordi	CCAAGCACCCCCGCGCAATTGAAGCCGCAACAAAATACTTCTTAACACAA
indochinensis	CCAAACACCCCCGTGCAATCGAAGCGACAACAAAATACTTCCTCACACAA
cornutus	CTAAACACCCACGAGCAAATGAAGCCGCAACAAAGTACTTTTTAACACAG
cyanopterus (Mindanao)	CAAAACACCCACGAGCAAATGAAGCCGCAACAAAATACTTCTTGACACAG
reticulatus (Samar)	CAAAACACCCACGAGCAAATGAAGCCGCAACAAAGTACTTCTTGACACAA
reticulatus (Bohol)	CAAAACACCCACGAGCAAATGAAGCCGCAACAAAGTACTTCTTGACACAA
maculatus	CAAAACACCCCCGTGCAATTGAAGCCGCTACAAAATATTTCCTAACACAA
mindanensis	CCAAACACCCTCGTGCAATTGAAGCTGCAACAAAATACTTCCTAACACAA
obscurus	CCAAGCACCCACGCGCAATTGAAGCGGCTACAAAATACTTCCTAACACAA
taeniopterus	CCAAACATCCACGCGCGATTGAAGCAGCTACAAAATACTTCCTAACACAA
ornatus (Samar)	CAAAACACCCACGAGCAAGTGAAGCCGCAACAAAATATTTTTTAACACAA
ornatus (Bohol)	CAAAACACCCACGAGCAAATGAAGCCGCAACAAAATATTTTCTTACACAA
fimbriatus (Borneo)	CAAAACACCCACGCGCAATTGAAGCCGCTACAAAGTACTTCCTAACACAA
cristatellus (Borneo)	CAAAACATCCACGTGCAACTGAAGCCGCTACAAAGTACTTTCTAACACAA
fimbriatus (Malay Pen.)	CAAAACACCCACGTGCAACTGAAGCCGCCACAAAATACTTCTTAACACAG
fimbriatus (Java)	CAAATCACCCACGTGCAACTGAGGCTGCTACAAAATACTTCTTGACACAA
melanopogon	CCAAACATCCCCGTGCAATTGAAGCTGCAACAAAATATTTCCTAACACAG
haematopogon	CCAAGCACCCACGTGCAATTGAAGCTGCAACAAAATACTTCCTAACACAA
guentheri	CAAAACATCCCCGGGCAAACGAAGCGGCAACAAAATACTTCCTAACACAA
quadrasi (Mindoro)	CAAAACACCCACGAGCAAACGAAGCCGCAACAAAATATTTCCTAACACAA
palawanensis	CTAAACACCCACGAGCAAATGAAGCCTCAACAAAATATTTCCTAACACAA
formosus	CCAAGCACCCGCGCGCAATTGAAGCAGCTACAAAATACTTTCTAACACAA
sumatranus (Borneo)	CTAAACACCCACGAGCAAATGAAGCCGCAACAAAATACTTCCTAACACAA
sumatranus (Malay Pen.)	CTAAGCACCCACGAGCAAACGAAGCCGCAACAAAATACTTCCTAACACAA
sumatranus (Sumatra)	CTAAGCACCCACGAGCAAATGAAGCCGCAACAAAATACTTCCTAACACAA
volans (Java)	CTAAGCACCCACGAGCAAATGAAGCCGCAACAAAATACTTCCTTACACAA
quadrasi (Sibuyan)	CAAAACATCCACGAGCAAACGAAGCCGCAACAAAATACTTTTTAACACAG
boschmai (Flores)	CTAAACACCCACGAGCAAATGAGGCCGCAACAAAATATTTTCTAACACAA
boschmai (Sumba)	CTAAGCACCCACGGGCAAATGAAGCCGCAACAAAATATTTTCTAACACAA
boschmai (Lembata 1)	CTAAACATCCACGGGCAAATGAAGCCGCAACAAAATATTTTCTGACCCAG
boschmai (Lembata 2)	CTAAACATCCACGGGCAAATGAAGCCGCAACAAAATATTTTCTGACCCAG
boschmai (Sumbawa)	CTAAACACCCACGAGCAAATGAAGCCGCAACAAAATATTTTCTAACACAA
timoriensis (Roti)	CTAAACACCCACGGGCAAATGAAGCCGCAACAAAATATTTTCTAACACAA
timoriensis (Timor)	CTAAACACCCACGGGCAAATGAAGCCGCAACAAAATATTTTCTAACACAA
beccarii	CAAAACACCCCCGAGCAATTGAAGCCGCAACAAAATACTTCCTAGCACAA
biaro	CCAAACACCCACGAGCAATTGAAGCCGCAACAAAATACTTCCTAGCACAA
"Tahulandang"	CCAAACACCCACGAGCAATTGAAGCCGCAACAAAATACTTCCTAGCACAA
bourouniensis	CAAAACACCCCCGAGCAACTGAGGCAGCAACAAAATATTTCCTTACACAG
caerhulians	CCAAGCACCCACGGGCAATTGAAGCCGCAACAAAATACTTCCTAGCACAG
spilonotus	CAAAGCACCCACGAGCAATTGAAGCCGCAACAAAATACTTCCTAGCACAG

	210 220 230 240 250
Aphaniotis fuscus	GCCACTGCTTCCTGCCTTCTACTATTTTCAGGAACTGTCAATGCCTGACA
Bronchocoela cristatella	TCCACCGCCTCCTGCCTAATCCTATTTGCAAGCACTATCAATGCCTGACA
Japalura splendida	ACTATTGCCTCCTGCCTATTACTATTTTCCTGCACCACTAATGCCTGATA
Japalura tricarinata	GCCATCGCCTCCTGCCTCATATTATCTTCCAGCATTGCCAGCGCCTGACA
maximus	GCTGTAGCCTCCTGCCTGCTCCTATCCTCAAGCATAGTAAATGCCTGACA
quinquefasciatus	GCCGTGGCCTCCTGCCTACTCCTAGCGTCCAGCATAGTAAACGCCTGACA
spilopterus (Luzon, SE Bicol Pen.)	GCCGTGGCCTCCTGTCTATTATTACTCTCAGGAATTATTAACGCCTGACA
spilopterus (Luzon, C Bicol Pen.)	GCCGTGGCCTCCTGTCTATTACTACTCTCAGGGATTATTAACGCCTGACA
spilopterus (Luzon, E coast)	GCCATCGCCTCCTGCCTACTACTATTCTCAAGCATTATTAATGCCTGACA
spilopterus (Polillo)	GCCATTGCCTCCTGCCTACTATTACTCTCAAGTATTATTAACGCCTGACA
spilopterus (Negros)	GCCGTAGCCTCCTGCCTATTATTGCTCTCGAGCATTATTAACGCTTGACA
spilopterus (Panay)	GCCGTACCCTCCTGCCTGTTGCTGCTCTCGAGCATTATTAACGCCTGACA
spilopterus (Cebu)	GCCGTAGCATCCTGCCTACTACTCCTCTCAAGCATTACTAACGCCTGACA
spilopterus (Siquijor)	GCCGTAGCATCCTGCCTACTATTGCTCTCGAGCATTATTAACGCCTGACA
bimaculatus	ACTGTAGCCTCCTGTCTACTACTGCCCGCAAGCATAATTAATGTCTGACA
blanfordi	GCTATTGCCTCCTGCCTACTTCTAGCATCAAGCACAATTAACGCCTGACA
indochinensis	GCTGTAGCCTCCTGCCTACTCCTGGCATCAAGCATAATAAACGCCTGACA
cornutus	GCCGTAGCCTCCTGCCTACTACTGCTCTCAAGCATAATTAACGCCTGACA
cyanopterus (Mindanao)	GCTGTAGCCTCCTGTCTACTTCTGTTCTCAAGTATCATTAATGCCTGACA
reticulatus (Samar)	GCTGTAGCCTCTTGCCTACTTCTGTTCTCAAGTATCATCAATGCCTGACA
reticulatus (Bohol)	GCTGTAGCCTCCTGCCTACTTCTGTTCTCAAGTATCATCAATGCTTGACA
maculatus	GCTGTAGCCTCTTGTCTTCTCCTATCATCGAGCATAATAAACGCCTGACG
mindanensis	GCTGTAGCCTCATGCCTTCTCCTATCATCAAGCATAGTAAACGCCTGACA
obscurus	GCCGTAGCCTCATGTCTTCTTCTAGCATCAAGCATGATAAACGCCTGGCA
taeniopterus	GCCGTGGCCTCATGCCTTCTTCTAGCATCAAGCATAGTAAACGCCTGACA
ornatus (Samar)	GCCGCAGCCTCCTGCTTATTACTACTCTCAAGCATTATTAACGCCTGACA
ornatus (Bohol)	GCTGTAGCCTCCTGTTTACTACTACTTTCAAGCATTATTAATGCCTGACA
fimbriatus (Borneo)	GCAGTAGCCTCTTGCTTACTTCTATCGTCGAGCATGATAAACGCCTGACA
cristatellus (Borneo)	GCAGTAGCTTCTTGCCTACTACTATCATCAAGCATAATAAACGCCTGACA
fimbriatus (Malay Pen.)	GCAGTAGCCTCTTGCTTACTTCTATCCTCGAGCATGATAAACGCCTGACA
fimbriatus (Java)	GCAGTAGCCTCTTGCTTACTTCTATCCTCAAGCATAATAAACGCCTGACA
melanopogon	GCCGTAGCCTCCTGCCTGCTACTAGCATCAAGCATAGTAAACGCCTGACA
haematopogon	GCTGTGGCCTCCTGCCTACTTCTGGCTTCAAGCATAATAAACGCCTGACA
guentheri	GCCGTAGCGTCCTGCCTATTACTACTCTCATGCATCATTAATGCTTGACA
quadrasi (Mindoro)	GCCGTAGCCTCCTGTCTACTACTACTTTCAAGCATTATTAACGTCTGACA
palawanensis	GCCGTGGCCTCCTGCCTACTATTACTATCAAGTATAATAAACGCTTGACA
formosus	GCCATAGCCTCATGCCTTCTTCTAGCATCAAGCATAGTAAACGCCTGACA
sumatranus (Borneo)	GCCGTCGCCTCCTGCCTACTCCTATTCTCGAGCATAATTAACGCCTGACA
sumatranus (Malay Pen.)	GCCGTCGCCTCCTGCCTACTCCTATTCTCAAGCATAATTAACGCCTGACA
sumatranus (Sumatra)	GCCGTCGCCTCCTGCCTACTCCTATTCTCAAGCATAATTAACGCCTGACA
volans (Java)	GCCGTAGCCTCTTGTCTACTCCTATTCTCAAGCATAATTAACGCCTGACA
quadrasi (Sibuyan)	GCCGTAGCCTCCTGCTTATTACTACTTTCAAGCATCATTAACGTCTGACA
boschmai (Flores)	GCCGTAGCCTCCTGTCTGCTCCTCTTTTCAAGCATAATTAACGCTTGACA
boschmai (Sumba)	GCCGTAGCTTCCTGCCTGCTCCTATTTTCAAGCATAATTAACGCTTGACA
boschmai (Lembata 1)	GCCGTAGCCTCCTGCCTACTCCTATTTTCAAGCATAATTAACGCTTGACA
boschmai (Lembata 2)	GCCGTAGCCTCCTGCCTACTCCTATTTTCAAGCATAATTAACGCTTGACA
boschmai (Sumbawa)	GCCGTAGCCTCCTGCCTTTTCCTGTTTTCAAGCATAATTAACGCTTGACA
timoriensis (Roti)	GCCGTAGCCTCCTGCCTGCTCCTATTTTCAAGCATAATCAACGCTTGACA
timoriensis (Timor)	GCCGTAGCCTCCTGCCTGCTCCTATTTTCAAGCATAATTAACGCTTGACA
beccarii	GCCGTAGCATCTTGCCTACTAATATTCTCAAGCATCATCAATGCTTGACA
biaro	GCCGTAGCATCTTGCCTACTACTTTCCTCAGCCATTATTAACGCTTGACA
"Tahulandang"	GCCGTAGCATCTTGCCTACTACTTTCCTCAGCCATTATTAACGCTTGGCA
bourouniensis	GCCGTAGCATCCTGCCTACTACTAGCCTCAGGCATTATCAACGCTTGACA
caerhulians	GCCGTAGCATCTTGCCTACTACTCTCCTCAGCCATTATTAACGCTTGACA
spilonotus	GCCGTAGCATCTTGCCTACTACTCTCCTCAGCCATTATTAACGCTTGACA

	260 270 280 290 300
Aphaniotis fuscus	AACAGGAACATGAAATATTTCACAACCATATAACGAACTATCGTCCATAC
Bronchocoela cristatella	AACCGGAGCATGAACAATTACACAAATGCCTGACAAACTTCCATCCACAC
Japalura splendida	CACAGGCACTTGAAGTATTACCCAAATAGACGACACATACACATCAACCC
Japalura tricarinata	AACTGGAAGCTGAGACATTACACAAATAACTAACAAATACTCATCCACAG
maximus	GACAGGAAGCTGAGACATCCTACAAATAACCAACAAACTAGCATCTACAA
quinquefasciatus	AACAGGAACCTGAGACATTCTACAAATAACCGACAAACTCGCATCCACAA
spilopterus (Luzon, SE Bicol Pen.)	AACAGGAACCTGAGACATCTTACAACTGACCAACAAACATGCGTCAACAA
spilopterus (Luzon, C Bicol Pen.)	AACAGGAACCTGAGATATCTTACAACTAACAAACAAACATGCATCAACAA
spilopterus (Luzon, E coast)	AACAGGAAGTTGAGACATCCTACAAATAACAAATAAGTACTCATCTATGA
spilopterus (Polillo)	AACAGGAACTTGAGACATTCTACAAATAACAAATAAGTACGCATCAATGA
spilopterus (Negros)	GACAGGAAGCTGAGACATCCTACAAATAACCAACAAATATGCATCCACAA
spilopterus (Panay)	GACAGGAAGCTGAGACATCCTACAAATAACCAACAAATATGCATCCACAA
spilopterus (Cebu)	AACAGGAAGCTGAGACATCCTACAAATAACCAACAAATATGCATCCACAA
spilopterus (Siquijor)	TACAGGAAGCTGAGACATCCTACAAATAAACGACAAATATGCTTCCTCAA
bimaculatus	AACAGGAACCTGAGACATCATACAAATAACCAACAAATACGCATCCACAA
blanfordi	AACAGGAAGCTGAGACATCCTACAAATGACCAATAAACTCACATCCACAA
indochinensis	AACAGGAACCTGAGACATCCTTCAAATAACCAACAAACTCGCATCCACAA
cornutus	AACAGGAAGCTGAGACATCTTACAAATAACCAACAAATACGCATCCATAA
cyanopterus (Mindanao)	AACAGGAAGCTGAGACATCCTACAAATAACCAACAAATACGCATCCGCAA
reticulatus (Samar)	AACAGGAAGCTGAAACATCCTACAGATAACCAACAAATACGCATCCACAA
reticulatus (Bohol)	AACAGGAAGCTGAGACATCCTACAATTAACCAACAAGTACGCATCCACAA
maculatus	AACAGGAAGCTGAGACATCTTACAAATAACCGATAAACTAACCACCACAA
mindanensis	AACAGGAAGCTGAGACATCCTACAAATAACTAACAAACTAGCATCAACAA
obscurus	GACAGGAAACTGAGACATCCTACAAATGACTAATAAACTCGCATCCACAA
taeniopterus	GACAGGAAGCTGAGACATCCTACAAATGACCAATAAACTTGCATCCACAA
ornatus (Samar)	AACAGGAAGCTGAGACATCCTTCAAATAACCGACAAATATGCATCCACAA
ornatus (Bohol)	AACAGGAAGCTGAGACATCCTACAAATAACCAACAAATACGCATCCACAA
fimbriatus (Borneo)	AACAGGGAGTTGAGACATCCTACAAATAACCAACCCCATAACATCTGCAA
cristatellus (Borneo)	AACAGGAAATTGAAGCATCCTACAAATAACCGACCCCCTAGCCTCCACAA
fimbriatus (Malay Pen.)	AACAGGAAGCTGAGACATCCTACAAATAACCAACCCGCTAACATCTACAA
fimbriatus (Java)	AACGGGAAGCTGAAACATCCTACAAATAACCAACCACCTAGCATCTACAA
melanopogon	AACGGGAAGCTGAGACATCCTACAAATGACTAACAAACTTACATCCACAA
haematopogon	GACGGGAAGCTGAGATATTCTACAAATAACCAACAAACTTGCATCTGTAA
guentheri	AACAGGAAGTTGAGACATCTTGCAAATAACCAACAAATACGCATCTGCAA
quadrasi (Mindoro)	AACAGGAAGCTGGGACATCCTACAAATAACCAACAAATACGCAATCACAA
palawanensis	GACAGGAAGTTGAGACATTCTACAAATAACCAATAAATATGCATCTACAA
formosus	GACAGGAAACTGAGACATCCTACAAATAACTAATAAACTCGCGTCCACAA
sumatranus (Borneo)	AACCGGAACCTGAGATATTCTACAAATAACCAACAAACACGCATCCACTA
sumatranus (Malay Pen.)	AACCGGAACCTGAGATATCCTACAAATAACCAACAAACATGCATCCACTA
sumatranus (Sumatra)	AACCGGAACCTGAGACATCCTGCAAATAACCAACAAACATGCATCCACTA
volans (Java)	GACAGGAACCTGAGACATCCTACAAATAACCGACAAATATGCAGCCACTA
quadrasi (Sibuyan)	AACAGGAAGCTGGGACATCCTACAAATAACCAATAAATACGCAAGCACAA
boschmai (Flores)	AACAGGAACCTGAGATATCCTGCAAATAACCGACAAATGGGCATCCGCCA
boschmai (Sumba)	AACAGGAACCTGAGATATCCTACAAATAACCGATAAATATGCATCCACCA
boschmai (Lembata 1)	AACAGGAACCTGAGACATTCTACAAATAACCGACAAATATGCATCCACCA
boschmai (Lembata 2)	AACAGGAACCTGAGATATTCTACAAATAACCGACAAATATGCATCCACCA
boschmai (Sumbawa)	AACAGGAACCTGAGACATCCTACAAATAACCGATAAATATGCATCCACTA
timoriensis (Roti)	AACAGGAACCTGAGACATCCTACAAATAACCGACAAATGTGCATCCACCA
timoriensis (Timor)	AACAGGAACCTGAGATATCCTACAAATAACCGACAAATGTGCATCCACCA
beccarii	AACAGGAACCTGAGATATCCTACAAATAACTAACAAATATGCAGCCACAA
biaro	AACAGGAAGCTGGGACATCCTACAAATAACTAACAAATATACATCTACAA
"Tahulandang"	AACAGGAAGCTGGGACATCCTACAAATAACTAACAAATATACATCTACAA
bourouniensis	AACAGGAAGCTGAGACATTCTACAAATAACTAACAAATACACATCCACAA
caerhulians	AACAGGAAGCTGGGACATCCTACAAATAACTAACAAATATACATCTACAA
spilonotus	AACAGGAAGCTGAGACATCCTACAAATAACTAACAAGTACACATCTACAA

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                                            310       320       330       340       350
                                             .         .         .         .         .
Aphaniotis fuscus                   TTATACTTATTGCCCTAATAATTAAAGCCGGAGCAGTCCCCACCCACTTT
Bronchocoela cristatella            TTATACTAATCGCACTCACAATAAAAATAGGAGCAGCCCCAATACACCTA
Japalura splendida                  TCGTACTCCTCGCCATTACGATAAAAGCCGGCACAGTCCCAACACACTTC
Japalura tricarinata                TAATAGCCATCGCCCTCACAATAAAAATAGGCTCAGTTCCACTACACTTC
maximus                             CAATAACTGTTGCCCTTACAATAAAAGCAGGGGCAGTCCCATTGCATTTC
quinquefasciatus                    TAATAACTGTTGCTCTTGCAATAAAAGCAGGGGCAGTCCCACTACATTTC
spilopterus (Luzon, SE Bicol Pen.)  TCATAATTATTGCCCTAGCAATAAAAATCGGGGCCACCCCACTCCATTTC
spilopterus (Luzon, C Bicol Pen.)   TCATAATTATTGCCCTAGCAATAAAAATCGGAGCCACCCCCCTCCATTTC
spilopterus (Luzon, E coast)        TCATGATTATTGCCCTCGCAATAAAAACCGGAACCGCTCCGCTCCACTTC
spilopterus (Polillo)               TTGTACTTATTGCCCTCGCAATGAAAACCGGAACCGCCCCCCTCCACTTC
spilopterus (Negros)                TAATAATCATTGCTCTCGCAATAAAAACTGGAACCGCCCCACTTCACTTT
spilopterus (Panay)                 TAATAATCATTGCTCTCGCAATAAAAACCGGAACCGCCCCACTTCACTTT
spilopterus (Cebu)                  CAATGATTATTGCTCTCGCAATAAAAACTGGAACCGCTCCACTTCATTTT
spilopterus (Siquijor)              TAATGATTATTGCCCTCGCAATAAAAACTGGAACCGCCCCACTTCACTTT
bimaculatus                         TTATACTTGTTGCCCTCTCAATAAAAATAGGAGCCGTACCACTACACTTC
blanfordi                           CAATAACAATCGCTATTGTGATAAAAGCAGGGGCTGTTCCTCTACACTTT
indochinensis                       CAATAACTATTGCCCTAGTAATAAAAGCGGGGGCTGTCCCATTGCACTTT
cornutus                            TCATGATCATTGCCCTCGCAATAAAAACCGGAACTGCCCCACTGCACTTC
cyanopterus (Mindanao)              TTATAATCGTGGCCCTTGCAATAAAAACCGGAACCGCCCCCTTACACTTT
reticulatus (Samar)                 TTATAATCGTGGCCCTTGCAATAAAAACCGGAACCGCCCCACTACACTTT
reticulatus (Bohol)                 TTATAATTGTGGCCCTTGCAATAAAAACCGGAACCGCCCCACTACACTTT
maculatus                           CAACACTTATTGCCCTCGCAATAAAAGCAGGGGCCATCCCCCTACACTTC
mindanensis                         CAATAACTATTGCCCTTGCAATAAAAGCAGGAGCAGTTCCACTACACTTC
obscurus                            CAATAACTATTGCCCTAGTAATAAAATCCGGAGCAGTCCCACTCCACTTC
taeniopterus                        CAATAACTCTCGCCCTAGTAATAAAAGCAGGAGCAGTCCCACTCCACTTT
ornatus (Samar)                     TCATAATCATCGCCCTAACAATAAAAATAGGAGCCGCCCCACTTCACTTT
ornatus (Bohol)                     TTATAGTCATCGCCCTTGCAATAAAAACAGGAACCGCTCCACTTCACTTT
fimbriatus (Borneo)                 CAATACTCGTGGCCCTAACAATAAAAGCCGGGGCCATCCCCCTACACTTC
cristatellus (Borneo)               CAATACTCCTAGCCCTAACAATAAAAGCAGGCGCCATCCCCCTACACTTC
fimbriatus (Malay Pen.)             CCATGCTAATCGCCCTAACAATAAAAGCCGGAGCTATCCCCCTGCACTTC
fimbriatus (Java)                   CCATGCTAGTAGCCCTAACAATAAAAGCCGGGGCCATCCCCCTACACTTC
melanopogon                         CAATAACTATTGCACTTGTAATAAAAGCAGGAGCAGTCCCACTACACTTC
haematopogon                        CAATAACCCTCGCCCTTGTGATAAAAGCCGGGGCCGTTCCACTACACTTT
guentheri                           TCATAGTCATTGCCCTCGCAATAAAAACCGGAACTGCTCCACTCCACTTC
quadrasi (Mindoro)                  TCATAATCATTGCCCTTGCAATAAAAATTGGAGTCGCCCCACTTCACTTT
palawanensis                        TTATAACTATTGCTCTTGCAATAAAAATCGGAGCTGCTCCGCTACATTTT
formosus                            CAATGACTGTTGCCCTAGTAATAAAAACAGGGGTAGTTCCACTCCACTTC
sumatranus (Borneo)                 TTATAATCCTCGCCCTAGCAATAAAAACCGGAGCTGCTCCCCTACACTTC
sumatranus (Malay Pen.)             TTATAATCCTCGCTCTAGCAATAAAAACTGGAGCCGCTCCCCTACACTTC
sumatranus (Sumatra)                TTATAATCCTCGCCCTAGCAATAAAAACCGGAGCTGCTCCCCTACACTTC
volans (Java)                       TTATAATCCTTGCCTTGGCAATAAAAACCGGAACCGCCCCCCTACACTTC
quadrasi (Sibuyan)                  TTATAATCATTGCCCTCGCAATAAAAATTGGAGCCGCCCCACTTCACTTC
boschmai (Flores)                   TTATAATCCTCGCCCTAGCAATAAAAATGGGAACCGCCCCATTACACTTC
boschmai (Sumba)                    TTATAATCCTAGCCCTGGCAATAAAAATAGGGGCTGCCCCTTTACACTTC
boschmai (Lembata 1)                TTATAATCCTAGCCCTAGCAATAAAAATGGGAGCCGCCCCCCTTCACTTC
boschmai (Lembata 2)                TTATAATCCTAGCCCTAGCAATAAAAATGGGAGTCGCCCCCCTTCACTTC
boschmai (Sumbawa)                  TTATAATTCTAGCCCTGGCAATAAAAACCGGGACTGCTCCCCTACACTTC
timoriensis (Roti)                  TTATAATCCTCGCCCTGGCAATAAAAATGGGAGCTGCCCCATTACACTTC
timoriensis (Timor)                 TTATAATCCTCGCCCTAGCAATAAAAATGGGAGCTGCCCCCCTACACTTC
beccarii                            TCATACTCATTGCCCTCGCAATAAAAGCAGGCGCCGTCCCCCTACACTTC
biaro                               TTACACTCATCGCCATTGCAATGAAAGCGGGGGCCGTCCCCCTGCACTTC
"Tahulandang"                       TTACACTCATCGCCATTGCAATAAAAGCGGGAGCCGTCCCCCTGCACTTC
bourouniensis                       TCATGCTCATTGCCATCGCAATAAAAGCAGGCGCCGTCCCACTACACTTC
caerhulians                         TCACACTCATTGCCATTGCAATGAAGGCGGGGGCCGTCCCTCTGCACTTC
spilonotus                          TTACACTCATTGCCATTGCAATGAAGGCGGGGGCCGTCCCACTGCACTTC
```

	360 370 380 390 400
Aphaniotis fuscus	TGACTACCAGAAGTAATACAAGGCACAACCATCATAACTGCAATAATTAT
Bronchocoela cristatella	TGACTTCCAGAAGTTATACAAGGTACAACACTTCTAACCTCACTACTAAT
Japalura splendida	TGACTGCCAGAAGTAATACAAGGAAGTACACTCACCACCACTATACTAAT
Japalura tricarinata	TGACTTCCAGAAGTAATACAGGGCAGCACACTATACACCACCTTAGTAAT
maximus	TGACTCCCAGAAGTAATACAAGGAAGCACTCTATACACTACCATGCTAAT
quinquefasciatus	TGACTCCCAGAAGTCATACAAGGCAGCACATTATACACCACCATGTTAAT
spilopterus (Luzon, SE Bicol Pen.)	TGACTACCAGAAGTCATACACGGCAGTACCATATACACCGCAATGCTAAT
spilopterus (Luzon, C Bicol Pen.)	TGACTACCAGAAGTCATACACGGCAGCACCATATACACCGCAATACTAAT
spilopterus (Luzon, E coast)	TGACTTCCAGAAGTCATGCACGGCAGTACCATATACACCGCCATACTTAT
spilopterus (Polillo)	TGACTTCCAGAAGTCATACACGGCAGTACCATGTATACCGCCATACTGAT
spilopterus (Negros)	TGACTCCCAGAAGTCATGCACGGAAGCACCATGTACACTGCCATGCTAAT
spilopterus (Panay)	TGACTCCCAGAAGTCATACACGGAAGCACCATGTACACTGCCATGCTAAT
spilopterus (Cebu)	TGACTCCCAGAAGTCATACACGGAAGCACTATATACACTGCCATACTGAT
spilopterus (Siquijor)	TGACTCCCAGAAGTTATACACGGGAGCACCCTATACACTGCCATGCTAAT
bimaculatus	TGACTGCCAGAGACTATACAAGGCAGCAGTATGTACACCGCCCTACTAAT
blanfordi	TGACTCCCAGAAGTCATACAAGGCAGTACCATATACACCGCCATACTAAT
indochinensis	TGACTACCAGAGGTTATACAAGGCAGCACTCTATATACCACCATGCTAAT
cornutus	TGACTCCCAGAAGTTATACACGGAAGCACCATATACACCGCCATACTAAT
cyanopterus (Mindanao)	TGACTGCCAGAAGTCATGCACGGTACCACCATATACACCGCCATACTAAT
reticulatus (Samar)	TGATTACCAGAAGTCATGCATGGTACCACCATATACACCGCCATACTAAT
reticulatus (Bohol)	TGACTGCCAGAAGTCATGCACGGTACCACCATACACACCGCCATACTAAT
maculatus	TGACTACCAGAAGTAATACAAGGCTGCACACTGCATACCGCCATATTAAT
mindanensis	TGACTACCAGAAGTCATACAGGGCAGCACTTTATTCACCACCATACTAAT
obscurus	TGACTTCCGGAGGTCATACAAGGCAGCACCCTGTACACTGCCATGCTAAT
taeniopterus	TGACTCCCAGAAGTTATGCAAGGCAGCACTCTATACACTGCCATACTAAT
ornatus (Samar)	TGACTCCCAGAAGTTATGCATGGCAGCACCCTATACACCGCCATACTAAT
ornatus (Bohol)	TGACTTCCAGAAGTCATGCACGGCAGCACCATATACACCGCCATATTAAT
fimbriatus (Borneo)	TGACTCCCAGAAGTTATGCAAGGCTGCACCCTATACACTGCCATGCTGAT
cristatellus (Borneo)	TGATTGCCAGAAGTAATACAAGGCTGCACTTTGTACACCGCCATACTAAT
fimbriatus (Malay Pen.)	TGACTCCCAGAAGTCATGCAAGGCTGCACCCTATATACCGCCATACTAAT
fimbriatus (Java)	TGACTCCCAGAAGTTATGCAAGGCTGCACCCTATACACCGCCATACTAAT
melanopogon	TGACTTCCAGAAGTCATACAAGGCAGCACCCTATACACCACCATACTAAT
haematopogon	TGATTACCAGAAGTCATACAAGGTAGCACCCTCTACACCACCATGCTGAT
guentheri	TGACTCCCAGAAGTTATACACGGCAGCTCCATGTACACGGCCATATTAAT
quadrasi (Mindoro)	TGACTCCCAGAAGTCATACACGGCAGCACCATGTACACCGCCATGTTAAT
palawanensis	TGACTCCCAGAAGTCATGCACGGCTGCACCATGCACACCGCCATACTAAT
formosus	TGACTTCCAGAAGTCATGCAAGGCAGCACTCTATACACTGCCATACTAAT
sumatranus (Borneo)	TGACTCCCAGAAGTTATACATGGCAGCACTATGTACACCGCTATACTAAT
sumatranus (Malay Pen.)	TGACTCCCAGAAGTTATACATGGCAGCACTATGTACACCGCTATACTAAT
sumatranus (Sumatra)	TGACTCCCAGAAGTTATACATGGCAGCACCATGTACACCGCTATACTAAT
volans (Java)	TGACTCCCAGAAGTCATGCATGGCAGCACTATGTATACTGCCATACTAAT
quadrasi (Sibuyan)	TGACTCCCAGAAGTTATACATGGCAGCACCATGTACACCGCCATATTAAT
boschmai (Flores)	TGACTTCCAGAAGTCATACATGGCAGCACAATGTACACCGCCATACTAAT
boschmai (Sumba)	TGATTCCCAGAAGTCATACATGGCAGTACAATATACACCGCCATACTAAT
boschmai (Lembata 1)	TGGCTCCCAGAAGTCATACATGGCAGCACAATATATACCGCCATATTAAT
boschmai (Lembata 2)	TGGCTCCCAGAAGTCATACATGGCAGCACAATATATACCGCCATATTAAT
boschmai (Sumbawa)	TGACTACCAGAAGTCATACATGGCAGCACCATGTACACTGCCATACTAAT
timoriensis (Roti)	TGACTCCCAGAAGTCATACATGGCAGCACAATGTACACCGCCATACTAAT
timoriensis (Timor)	TGACTCCCAGAAGTCATACATGGCAGCACGATGTACACCGCCATGCTAAT
beccarii	TGACTACCAGAAGTTATACAGGGCAGTACCATATACACCGCCATACTAAT
biaro	TGATTGCCAGAAGTAATACAAGGCAGCACTATATACACTGCCATAATAAT
"Tahulandang"	TGATTACCAGAAGTAATACAAGGCAGCACCATATACACTGCCATAATAAT
bourouniensis	TGAATACCAGAAGTCATACAAGGCAGCACCCTATACACCGCCATGCTTAT
caerhulians	TGATTACCAGAAGTCATACAAGGCAGCACCATATACACTGCCATAATAAT
spilonotus	TGATTACCAGAAGTAATACAAGGCAGCACCATATACACTGCCATAGTAAT

	410 420 430 440 450
Aphaniotis fuscus	CGCTACCTGACAAAAAATCGCCCCTACAATCCTAATTTTTTACTATCAA
Bronchocoela cristatella	CTCAACCTGACAAAAAATCGCCCCAATAGTATTAATTTTTACTACATCCA
Japalura splendida	ATCAACCTGACAAAAAATAGCTCCAATAGCCCTAATCTACTCCGTATCAA
Japalura tricarinata	CTCAACATGACAAAAACTAGCCCCCTTCGCCCTACTTTATTTCATATCAA
maximus	CTCCACATGACAAAAAATCGCCCCCATAGCACTTATATACTCAATATCAA
quinquefasciatus	TTCTACATGACAAAAAATTGCCCCAATAACATTACTCTACTCAATGTCAA
spilopterus (Luzon, SE Bicol Pen.)	CTCAACCTGACAAAAAATGGCCCCCATAGCGCTCTTCTACTCAATTTCTA
spilopterus (Luzon, C Bicol Pen.)	TTCAACCTGACAAAAAATAGCCCCCGTAGCACTCTTCTACTCAATTTCTA
spilopterus (Luzon, E coast)	TTCAACTTGACAAAAAATAGCTCCAATAGCACTCCTCTATCAAATCTCGA
spilopterus (Polillo)	TTCAACCTGACAAAAAATGGCCCCAATAGCACTCCTTTACCAAATCTCAA
spilopterus (Negros)	CTCAACTTGACAAAAAATAGCTCCAATAGCACTCCTTTATTCAATCTCAA
spilopterus (Panay)	CTCAACTTGACAAAAAATAGCCCCAATAGCACTCCTTTATTCAATCTCAA
spilopterus (Cebu)	CTCAACTTGACAAAAAATAGCCCCCATAGCACTCCTCTATTCAATCTCAA
spilopterus (Siquijor)	CTCAACTTGACAAAAAATAGCTCCAATAGCACTCCTCTATTCAATCTCAA
bimaculatus	TTCAACCTGACAAAAAATAGCCCCAATAGCACTACTCTACTCAATATCAA
blanfordi	CTCCACTTGACAAAAAATCGCCCCAATGGCACTCCTCTATTCAATATCAA
indochinensis	TTCCACTTGACAAAAGATCGCCCCAATAGCACTTCTTTACTCAATATCAA
cornutus	CTCAACTTGACAAAAAATAGCCCCAATAGCACTCCTCTATCAAATTTCAA
cyanopterus (Mindanao)	TTCAACTTGACAAAAAATAGCTCCAATAGCACTTCTCTATTTGACCTCTA
reticulatus (Samar)	TTCAACTTGACAAAAAATAGCTCCAATAACACTCCTCTATTTAACCTCTA
reticulatus (Bohol)	TTCGACTTGACAAAAAATAGCTCCAATAACACTCCTCTATCTGACCTCTA
maculatus	CTCCACCTGACAAAAAATTGCCCCCATAGCCCTCCTCTATCTAATGTCAA
mindanensis	CTCCACATGACAAAAAGTCGCCCCAATAGCACTACTCTACTCAATCTCTA
obscurus	CTCCACCTGACAAAAAATTGCCCCAATGGCACTTCTCTATTCAATATCCA
taeniopterus	TTCCACTTGACAAAAAATTGCCCCAATAGCACTTCTCTATTCAATATCCA
ornatus (Samar)	TTCAACCTGACAAAAAATTGCTCCTATAGCACTCCTTTATCTAATCTCGA
ornatus (Bohol)	TTCAACCTGACAAAAAATCGCTCCTATAACACTTCTTTATCTAATCTCGA
fimbriatus (Borneo)	CGCCACCTGACAAAAAATCGCTCCAATAGCCCTTATATATCTAATGTCAA
cristatellus (Borneo)	TTCCACCTGACAAAAAATCGCCCCTATAGCCCTACTATATATAATCTCAA
fimbriatus (Malay Pen.)	CTCCACCTGACAAAAAATTGCCCCAATAGCCCTAATCTATCTAATGTCAA
fimbriatus (Java)	CTCCACCTGACAAAAAATCGCCCCAATGGCCCTAATCTATCTAATGTCAA
melanopogon	TTCCACTTGACAAAAAATCGCCCCAATAACACTTCTCTATTCAATATCAA
haematopogon	CTCCACTTGACAAAAGGTTGCCCCAATAGCACTTCTCTATTCAATATCAA
guentheri	TTCAACTTGACAGAAAATAGCTCCAATAGCACTCCTCTACCTAATTTCAA
quadrasi (Mindoro)	ATCAACCTGACAAAAAATGGCTCCAATAGCACTTCTTTATTTAATCGCAA
palawanensis	TTCAACTTGACAAAAAATGGCCCCAATAGCACTTCTTTATTTAATTTCAA
formosus	CTCCACTTGACAAAAAATCGCCCCAATAGCACTTCTCTATTCAATATCTA
sumatranus (Borneo)	CTCGACTTGACAAAAAATTGCCCCAATGACACTTCTGTACCTTATATCAA
sumatranus (Malay Pen.)	TTCAACTTGACAAAAAATTGCTCCTATAGCACTCCTGTACCTTATGTCAA
sumatranus (Sumatra)	CTCGACTTGACAAAAAATTGCCCCTATGGCACTCCTGTACCTTATGTCAA
volans (Java)	TTCAACTTGACAAAAAATTGCTCCCATAACACTCCTCTATCTCATATCAA
quadrasi (Sibuyan)	GTCAACTTGACAAAAAATGGCTCCAATAGCACTTTTTTATTTAATCTCAA
boschmai (Flores)	CTCAACTTGACAAAAAATCGCCCCCATAACACTTTTGTACCTTATATCAA
boschmai (Sumba)	CTCAACTTGACAAAAAATCGCTCCTATAACACTTTTATACCTTATATCAA
boschmai (Lembata 1)	CTCAACCTGACAAAAAATTGCCCCAATAACACTCCTGTACCTTATATCAA
boschmai (Lembata 2)	CTCAACTTGACAAAAAATTGCCCCAATAACACTCCTGTACCTTATATCAA
boschmai (Sumbawa)	TTCAACTTGACAAAAAATTGCCCCCATAACACTCTTGTACCTCATATCTA
timoriensis (Roti)	CTCAACTTGACAAAAAATCGCCCCTATAACACTTTTGTACCTTATATCAA
timoriensis (Timor)	CTCAACTTGACAAAAAATCGCCCCTATAACACTTTTGTACCTTATATCAA
beccarii	TTCGACCTGACAAAAGATAGCTCCAATAGTTCTTCTTTATTCAATATCAA
biaro	CTCAACCTGACAAAAAATAGCCCCCATAGCCCTGCTTTATCTAATGTCAA
"Tahulandang"	CTCAACCTGACAAAAAATAGCCCCCATAGCCCTCCTTTATCTAATGTCAA
bourouniensis	CTCAACCTGGCAAAAAGTCGCCCCAATAACACTTCTTTATCTAATTTCAA
caerhulians	CTCAACCTGACAAAAAATAGCTCCTATAGCCCTTCTTTATCTAATGTCAA
spilonotus	CTCAACCTGACAAAAAATAGCCCCCATAGCCCTCCTTTATCTAATATCCA

	460 470 480 490 500
Aphaniotis fuscus	ACCATGCCCAACCGTATATTGCAATTACCCTCGGACTTCTATCAACATCT
Bronchocoela cristatella	ATCACCTATCATCAAACATCACCCTAATCATAGGACTTCTATCAACATAT
Japalura splendida	ACCACGCCTCACCAAACATTACACTAATGCTTGGACTACTGTCAACAACC
Japalura tricarinata	ACCACATACAACCCGTTATTATCTTAACACTTGGAATCCTATCAACAACA
maximus	ACCACATACAACCAGCTATCACTATCACACTAGGTATACTCTCAACAACA
quinquefasciatus	ACCACATACAACCAATTATCACCATTACACTAGGCATGCTCTCAACAACA
spilopterus (Luzon, SE Bicol Pen.)	ATCACATACAGTCTTCGATCGCCCTCATTATCGGCATCCTTTCGACAATG
spilopterus (Luzon, C Bicol Pen.)	ATCACATACAATCTTCGATCGCCCTCATTATTGGCATCCTTTCGACAATG
spilopterus (Luzon, E coast)	ACCATGTACAACCCGCCGTCACCCTTACACTCGGCATCCTCTCAACAACA
spilopterus (Polillo)	GCCACGTACAGCCCGCCCTTGCCCTTACACTCGGCATCCTCTCAACAACA
spilopterus (Negros)	ACCATATACAGCCTGTCACCGTTCTCACACTGGGCATTCTCTCAACTACA
spilopterus (Panay)	ACCATATACAGCCTGTCATCGTTCTCACACTGGGCATTCTCTCAACTACA
spilopterus (Cebu)	ACCACATACAGCCTATTATTGTCCTTACACTTGGTATTATTTCAACCATA
spilopterus (Siquijor)	GCCATATACAACCTGTCATCGCTCTCACACTTGGCATCCTCTCAACCATA
bimaculatus	CCCACATCCAACCGACCTTCGCCCTTATGCTAGGCCTACTCTCAACAGTA
blanfordi	ATCATATACAACCAATTATTGCCATCACACTGGGCCTACTATCCACAACA
indochinensis	ACCACACACAACCAATTATTATTGTTACACTAGGTATTCTTTCCACAACA
cornutus	ACCACATGCAATCTACCATTGCCCTCACACTTGGCATTCTATCAACAACA
cyanopterus (Mindanao)	ATCATTTACAGCCCACCATTACCCTCACACTTGGTGTTATATCAGCAATG
reticulatus (Samar)	ATCATCTACAGCCCGCCATTACCCTCACACTGGGTGTTGTATCCGCAATG
reticulatus (Bohol)	ATCACCTACAGCCCACCATCACCCTCACACTGGGTGTTGTATCAGCAATG
maculatus	ACCACACACAACCCATTGTAACCATAACACTCGGCATGCTCTCCACAACC
mindanensis	ACCATACACAACCAACTATCACCATTACACTAGGCATACTCTCGACAATA
obscurus	ACCATTTACAACCAACTATCACCATTACACTTGGTGTACTTTCCACAACA
taeniopterus	ACCACTTACAACCAACTATCACCATAACACTTGGTGTACTTTCCACAACA
ornatus (Samar)	ACCACATACAATCCACTATCCCCCTCACCCTTGGTATTATTTCGACAATA
ornatus (Bohol)	ACCACATACAATCCACTATCGTCCTTACCATCGGCATTATTTCAACAATA
fimbriatus (Borneo)	ACCACACACAACCACTAATTACTATAACACTCGGCATACTCTCAACAATG
cristatellus (Borneo)	GCCACGTACAGCCCCTAGTTGCTCTGACACTAGGCACACTATCAACAATA
fimbriatus (Malay Pen.)	ACCATGCCCAACCACTAATTACCCTAACACTCGGCATGCTCTCAACAATA
fimbriatus (Java)	ACCACACCCAACCACTAATCACCCTTACACTCGGCATGCTCTCAACAATG
melanopogon	ACCACATACAACCAATTATCACCATTACACTTGGCGTACTCTCCACAACA
haematopogon	ACCACATACAACCGACTATCACCATTACACTAGGCGTACTTTCCACAACA
guentheri	GCCACATACAATCTCCCATCGTCCTCATATTAGGCATTCTTTCAACGACA
quadrasi (Mindoro)	ATCACATACAACCTATAACCACCCTGACACTCGGAATTCTTTCAACAATA
palawanensis	ACCACATGCAACCTACTCTTACTCTCACATTAGGCATTTTCTCAACAATA
formosus	ACCACCTACAACCGATTGTCACCATAACACTTGGTGTACTCTCCACAACA
sumatranus (Borneo)	ACCACATACAGCCTACCATCACCCTTACACTCGGTATTCTTTCAACAACA
sumatranus (Malay Pen.)	ACCATATACAACCTGCCATCACCCTTACACTCGGTATTCTTTCAACAACG
sumatranus (Sumatra)	ACCATATACAGCCTGCCATCACCCTTACACTCGGTATTCTTTCAACAACA
volans (Java)	ACCATATACAGCCTGTCGTCACCCTCACACTCGGCATACTTTCAACTATA
quadrasi (Sibuyan)	ATCACACACAACCTTTAATTACCCTAACACTCGGCATTATTTCAACAATA
boschmai (Flores)	ATCATACACAACCTGTCATTACCCTTACACTCGGCCTACTTTCAACGACA
boschmai (Sumba)	ATCATACACAACCTGCCATTGCCCTTACACTCGGCCTACTTTCAACAACA
boschmai (Lembata 1)	ATCATACACAATCCACCATTGCCCTTACACTCGGCCTACTTTCAACAACA
boschmai (Lembata 2)	ATCATACACAATCCACCATTGCCCTTACACTCGGCCTACTTTCAACAACA
boschmai (Sumbawa)	ATCATACACAACCTGCCATTACCATTACACTCGGCTTACTCTCAACAACA
timoriensis (Roti)	ATCACACACAACCTACCATTGCCCTTACACTCGGCCTACTTTCAACAACA
timoriensis (Timor)	ATCATACACAACCTACCATTGCCCTTACACTCGGCCTACTTTCAACAACA
beccarii	GCCATGTACAACCAAGCACAACCCTTGTACTAGGCTTGCTTTCAACAACA
biaro	ACCACATAGAAACCGCTGCCACCCTCACACTAGGCATGCTCTCAACAACG
"Tahulandang"	ACCACATAGAGCCCACTGCCACCCTCACACTGGGCATGCTCTCAACAACG
bourouniensis	ACCATGTACAACCAATCATCACCCTTATACTAGGCATACTTTCAACAACA
caerhulians	ACCACATAGAACCCGCTGCCACTCTCACACTAGGTATGCTTTCAACAACG
spilonotus	ACCACTTAGAACCCACTGCCACCCTCATACTAGGCATACTCTCAACAACG

	510 520 530 540 550
Aphaniotis fuscus	TTTGGTGGTTGAGGTGGAATAAATCAAACACAACTACGAAAAATACTAGC
Bronchocoela cristatella	CTAGGAGGATGAGGCGGAATAAATCAAACCCACCTACGGAAAATAATAGC
Japalura splendida	TTCGGCGGATGAGGGGGAATAAACCAGACACAGCTACGAAAAATAATAGC
Japalura tricarinata	TTCGGAGGCTGAGGGGGAATAAATCAAACCCAACTACGAAAAATAATAGC
maximus	TTCGGCGGTTGAGGGGGAATAAACCAAACCCAACTACGAAAGATAATAGC
quinquefasciatus	TTCGGAGGTTGAGGGGGTATTAACCAAACCCAACTACGAAAAATAATGGC
spilopterus (Luzon, SE Bicol Pen.)	GTTGGAGGCTGAGGGGGTATTAACCAAACTCAACTACGGAAAATACTAGC
spilopterus (Luzon, C Bicol Pen.)	GTCGGTGGCTGAGGGGGTATTAACCAAACTCAACTGCGGAAAATACTAGC
spilopterus (Luzon, E coast)	ATCGGCGGCTGAGGGGGCATTAACCAAACCCAACTGCGAAAAATACTAGC
spilopterus (Polillo)	ATCGGCGGCTGAGGCGGCATTAACCAAACCCAGCTACGGAAAATACTAGC
spilopterus (Negros)	ATCGGCGGTTGAGGTGGCATTAACCAAACCCAACTACGAAAAATACTAGC
spilopterus (Panay)	ATCGGCGGTTGAGGGGGCATTAACCAAACCCAACTACGAAAAATACTAGC
spilopterus (Cebu)	ATCGGTGGTTGAGGAGGCATTAACCAAACCCAACTACGAAAAATACTAGC
spilopterus (Siquijor)	GTCGGCGGTTGGGGCGGCATTAACCAGACCCAACTACGGAAAATACTAGC
bimaculatus	TTTGGGGGCTGAGGCGGTATTAACCAAACTCAATTACGAAAAATAATAGC
blanfordi	TTCGGCGGTTGAAGCGGCATTAATCAAACCCAACTGCGTAAAATAATAGC
indochinensis	TTCGGCGGCTGAGGCGGAATTAATCAAACCCAGCTACGAAAAATAATAGC
cornutus	ATCGGCGGCTGAAGGGGCATCAACCAAACCCAATTACGAAAAATACTGGC
cyanopterus (Mindanao)	ATTGGGGGCTGAGGGGGCATTAATCAAACTCAACTACGAAAAATAATAGC
reticulatus (Samar)	ATCGGGGGCTGAGGAAGCATTAACCAAATTCAACTACGAAAAATGCTAGC
reticulatus (Bohol)	ATTGGGGGCTGGGGGGGCATTAACCAAACTCAACTACGAAAAATGCTAGC
maculatus	TTTGGCGGATGGGGCGGAATTAACCAAACCCAACTTCGAAAAATAATAGC
mindanensis	TTTGGTGGTTGAAGGGGTATTAACCAAACTCAACTACGAAAAATAATAGC
obscurus	TTCGGAGGCTGAGGCGGAATTAATCAAACCCAACTACGAAAAATAATAGC
taeniopterus	TTTGGAGGCTGAGGCGGAATTAATCAAACTCAACTGCGAAAAATAATAGC
ornatus (Samar)	ATCGGAGGCTGAGGAGGCATTAACCAGACCCAGCTACGAAAAATGCTAGC
ornatus (Bohol)	ATCGGAGGATGAGGAGGCATTAACCAGACTCAACTACGAAAAATGCTAGC
fimbriatus (Borneo)	TTTGGGGGCTGAGGCGGAATCAATCAAACCCAGCTACGAAAAATAATGGC
cristatellus (Borneo)	TTTGGAGGCTGAGGAGGGATCAACCAAACCCAACTGCGAAAAATAATAGC
fimbriatus (Malay Pen.)	TTCGGAGGCTGAGGCGGGATCAACCAAACCCAACTACGAAAAATAATAGC
fimbriatus (Java)	TTGGGAGGTTGAGGCGGAATAAACCAAACCCAACTACGAAAAATAATAGC
melanopogon	TTTGGCGGTTGAGGCGGAATTAACCAAACCCAGCTACGAAAAATAATAGC
haematopogon	TTCGGCGGCTGAGCCGGCATTAATCAAACCCAACTGCGAAAAATAATAGC
guentheri	ATCGGCGGCTGAGGAGGCATCAACCAAACCCAGCTACGAAAGATGTTAGC
quadrasi (Mindoro)	ATCGGCGGCTGAGGGGGCATTAACCAAACTCAGCTACGAAAAATACTAGC
palawanensis	ATCGGCGGCTGAGGTGGAATTAACCAAACTCAACTACGAAAAATACTAGC
formosus	TTCGGAGGCTGGGGCGGAATTAATCAAACCCAACTACGAAAAATAATAGC
sumatranus (Borneo)	ATCGGCGGCTGAGGGGGCATCAACCAAACCCAACTACGAAAAATACTTGC
sumatranus (Malay Pen.)	ATCGGCGGTTGAGGAGGCATCAACCAAACCCAGCTACGAAAGATACTTGC
sumatranus (Sumatra)	ATCGGCGGCTGAGGAGGCATCAACCAAACCCAACTACGAAAGATACTTGC
volans (Java)	GTCGGCGGCTGAGGGGGCATCAACCAAACCCAGCTACGAAAAATACTAGC
quadrasi (Sibuyan)	ATCGGAGGCTGAGGGGGCATTAACCAAACCCAACTACGGAAAATATTAGC
boschmai (Flores)	ATTGGCGGCTGAGGAGGAATCAACCAAACTCAACTACGAAAAATACTAGC
boschmai (Sumba)	ATTGGCGGCTGAGGGGGAATCAACCAAACCCAACTACGAAAAATACTAGC
boschmai (Lembata 1)	ATTGGTGGCTGAGGAGGAATCAACCAAACCCAACTACGAAAAATACTAGC
boschmai (Lembata 2)	ATTGGTGGCTGAGGAGGAATCAACCAAACCCAACTACGAAAAATACTAGC
boschmai (Sumbawa)	ATCGGTGGCTGAGGCGGGATCAACCAAACCCAATTACGAAAAATACTAGC
timoriensis (Roti)	ATTGGCGGCTGAGGGGGAATCAACCAAACCCAACTACGAAAAATACTAGC
timoriensis (Timor)	ATTGGCGGCTGAGGGGGAATCAACCAAACCCAACTACGAAAAATATTAGC
beccarii	ATTGGCGGTTGAGGCGGAATTAATCAGACCCAACTACGAAAGATAATAGC
biaro	ATTGGCGGCTGAGGGGGGATCAACCAAACCCAACTACGAATAATAATAGC
"Tahulandang"	ATTGGCGGCTGAGGGGGGATCAACCAAACCCAACTACGAAAAATAATAGC
bourouniensis	ATCGGAGGCTGAGGGGGAATCAATCAAACCCAACTACGAA?AATAATAGC
caerhulians	GTCGGCGGCTGAGGGGGGATCAACCAAACCCAGCTACGAAAAATAATAGC
spilonotus	ATCGGGGGCTGAGGGGGGATCAACCAAACCCAGCTACGAAAAATAATAGC

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                                           560       570       580       590       600
                                             .         .         .         .         .
Aphaniotis fuscus                   CTTCTCATCAATCGCCAATATAGGGTGAACTATGATAACTCTAACATCAG
Bronchocoela cristatella            CTTTTCATCAATTGCCAACATAGGGATGAACTTAATAACCCTAACTTCAG
Japalura splendida                  CTATTCATCAATCACGAACATAGGCTGAACAGTAATAATCCTAGCTATAC
Japalura tricarinata                CTACTCATCAATTACCAACGTAGGTTGAACACTGATGACCCTTACATCAG
maximus                             CTATTCATCAATCACCAACTTGGGCTGAGCATTAATCGTAGTGCCATTCG
quinquefasciatus                    CTACTCATCAATCACCAATATCGGATGAGCCCTAATCGTAATCCCATTCG
spilopterus (Luzon, SE Bicol Pen.)  CTACTCATCTATCTCCAACTTAGGCTGGGCCATGATGATTATTTCATTTG
spilopterus (Luzon, C Bicol Pen.)   CTACTCATCAATCTCCAACTTAGGCTGAGCCATAATAATTATCTCATTCG
spilopterus (Luzon, E coast)        TTACTCATCAATCTCAAACTTAGGCTGAGCCATAATAGTTATCTCATTCG
spilopterus (Polillo)               CTACTCATCAATCTCAAATTTAGGCTGAGCCATAATAGTTATCTCATTTG
spilopterus (Negros)                TTACTCATCTATCTCAAACTTAGGTTGAGCTATAATAGTCATTTCATTCG
spilopterus (Panay)                 TTACTCATCTATCTCAAACTTAGGCTGAGCTATAATAGTTATTTCATTCG
spilopterus (Cebu)                  TTACTCATCCATCTCAAACTTAGGTTGAGCTATAATAGTTATTTCATTTG
spilopterus (Siquijor)              CTACTCATCTATCTCAAACCTAGGTTGAGCTATAATAGTCATCTCGTTCG
bimaculatus                         TTACTCATCAATTACCAACTTAGGCTGAGGCTTAATAATTATCTCATTCG
blanfordi                           CTTCTCATCAATTACCAACCTAGGCTGAGCACTAATTGTGGCCCCATTTG
indochinensis                       CTTCTCCTCAATCACCAACCTTGGCTGAGCACTAATTGTAACCCCATTTG
cornutus                            CTACTCATCAATTTCAAACTTAGGTTGAGCCATAATAATTATCCCCTTCG
cyanopterus (Mindanao)              TTACTCCTCAATTTCAAACTTAGGCTGAGCAATGGTAGTAGTCTCGTTTG
reticulatus (Samar)                 CTACTCGTCAATTTCAAACTTAGGTTGAGCAATGGTAGTAATCTCGTTTG
reticulatus (Bohol)                 CTATTCATCAATCTCAAACCTGGGTTGAGCAATGGTAGTAATCTCGTTTG
maculatus                           CTACTCATCAATTACCAACCTCGGTTGAGCCCTAATAGTAATCTCACTCG
mindanensis                         CTACTCATCAATCGCTAACCTCGGCTGAGCATTAATCGTGATCTCATTCG
obscurus                            CTACTCATCAATCACCAACCTGGGCTGGGCTTTAATCGTGGCCCCATTTG
taeniopterus                        CTACTCATCAATTACTAATCTAGGTTGAACATTAACTGTAGCCCCATTCG
ornatus (Samar)                     CTACTCGTCAATTTCAAATTTAGGCTGAGCCATGATAATTGTCCCATTTG
ornatus (Bohol)                     CTACTCGTCCATTTCAAACCTAGGCTGGGCCATAATAATTATCCCATTCG
fimbriatus (Borneo)                 TTACTCATCAATTACTAACCTAGGCTGAGCCCTAATAGTTATCGCATTCG
cristatellus (Borneo)               CTACTCATCGATCACCAACCTAGGATGAGCCCTAATAGTCATCCCATCCG
fimbriatus (Malay Pen.)             CTACTCCTCAATCACTAACCTAGGCTGATCCCTAATAGTTATTTCACTCG
fimbriatus (Java)                   CTACTCATCAATTACTAACCTAGGCTGATCCCTAATAGTTATCTCACTTG
melanopogon                         CTACTCATCAATTGCTAACCTCGGCTGAGCACTAATAATAACCCCATTTG
haematopogon                        CTACTCATCAATTACCAACCTCGGCTGAGCACTAATTATTGCCCCGTTTG
guentheri                           TTATTCATCAATCTCAAATCTAGGCTGGGCCATAGTAATTATCCCATTCG
quadrasi (Mindoro)                  ATACTCATCAATTTCAAACCTAGGCTGAGCCATAATAATTGTCTCATTTG
palawanensis                        CTACTCATCTATCTCGAACTTAGGTTGAGCAATAATAATTATCTCATTCG
formosus                            CTACTCATCAATCACCAACCTAGGTTGAGCACTAATCGTGGCCCCATTTG
sumatranus (Borneo)                 TTATTCCTCAATCTCCAACTTAGGCTGAGCTATAATAATTGTACCATTTG
sumatranus (Malay Pen.)             TTACTCCTCAATCTCCAACTTAGGCTGGGCCATAATAATTGTATCATTTG
sumatranus (Sumatra)                TTATTCCTCAATCTCCAACTTAGGCTGGGCCATAATAATTGTGTCATTTG
volans (Java)                       TTACTCCTCAGTCTCCAACTTAGGCTGAGCCATAATAATTGTTTCATTTG
quadrasi (Sibuyan)                  ATATTCATCAATTTCAAACTTAGGCTGAGCCATGATAATTATTTCATTTG
boschmai (Flores)                   TTATTCATCAATCTCCAATTTAGGTTGAGCCATAATAATTGTGTCATTTG
boschmai (Sumba)                    TTACTCTTCAATCTCCAATTTAGGTTGAGCCATAATAATTGTATCATTTG
boschmai (Lembata 1)                TTACTCCTCAATCTCCAATTTAGGCTGAGCCATAATAGTTGTATCATTTG
boschmai (Lembata 2)                TTACTCCTCAATCTCCAATTTAGGTTGAGCCATAATAGTTGTATCATTTG
boschmai (Sumbawa)                  TTACTCCTCAATCTCCAATTTAGGCTGAGCCATAATAATTTTATCATTTG
timoriensis (Roti)                  TTATTCCTCAATCTCCAATTTAGGTTGAGCCATAATAATTGTGCCATTTG
timoriensis (Timor)                 TTACTCCTCGATCTCCAATTTAGGTTGAGCCCTAATAATTGTGTCATTTG
beccarii                            ATACTCATCGATCACTAACTTAGGCTGGGCATTAATAGTCATTTCACTCG
biaro                               ATACTCATCTATTACCAACCTAGGCTGAGCACTAATAGTTGTCTCACTAG
"Tahulandang"                       ATACTCATCTATTACCAACCTAGGCTGAGCACTAATAGTTATCTCACTAG
bourouniensis                       ATACTCATCAATCACCAACCTAGGCTGAGCATTAATAGTTCTTTCGCTCG
caerhulians                         ATATTCATCTATTACCAACTTAGGCTGAGCACTAATAGTTGTCTCACTGG
spilonotus                          ATACTCATCTATTACCAACTTAGGCTGAGCACTAATAGTTATTTCGCTAG
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                                            610       620       630       640       650
                                             .         .         .         .         .
Aphaniotis fuscus                   ACCCAAAAACATCAATATTTAACATTTTTATCTATATCCTCATGACAATC
Bronchocoela cristatella            AACCAAAAATATCAATAATTAACATCATAACATATATACTCCTAACAACC
Japalura splendida                  AACCAAAGGCATCAATAATTAGCATCTTTACATACATCATCACAATTATC
Japalura tricarinata                AACCAAATACATCTGCAATCAACATTATAACATATATTCTCCTGATAATC
maximus                             AACCAAACCTATTAGCAATTAATATTCTACTATACATTCTCATAATAATA
quinquefasciatus                    AACCAAACATGTTTACAATTAGCATTCTAATTTACATCCTCATAATAGTA
spilopterus (Luzon, SE Bicol Pen.)  AACCGAACACATTCATGATCAACATTCTACTGTATATTCTTATAATAATT
spilopterus (Luzon, C Bicol Pen.)   AACCAAACACATTCATAATCAACATTCTGCTGTATATTCTTATGATAATT
spilopterus (Luzon, E coast)        AACCAAACATATTCACAATTAACATTCTAACATACATTCTCATGACAATC
spilopterus (Polillo)               AACCAAACACATTCACAATTAACATTCTAACATATATTCTTATGACAATC
spilopterus (Negros)                AACCAAATACTTTTACAATTAACATCATAGTGTATATTCTGATAATAATT
spilopterus (Panay)                 AACCAAATACTTTTACGATTAACATCATAGTGTATATTCTGATAATAATT
spilopterus (Cebu)                  AACCAAACACTTTCACAATTAACATCATAATGTATATTCTGATAATAATT
spilopterus (Siquijor)              AACCAAACACTTTCACAATTAACATCCTAGTATATATCCTGATAATAATC
bimaculatus                         AACCAGATACATTCACAATTAACATCCTATTGTACATCCTCATAATAATA
blanfordi                           AACCAAACATGTTCATAATCAGTATTCTAGTGTATATTCTGATAATAGCC
indochinensis                       AACCAAACATATTCGCAATCACCATTTTAACTTACATTTTAATAATAATC
cornutus                            AACCAAACACATTCACAATTAACATCCTAGTATACATCATCATAATAATT
cyanopterus (Mindanao)              AGCCAAACACGTTCACAATCAACATTTTAACCTATATCCTTATGATAGTC
reticulatus (Samar)                 AACCAAATGCATTCACAATCAACATCTTAACCTATGTCCTTATGATAGTC
reticulatus (Bohol)                 AGCCAAACACATTCACAATTAACATCATAACCTATGTCCTTATGATAATC
maculatus                           AACCAAACACATTCGCAATTAATATTCTAGTATATATCCTTATAATAGTA
mindanensis                         AACCAAACCTGTTCACAATTAGCATTATAATATACATCCTCATAATAATA
obscurus                            AACCTAACATGCTCATAATAGGTATCCTAGTATATATTCTCATAATAGTA
taeniopterus                        AACCTAACTTACTCATTATGGGCATTCTAATGTACATTCTCATAATAGTA
ornatus (Samar)                     AACCAAACACATTCGCAATCAACATTTTAGTATACATTCTTATGATAATC
ornatus (Bohol)                     AACCAAACACATTCACAATCAACATTTTAGTGTACATTCTTATGATAATT
fimbriatus (Borneo)                 AACCAAACACATTCGCAATTAATATCCTAATGTACATCCTCATAATAATA
cristatellus (Borneo)               ACCCAAACACATTCGCAATCAATATTCTATTATACATCCTCATAATAATG
fimbriatus (Malay Pen.)             AACCAAACACATTCGCAATTAACATCCTGATATACATTCTCATAATAATG
fimbriatus (Java)                   AACCAAACACATTCGCAATTAACATCCTAATGTACATCCTCATAATAATG
melanopogon                         AACCAAACATGTTCGCAATCAGCATCTTAGTCTATATTCTAATAATAATA
haematopogon                        AACCAGATATATTCGCGATCAGCATTCTAGTGTATATTCTAATAATAATA
guentheri                           AACCAAACGTATTTACAATCAACATCCTAATATACATTCTCATGATAATT
quadrasi (Mindoro)                  AACCAAACACATTTACAATTAACATTTTAGTATATATCCTTATAACAATT
palawanensis                        AACCAAACACCTTCACAATTAATATTTTAGTGTATATTCTCATAATAATT
formosus                            AACCTAACCTGCTCATAGTGAGTATCCTGGTATATATTCTCATAATAGTA
sumatranus (Borneo)                 AACCAAACACATTCACAATCAATATTCTAATCTATATTCTCATAACAATT
sumatranus (Malay Pen.)             AACCAAACACATTCACAGCTAATATTCTAATCTATATTCTCATGACAATT
sumatranus (Sumatra)                AACCAAACACATTCACAGCTAATATTCTAATCTATATTCTCATGACAATC
volans (Java)                       AACCAAATACATTCACTATTAACATCCTAATTTATATTCTCATAACGATT
quadrasi (Sibuyan)                  AACCAAACACATTTACAATTAACATTTTAGTATATATTCTTATAACAATT
boschmai (Flores)                   AACCAAACATATTCACAATTAACATTCTAATCTACATTCTTATAACAATT
boschmai (Sumba)                    AACCAAACACATTCACAATTAACATTCTAATCTACATTCTTATAACAATT
boschmai (Lembata 1)                AACCAAACACATTCACAATTAACATTCTAATCTACATTATTATAACAATT
boschmai (Lembata 2)                AACCAAACACATTCACAATTAACATTCTAATCTACATTATTATAACAATT
boschmai (Sumbawa)                  AACCAAACACATTCACAATTAATATTTTAATCTACATTCTCATAACAATT
timoriensis (Roti)                  AACCAAACACATTCACAATTAATATTCTAATCTACATTCTTATAACAATT
timoriensis (Timor)                 AACCAAACACATTCACAATCAATATTCTAATCTACATTCTTATAACAATT
beccarii                            AGCCAAACATCTTCGTTATTAACATTTTAATATACATTCTAATAATAATC
biaro                               AACCAAACACATTTGCCATTAACATTCTAATATACATTCTCATAATAATT
"Tahulandang"                       AACCAAACACATTTGCCATTAACATTCTAATGTACATTCTCATAATAATT
bourouniensis                       AACCAAACATATTCGCCATTAATATTTTGGTATACATCCTCATAATAGTA
caerhulians                         AACCAAACACGTTTGCCATTAATATTTTAATATACATTCTCATAATAATT
spilonotus                          AACCAAACACATTTGCCATTAATATTTTAATATACATTCTCATAATAATT
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	660 670 680 690 700
Aphaniotis fuscus	CCTACATTTTTACTTATAATACTAACATCAACAAAAACACTACAAAACAT
Bronchocoela cristatella	CCTACCTTTATTCTACTAGCACAGACATCAACAAAAACACTCCAAGACAT
Japalura splendida	CCAACAATCCTAATAATAGAGCTCACTTCAACAAAAACACTACAAAACAT
Japalura tricarinata	CCGACATTCCTTCTCATAATTCTAACAACAACCAAGACATTACAAAATAT
maximus	GCAACATTTCCTCTTCTAGCTATAACAACAACAAAAACACTACAAAACCT
quinquefasciatus	CCAACATTCCCACTACTCGCCATAACAACAACCAAAACACTACAAAACCT
spilopterus (Luzon, SE Bicol Pen.)	CCAACATTCACCATCCTAGCTGCAATGGCCACCAAAACACTACAAAACCT
spilopterus (Luzon, C Bicol Pen.)	CCAACATTCACTATTCTAGCTGCAATGGCAACCAAAACACTACAAAACCT
spilopterus (Luzon, E coast)	CCAACATTTATGATCTTAACCACGACAACCACCAAAACACTTCAAAACCT
spilopterus (Polillo)	CCAACATTCATGATCTTAACCTCAACAGCCACCAAAACACTTCAAAACCT
spilopterus (Negros)	CCAACATTCACAATTTTAGCTGTAACAACCACTAAAACCCTACAAAACCT
spilopterus (Panay)	CCAACATTCACAATTTTAGCTGTAACAACCACTAAAACCCTACAAAACCT
spilopterus (Cebu)	CCAACATTCACAATTTTAACTGTAATAGCCACTAAAACACTACAAAACCT
spilopterus (Siquijor)	CCGACATTCACAATTCTAACTGTGGTAGCCACTAAAACGCTACAAAATCT
bimaculatus	CCAACATTCCCGATTCTAGCAACAATAGCCACAAAAACCCTACAAAACCT
blanfordi	CCGACATTCCCCCTTTTAGCAGGAATAACAACCAAAACACTACAAAACCT
indochinensis	CCAACATTTACCCTAATAGTAATATTAGCAACAAAAACATTACAAAACCT
cornutus	CCCACATTTACAATCTTAGCCACAACAACCACCAAAACACTACAAAACCT
cyanopterus (Mindanao)	CCAACATTCACAATCTTAGCTGCAATGGCCACCAAAACACTGCAAAATCT
reticulatus (Samar)	CCAACATTCACGATTTTAGCTGCAATGGCCACCAAGACACTGCAAAACCT
reticulatus (Bohol)	CCAACGTTCACGATCTTAGCTGCAATGGCCACCAAAACACTACAAAACCT
maculatus	CCAACATTCCACATTTTAACTATAACCGCCACTAAAACACTACAAAACCT
mindanensis	CCAACATTCCCACTTTTAGCCATAACAGCAACTAAAACACTACAAAACCT
obscurus	CCTACATTCCCCCTATTAGCAGTAATAATGATTAAAACACTGCAAAACCT
taeniopterus	CCTACATTCCCCCTATTAGCAACAATAATAGTTAAAACACTACAAAACTT
ornatus (Samar)	CCAACATTCACTATTTTAATCGTGATAGCCACCAAAACACTGCAAAATCT
ornatus (Bohol)	CCAACATTCACTATTTTAATTGCAATAGCCACCAAAACATTGCAAAACCT
fimbriatus (Borneo)	CCCACCTTTCCAATTTTAGCTATAACCGCAACCAAGACATTAAAAAACCT
cristatellus (Borneo)	CCAGCCTTCCCAATTTTAGCTGCGACCGCAACCAAAACAATACAAAACCT
fimbriatus (Malay Pen.)	CCCGCCTTTCCAATTTTGGGCATAACCGCAACCAAAACACTACAAAACCT
fimbriatus (Java)	CCCACATTTCCAATTTTGGCCATAACCGCAACCACGACACTAAAAAACCT
melanopogon	CCAACATTTCCACTTTTAGCAATAATAGCAACTAAAACACTACAAAACCT
haematopogon	CCAACATTCCCCCTATTAACCATGCTAGCAACCAAAACATTACAAAACTT
guentheri	CCAACATTCACAATCTTAGCTGCAATGGCTACCAAAACACTACAAAATTT
quadrasi (Mindoro)	CCAACATTCACAATCTTAGCCGCAATGGCCACCAAAACATTACAAAGCTT
palawanensis	CCAACATTCACAATCTTAGCTACAATATCCACCAAAACATTACAAAACCT
formosus	CCTACATTCCCACTATTAACAGTAATAATAGTTAAGACACTACAAAACCT
sumatranus (Borneo)	CCAACATTCACAATTTTAACTGCATCAGCCACCAAAACACTACAAAATCT
sumatranus (Malay Pen.)	CCAACATTTACAATTTTAATTGCGTCAGCCACCAAAACACTCCAAAATCT
sumatranus (Sumatra)	CCAACATTTACAATTTTAACTGCATCAGCCACCAAAACACTACAAAATCT
volans (Java)	CCAACATTCACAATTTTAACAGCAATAGCCACCAAAACATTACAAAACCT
quadrasi (Sibuyan)	CCAACATTCACAATCTTAGCCGCAATAGCCACCAAAACATTACAAAGCTT
boschmai (Flores)	CCAACATTCACAATTTTGGCCACAACAGCCACCAAGACATTACAAAATTT
boschmai (Sumba)	CCAACATTCACAATTTTGGCCACAACAGCCACCAAAACATTACAAAATTT
boschmai (Lembata 1)	CCAACATTTACAATTTTAGCTACAACAGCCACCAAGACATTACAAAACTT
boschmai (Lembata 2)	CCAACATTTACAATTTTAGCTACAACAGCCACCAAGACATTACAAAACTT
boschmai (Sumbawa)	CCAACATTCATAATCTTAGCTGCAACAGCCACCAAAACATTACAAAACCT
timoriensis (Roti)	CCAACATTCACAATTTTGGCTACAACAGCCACCAAGACATTACAAAACTT
timoriensis (Timor)	CCAACATTCACAATTTTGGCCACAACAACCACCAAGACATTACAAAACTT
beccarii	CCAACATTTCCAATATTAGCTGCAACATCCACAAAAACACTTCAAAACCT
biaro	CCAACATTTCCAATCTTAGCTGCAACATCCACAAAAACACTACAAAACCT
"Tahulandang"	CCAACATTTCCAATCTTAGCTGCAACATCCACAAAAACACTACAAAACCT
bourouniensis	CCAACCTTTCCAATCTTAGCCGCAACATCCACCAAAACACTTCAAAACCT
caerhulians	CCAACATTTCCAATCTTAGCCGCAACATCCACAAAAACACTACAAAACCT
spilonotus	CCAACATTTCCAATCTTAGCCGCAACATCCACAAAAACACTACAAAACCT

	710 720 730 740 750
Aphaniotis fuscus	AGCAATTATATGAACTACATCACCAACAATATCAATAATAATAACTATCA
Bronchocoela cristatella	GACAACCATATGAACAACCTCCCCAACATCATCTATCACACTAACTTTTC
Japalura splendida	GACAACCTCCTGATCAACATCTCCTACCACCACCACCATATTAGCACTTC
Japalura tricarinata	ATCAACCACTTGAACCACATCTCCAACTGCAACCACAACACTAACAATCT
maximus	ATCAACCTCTTGAACTATCTCTCCGATCGGAACCACAACACTGATAATCT
quinquefasciatus	ATCAACCTCCTGAACTACATCCCCAACCGGAACCACAATACTAATAATTC
spilopterus (Luzon, SE Bicol Pen.)	TTCAACATCTTGAACCACCTCACCAACCGGAACAACCATCCTAATAATCC
spilopterus (Luzon, C Bicol Pen.)	TTCAACATCTTGAACTACCTCTCCAACCGGAACAACCATGCTAATAATCC
spilopterus (Luzon, E coast)	ATCAGCCTCTTGAACCTCTTCACCAGTGGGAACAACTATACTAATGATCT
spilopterus (Polillo)	GTCAGCCTC?TGAACCTCTTCACCAATAGGAACAACTATACTAATGATTC
spilopterus (Negros)	ATCAGCATCTTGGACCACCTCACCAACAGGAACAACCATACTTATAATTT
spilopterus (Panay)	ATCAGCATCTTGGACCACCTCACCAACAGGAACAACCATACTTATAATTC
spilopterus (Cebu)	GTCAGCATCTTGAACCACCTCACCAACAGGAACAACCATACTTATAATCC
spilopterus (Siquijor)	ATCAGCATCTTGAACCACCTCACCAACAGGGACAACCATACTTATAGTCC
bimaculatus	ATCCTCATCTTGAACCACATCCCCTATCGGATCAACAATGCTAATAATTC
blanfordi	GTCAGCCTCCTGAACTACATCCCCAACAGGGACTACAACACTAATAATCC
indochinensis	ATCAACCTCCTGAACTACATCTCCAACCGGAACCACACTATTAATAATCT
cornutus	GTCAGCATCTTGAACTACCTCACCAATCGGAACAACCATGTTAATAATCC
cyanopterus (Mindanao)	ATCAACATCTTGAACGACCTCACCAACCGGAACAACCACTCTAATAATAC
reticulatus (Samar)	GTCAACATCTTGGACGACCTCACCAACCGGAACAACCATTCTAATAATAC
reticulatus (Bohol)	GTCAGCCTCTTGGACGACCTCACCAACCGGAACAGCCGTTCTAATGATAC
maculatus	TTCATCCTCCTGAACTACCTCACCAACCGGAACCGTAACACTAATAATTC
mindanensis	GTCAACCTCTTGAACCACATCTCCAATTGGAACTACAACACTAATAATCT
obscurus	TTCAACTTCCTGAACTACATCCCCAACCGGGACCACAACACTAATGATCT
taeniopterus	ATCTACTTCCTGAACCACGTCCCCAACTGGAACCACAACACTAATGATCT
ornatus (Samar)	ATCAACATCTTGAACCACCTCACCAACCGGAACAACCATATTAATGATCT
ornatus (Bohol)	ATCAACATCTTGAACCACCTCACCAACCGGGACAACCATATTAATGATTT
fimbriatus (Borneo)	CTCAGCCTCCTGAACAACATCCCCAGCCGGAACTACAACATTAATAATTC
cristatellus (Borneo)	GTCAACCTCATGAACAACATCCCCAACCGGAACTACAACACTAATGATCC
fimbriatus (Malay Pen.)	ATCAACCTCCTGAACAACATCCCCAACAGGAACTACAACATTAATAATTC
fimbriatus (Java)	ATCAACCTCCTGAACAACATCCCCAACAGGAACTACAACATTAATAATTC
melanopogon	GTCAGCCTCATGAACCACATCTCCAACCGGAACTACAACACTAATAATTT
haematopogon	ATCGACCTCATGAACTACATCTCCAACCGGAGCCACACTATTAATAACCT
guentheri	ATCAGCATCCTGAACCACCTCACCAACCGGAACAACCTTATTAATAGTCT
quadrasi (Mindoro)	ATCAGCATCTTGAACTACCTCACCAATCGGAACAACCATACTAATAATTT
palawanensis	ATCAACATCTTGAACTACCTCACCAATCGGAACAACCATATTAATGATTC
formosus	TTCAACCTCCTGAACCACATCCCCAACCGGAACTACAACGCTAATGATCT
sumatranus (Borneo)	ATCAACATCTTGAACTACCTCACCAACCGGAACAACAATACTAACAATTC
sumatranus (Malay Pen.)	ATCAACGTCCTGAACTACCTCACCAACCGGAACAACAGTACTAATAATTC
sumatranus (Sumatra)	ATCAACGTCTTGAACTACCTCACCAACCGGAACAACAATACTAATAATTC
volans (Java)	ATCAGCATCTTGAACCACCTCACCAACCGGAACAACAATACTAATAGTAC
quadrasi (Sibuyan)	ATCAGCATCTTGAACTACCTCACCAACCGGAACAACCGTACTAATAATTC
boschmai (Flores)	ATCAGCATCTTGAACTACCTCCCCGGTTGGAACAACCATACTAATAATAC
boschmai (Sumba)	ATCAGCATCTTGAACTACTTCCCCAGTTGGAACAACCATACTAATGATAT
boschmai (Lembata 1)	ATCAGCATCTTGAACTACTTCTCCAGTTGGAACAACAATGCTAATAGTAC
boschmai (Lembata 2)	ATCAGCATCTTGAACTACTTCTCCAGTTGGAACAACAATGCTAATAGTAC
boschmai (Sumbawa)	ATCAGCATCTTGAACTACCTCCCCAATTGGAACAACAATACTAATGGTAC
timoriensis (Roti)	ATCAGCATCTTGAACTACCTCCCCAGTTGGAACAACCATACTAATAATAC
timoriensis (Timor)	ATCAGCATCTTGAACTACCTCCCCAGTTGGGACAACCATACTAATAATAC
beccarii	ATCAACATCTTGAACCACATCACCCGTCGGAACCACAATATTAATGGCCC
biaro	ATCAACATCTTGAACCACATCACCACTCGGAACCACAATATTAATAGGCC
"Tahulandang"	ATCAGCATCTTGAACCACATCACCACTCGGAACCACAATATTAATAGGCC
bourouniensis	TTCAACATCTTGAACCACTTCACCACTCGGAACAACAATATTAATGGTCT
caerhulians	ATCAACATCTTGAACCACATCACCGTTAGGGACCACAATATTAATAGGCC
spilonotus	ATCAACATCTTGAACCACATCACCACTCGGAACCACAATATTAATAGGCC

	760 770 780 790 800
Aphaniotis fuscus	TTTTACTTTCAATAGCCGGTTTACCACCACTGACAGGTTTCGTACCAAAA
Bronchocoela cristatella	TATTATTATCAATAGCCGGACTTCCACCATTAACAGGATTCATGCCAAAA
Japalura splendida	TACTTCTATCAACAGCCGGCCTACCACCTCTTACAGGATTCATTCCAAAA
Japalura tricarinata	TATTGCTCTCAACAGCCGGACTTCCACCACTCACCGGGTTTTTACCAAAA
maximus	TACTTCTATCAATTGCCGGACTTCCCCCCCTCACAGGATTTTTACCAAAA
quinquefasciatus	TACTACTATCAATTGCCGGACTCCCACCTCTCACAGGATTCCTGCCAAAA
spilopterus (Luzon, SE Bicol Pen.)	TATTATTATCAATTGCTGGACTCCCACCTCTCACAGGCTTTTTGCCAAAG
spilopterus (Luzon, C Bicol Pen.)	TATTATTATCAATTGCTGGACTCCCACCTCTCACAGGCTTTTTGCCAAAG
spilopterus (Luzon, E coast)	TACTATTATCAACTGCTGGACTTCCACCACTTACAGGATTCCTGCCAAAA
spilopterus (Polillo)	TACTGCTATCAACTGCCGGACTTCCTCCACTTACAGGATTTCTGCCAAAA
spilopterus (Negros)	TACTACTATCAATTGCCGGACTTCCTCCACTCACAGGTTTCCTACCGAAA
spilopterus (Panay)	TACTACTATCAATTGCCGGACTTCCTCCACTCACAGGTTTCCTGCCAAAA
spilopterus (Cebu)	TGTTACTATCAATTGCTGGACTTCCTCCACTTACAGGCTTCCTGCCAAAA
spilopterus (Siquijor)	TATTACTATCAGTTGCCGGACTCCCTCCACTTACAGGCTTTCTGCCTAAA
bimaculatus	TACTACTATCTATTGCCGGACTTCCACCACTCACTGGATTTTTACCAAAA
blanfordi	TTCTACTATCAATTGCCGGACTCCCCCCACTCACAGGATTCCTGCCTAAA
indochinensis	TACTACTATCAGTTGCCGGCCTTCCACCACTCACAGGGTTTTTACCAAAA
cornutus	TACTACTGTCAATTGCCGGACTTCCACCACTCACAGGCTTCCTACCAAAA
cyanopterus (Mindanao)	TACTGTTATCGACTGCCGGCCTTCCACCACTCACAGGCTTCCTACCAAAA
reticulatus (Samar)	TACTGCTATCAACTGCCGGCCTCCCACCACTCACAGGCTTCCTACCAAAA
reticulatus (Bohol)	TACTACTATCAACTGCCGGCCTCCCGCCACTCACAGGCTTCCTCCCAAAA
maculatus	TTTTACTATCCATTGCCGGACTCCCCCCACTTACAGGATTCCTACCAAAA
mindanensis	TACTACTATCAATTGCCGGACTCCCGCCACTCACAGGGTTTTTACCAAAA
obscurus	TATTATTATCAATTGCCGGGCTCCCCCCCCTCACTGGATTTCTGCCAAAA
taeniopterus	TATTACTATCAATTGCCGGACTCCCCCCCCTCACTGGATTTTTACCAAAA
ornatus (Samar)	TATTATTGTCTATTGCTGGACTCCCACCCCTTACGGGCTTCCTCCCAAAA
ornatus (Bohol)	TATTACTATCTATTGCTGGACTCCCCCCTCTTACAGGCTTTCTCCCAAAA
fimbriatus (Borneo)	TACTACTATCTATTGCCGGCCTCCCCCCCCTCACAGGATTTTTACCAAAA
cristatellus (Borneo)	TGTTATTATCAATTGCCGGACTCCCCCCCCTCACAGGATTTCTGCCAAAA
fimbriatus (Malay Pen.)	TACTACTATCAATTGCCGGACTCCCCCCCCTCACAGGATTTCTACCAAAA
fimbriatus (Java)	TATTACTATCAATTGCCGGGCTCCCCCCCCTCACAGGATTTCTACCAAAA
melanopogon	TGCTACTATCAATTGCAGGATTACCCCCACTTACAGGATTCCTACCAAAA
haematopogon	TACTGCTCTCAATTGCCGGACTCCCACCACTTACAGGGTTTCTCCCAAAA
guentheri	TACTACTATCAATTGCCGGGCTACCCCCACTCACAGGCTTTCTACCAAAA
quadrasi (Mindoro)	TATTACTGTCAATTGCCGGGCTTCCCCCACTCACAGGCTTCCTACCTAAA
palawanensis	TATTACTATCAACTGCCGGATTACCCCCACTTACAGGCTTCCTACCAAAA
formosus	TATTATTATCAATTGCCGGACTCCCCCCCCTCACTGGATTTTTGCCAAAA
sumatranus (Borneo)	TACTCCTATCAATTGCCGGTCTACCCCCACTCACAGGCTTCATGCCAAAA
sumatranus (Malay Pen.)	TACTCCTATCAATTGCCGGCCTACCCCCACTCACAGGCTTCATGCCAAAA
sumatranus (Sumatra)	TACTTCTATCAATTGCCGGCTTACCCCCACTCACAGGCTTCATGCCAAAA
volans (Java)	TACTTCTATCAATTGCCGGACTACCCCCACTCACAGGCTTCATGCCAAAA
quadrasi (Sibuyan)	TACTGTTATCAATTGCCGGTCTTCCTCCACTCACAGGCTTCTTACCTAAA
boschmai (Flores)	TATTTTTATCAATTGCCGGACTACCACCACTCACAGGATTCATACCAAAA
boschmai (Sumba)	TGTTCCTATCAATTGCCGGACTACCCCCACTTACAGGCTTCATGCCAAAA
boschmai (Lembata 1)	TATTTCTATCAATTGCCGGACTACCTCCACTCACAGGGTTCATGCCAAAA
boschmai (Lembata 2)	TATTTCTATCAATTGCCGGACTACCCCCACTCAC????????????????
boschmai (Sumbawa)	TATTTCTATCAATTGCCGGGCTGCCCCCACTCACAGGCTTCATGCCAAAA
timoriensis (Roti)	TATTCCTATCAATTGCCGGACTCCCACCACTCACAGGCTTTATGCCAAAA
timoriensis (Timor)	TATTCCTATCAATTGCCGGACTACCCCCACTCACAGGCTTTATGCCAAAA
beccarii	TACTCCTATCAATTGCTGGACTCCCACCACTCACGGGGTTCTTACCAAAA
biaro	TACTCCTATCAATTGCAGGACTTCCCCCCCTCACAGGCTTTTTACCAAAA
"Tahulandang"	TACTCCTATCAATTGCCGGACTTCCCCCCCTCACAGGCTTTTTACCAAAA
bourouniensis	TACTTCTTTCAATTGCCGGACTTCCACCACTGACAGGATTCTTACCAAAA
caerhulians	TACTCCTATCAATTGCCGGACTCCCCCCCCTCACAGGCTTTCTACCAAAA
spilonotus	TACTCCTATCAATTGCCGGACTCCCACCACTCACAGGCTTTTTACCAAAA

	810 820 830 840 850
Aphaniotis fuscus	CTAATAATCCTAAACGAACTAGTAACACAAAACCTAACTACAACCGCCAT
Bronchocoela cristatella	CTACTAATTTTAAACGAACTTATCTCACAAAATATAACAGCTATCTCCAT
Japalura splendida	CTACTAATCTTAAATGAACTAGTGACCCAAAACCTTACACCTACTGCTGT
Japalura tricarinata	CTACTAATTTTAAACGAACTAGTAACACAAAAACTCACACCCATTGCCGT
maximus	CTACTCATTTTAAATGAACTTGTAATGCATAACCTCACACCACTTGCCAC
quinquefasciatus	CTGCTCATTTTAAATGAACTTGTAATACAAAACCTCACACCAATCGCCAC
spilopterus (Luzon, SE Bicol Pen.)	CTGCTCATTCTAAACGAACTCGTAATGCAAACCCTCACCCCCATCGCCGT
spilopterus (Luzon, C Bicol Pen.)	CTGCTCATTCTAAACGAACTCGTAATACAAACCCTCACCCCCATCGCCGT
spilopterus (Luzon, E coast)	TTACTCATTTTAAACGAACTAGTAACACAAACCTTGACACCAATTGCCAC
spilopterus (Polillo)	TTACTAATTTTAAACGAACTAGTAACACAAGCCTTAACACCAATCGCCAC
spilopterus (Negros)	CTACTTATTTTAAACGAACTAGTAACACAAACCCTAACACCCCTCGCCAC
spilopterus (Panay)	CTACTTATTTTAAACGAACTAGTAACACAAACCCTAACACCCCTCGCCAC
spilopterus (Cebu)	TTACTTATTTTGAACGAATTAGTAACACAAACCCTAACACCCCTTGCCAC
spilopterus (Siquijor)	CTACTAATTTTGAATGAATTAGTAACACAAACCCTAACACCCCTCGCCAC
bimaculatus	CTACTTATCCTAAATGAACTCGTAGCACAAACCCTCACACCAATTGCCGC
blanfordi	CTACTCATTCTAAATGAACTTGTAACCCAAAATCTCACGCCAATCGCCAC
indochinensis	CTACTAATTCTAAACGAACTTGTAACACAAAACCTCACCACAATCGCCAC
cornutus	CTACTCATTTTAAACGAATTAGTAACACAAACCCTAACTCCCATCGCCAC
cyanopterus (Mindanao)	TTGCTTATTCTAAATGAACTAGTAACACAAACCCTTACACCCATCGCCGT
reticulatus (Samar)	TTGCTTATCTTAAATGAGCTAGTAGCACAAACCCTCACACCCATCGCCAT
reticulatus (Bohol)	TTGCTTATCTTAAATGAGCTAGTAACACAGACCCTCACACCTATCGCCAT
maculatus	TTACTTATTTTAAACGAACTTGTAACGCAGAACCTCACACCAATTGCCAC
mindanensis	CTACTTATTTTAAATGAACTTGTATCACAAAACCTTACCCCAATCGCCAC
obscurus	CTCCTCATCTTAAACGAACTTGTAGCACAAAACCTCACACCAATCGCCAC
taeniopterus	CTCCTCATCTTAAACGAACTTGTAACACAAAACCTCACACCAATCGCCAC
ornatus (Samar)	TTGCTCATCCTAAACGAACTTGTGGCACAAACCCTAATACCCATCGCCAC
ornatus (Bohol)	TTACTCATCCTAAACGAACTTGTAGCACAGACTCTAGTACCCATCGCCAC
fimbriatus (Borneo)	CTGCTGATCCTAAACGAACTTGTAATGCAAAACCTCACACCAATTGCCAC
cristatellus (Borneo)	CTGCTGATTATTAACGAACTTGTAATGCAAGGCCTCACACCAATCGCCAC
fimbriatus (Malay Pen.)	CTGCTAATCCTAAACGAACTTGTTATGCAAAACCTCACACCAATTGCCAC
fimbriatus (Java)	CTACTAATCCTAAACGAACTTGTAATTCAAAACCTTACACCAATTGCCAC
melanopogon	CTCTTAATTTTAAACGAGCTTGTGGCACAAAACCTCACACCAATTGCCAC
haematopogon	CTCCTAATCCTAAATGAACTTGTAATACAAAATCTCACGCCAATCGCTGC
guentheri	CTTCTCATCTTAAACGAACTCGTAACACAAACCCTAACACCCATCGCCAT
quadrasi (Mindoro)	TTACTTATTCTAAACGAACTCGTAGCACAAACCCTCACACCCATCGCTAT
palawanensis	TTATTAATTCTAAATGAACTCCTAGCACAAACCCTAACACCCATTGCCAC
formosus	CTCCTCATCTTAAACGAACTCGTAGCACAAAACCTCACACCAGTCGCCAC
sumatranus (Borneo)	CTACTTATCCTAAATGAACTCGTAATACAAACCCTCACACCTCTTGCTAT
sumatranus (Malay Pen.)	TTACTTATCCTAAATGAACTCGTAATACAAACCCTCACACCACTTGCCAT
sumatranus (Sumatra)	CTGCTTATCCTAAACGAACTCGTAATACAAACCCTCACACCTCTTGCCAT
volans (Java)	CTACTCATCCTAAATGAACTCGTAACACAAACCCTCACACCCCTTGCCAT
quadrasi (Sibuyan)	CTGCTCATTTTAAACGAACTCGTAGCACAAACTCTCACACCCATCGCTAC
boschmai (Flores)	TTGCTTATCCTAAATGAACTTGTAACACAAACCCTCACACCTCTTGCCAC
boschmai (Sumba)	TTGCTTATCCTAAATGAACTTGTAACACAAACCCTCACACCTATTGCCAT
boschmai (Lembata 1)	TTACTTATTCTAAATGAACTTGTAACACAAACCCTCACACCCCTTGCTAT
boschmai (Lembata 2)	??
boschmai (Sumbawa)	TTACTTATCCTAAATGAACTAGTAACACAAACCCTTACACCCCTTGCCGT
timoriensis (Roti)	TTGCTTATTCTAAATGAACTCGTAACACAAACCCTCACACCTCTTGCCAT
timoriensis (Timor)	TTGCTTATTCTAAATGAACTCGTAACACAAACCCTCACACCTCTTGCCAT
beccarii	CTTCTCATCCTAAATGAACTTGTAACACAAGCCCTTACACCAATCGCCGC
biaro	CTTCTCATCCTAAACGAACTCGTAACACAAGCCCTCACGCCAATCGCAGC
"Tahulandang"	CTTCTCATCCTGAACGAACTCGTAACACAAGCCCTCACGCCAATCGCAAC
bourouniensis	CTCCTGATTTTAAACGAACTTGTAATGCAAGCCCTTACCCCAATTGCTGC
caerhulians	CTTCTCATTCTAAACGAACTCGTAACACAAGCCCTCACGCCAGTCGCAGC
spilonotus	CTTCTCATCCTAAACGAACTCGTAACACAAGCCCTTACACCTGCCGCAGC

	860 870 880 890 900
Aphaniotis fuscus	TATTACAACAATAACCTCCCTACTAACCTTAGTATTCTACCTACGAATTA
Bronchocoela cristatella	TGCCACAACAATGGCCTCCCTATTATCACTAATTTTTTACCTACGAATCA
Japalura splendida	GGGTGCAGCCACAGCTTCACTCCTAAGTATAATCTTTTATTTACGCATGG
Japalura tricarinata	CATTTCCACAATGACCACCCTATTGAACTTAACCTTTTACCTGCGAACAG
maximus	CATGGCAGCAATGACATCCCTATTAAACCTCGTATTCTACCTACGAACCG
quinquefasciatus	CCTAACAGCAATAACATCCCTACTAAACCTCGTATTTTACCTACGAACCG
spilopterus (Luzon, SE Bicol Pen.)	CATTACAATAATGACCTCCCTACTAAACCTCGTATTTTACCTACGAGCCA
spilopterus (Luzon, C Bicol Pen.)	CATTACAATAATGACCTCCCTACTAAACCTCGTATTTTACCTACGAGCCA
spilopterus (Luzon, E coast)	CATCACAATAATAACTTCCTTGCTAAATCTTGTATTTTACCTCCGGGCCA
spilopterus (Polillo)	CATCACAATAATAACTTCCTTGCTAAATCTTGTATTTTACCTTCGGGCCA
spilopterus (Negros)	TATTACAATAATAACCTCCTTATTAAACCTCATGTTTTACCTACGAACCA
spilopterus (Panay)	TATTACAATAATAACCTCCTTATTAAACCTCATGTTTTACCTACGAACCA
spilopterus (Cebu)	CATTACAATAATAACCTCTCTACTAAATCTAATGTTTTACCTACGAACCA
spilopterus (Siquijor)	CATTACAATAATAACCTCCTTATTAAACCTTATATTTTACCTGCGAACCA
bimaculatus	TATCACTGCAATAACCTCCCTACTAAACCTAGTGTTTTACCTACGAACTG
blanfordi	CTTTACAGCAATAACATCCCTATTAAACCTAGTATTTTACCTGCGAACCG
indochinensis	TATGACAGCAATAACATCCCTGCTAAACCTAGTATTCTACCTTCGAACAG
cornutus	CATTGCGACAATAACTTCCCTATTAAACCTTGTGTTTTACCTACGAGCTA
cyanopterus (Mindanao)	CATCACAGCACTGACCTCCTTGATGACTCTAGTATTTCACCTGCGAACTG
reticulatus (Samar)	CATCACAACGCTGACCTCCCTGCTAACTCTAGTATTTTACCTGCGAACCG
reticulatus (Bohol)	CATCACAACACTGACCTCCTTGCTGACTCTAGTATTTTACCTGCGAACCG
maculatus	CATGACAGCAATAACCTCCCTATTAAACCTGATCTTTTACCTTCGAACCA
mindanensis	TATCACGGCAATTACATCTCTACTAAACCTCGTATTCTACCTACGAACCG
obscurus	CATAACTGCAATTACATCCCTTTTAAACCTGGTGTTTTACCTACGAACCG
taeniopterus	TATAACTGCAATTACATCCCTTTTAAACCTCGTATTTTACCTACGAACCG
ornatus (Samar)	CATCACAACCATAACTTCTCTGTTAAATCTCGTATTTTATTTACGAGCCA
ornatus (Bohol)	CATCACAACCATAACCTCCCTATTAAACCTCGTATTTTATTTGCGGGCCA
fimbriatus (Borneo)	CGTAACAGCAATGACCTCCCTATTAAACCTCGTATTTTACCTACGAGCCA
cristatellus (Borneo)	CGTAACAGCAATAACCTCTCTACTAAACCTCGTCTTTTACCTACGAGCCA
fimbriatus (Malay Pen.)	CGTGACAGCAATAACCTCCCTACTGAACCTCATGTTTTACCTGCGAACCA
fimbriatus (Java)	CGTGACAGCAATAACCTCCCTACTAAACCTCATATTCTACCTGCGAGCCA
melanopogon	CATAACAGCAATAACATCCCTACTAAGCCTAGCATTCTATCTACGAACCG
haematopogon	TTTAACAGCAATAACATCCCTATTAAACTTAGTATTCTACCTTCGAACCA
guentheri	TGTCACAACAATAACTTCTCTATTAAACCTCGTGTTTTATCTGCGGGCCA
quadrasi (Mindoro)	TATTACAACAATAACCTCCCTACTAAATCTGATATTTTACCTACGAGCCA
palawanensis	CATTACAACAATGACTTCTCTCTTAAACCTTGTTTTCTATCTACGAACCA
formosus	CATAACCGCAATTACATCCCTTTTAAACTTGGTATTTTACCTACGAACCG
sumatranus (Borneo)	CATCACAACTATAACCTCCCTATTAAACCTCGTATTTTACCTACGAACCA
sumatranus (Malay Pen.)	CATTACAACTATGACCTCCCTATTAAACCTCGTATTTTACTTACGAACCA
sumatranus (Sumatra)	CATTACAACCATGACCTCCCTATTAAACCTCGTATTTTACTTACGAACCA
volans (Java)	CATTACAGCTATAACCTCCCTATTAAACCTCGTATTTTACCTACGAACCA
quadrasi (Sibuyan)	TATTGCAACAATGACCTCCCTACTAAATCTGATGTTTTACTTACGAGCCA
boschmai (Flores)	CATTACAGCTATAACCTCCCTATTAAATCTAGTGTTCTATCTACGAACCG
boschmai (Sumba)	CATTACAGCCATAACCTCCCTATTAAACTTAGTGTTCTACCTACGAACCG
boschmai (Lembata 1)	CATTACAACTATAACTTCCCTATTAAACCTAGTATTCTACCTACGAACCG
boschmai (Lembata 2)	??
boschmai (Sumbawa)	CATTACAGCTATGACCTCCCTACTAAATCTCGTGTTCTACTTACGAACAA
timoriensis (Roti)	CATTACAGCTATAACCTCCCTATTGAACCTAGTATTCTACCTACGAACCG
timoriensis (Timor)	CATTACAGCTATAACCTCCCTATTAAACCTAGTATTCTACCTACGAACCG
beccarii	TATCACTGCAATAACCTCTATGCTAAACCTAGTATTTTACTTGCGAGCTA
biaro	TATTACCGCAATAACCTCAATACTCAACCTAGTATTTTACCTGCGAGCCA
"Tahulandang"	TATCACCACAATAACCTCAATACTCAACCTAGTATTTTACCTGCGAGCCA
bourouniensis	CATCACAGCAATAACCTCCATATTAAACCTAATGTTTTACCTACGAGCCA
caerhulians	TATTACCGCAATAACCTCAATACTTAACCTAGTATTTTACCTGCGAGCCA
spilonotus	TATTACCGCAATAACCTCAATACTTAACCTAGTATTTTACCTGCGGGCCA

	910 920 930 940 950
Aphaniotis fuscus	CATATTTAACTACATTATTAAATCCTCCAAGCTCATCTACATCTACAACA
Bronchocoela cristatella	GCTACCTAACCTCACTACTCAATACACCCAGCTCCTCAACATCAACAACA
Japalura splendida	CCTACCTAACGGCCCTGCTAAACTCTCCTGGCTCTGCCACATCAACGATG
Japalura tricarinata	CATACATGACAACATTACTTAACTCTCCTGCCTCTGCCACATCAACAATA
maximus	CGTACATAACTACGCTTCTCACTTCTCCTGGCTCTGCCACATCATCAATG
quinquefasciatus	CGTATATAACTACGCTTCTTACTTCTCCTGGCTCTGCCACATCATCCATG
spilopterus (Luzon, SE Bicol Pen.)	TGTACATGACTACACTTCTTAACTCTCCTGCTTCTGCCACAGCATCCATA
spilopterus (Luzon, C Bicol Pen.)	TGTACATGACTACACTTCTTAACTCTCCTGCTTCTGCCACAGCATCCATA
spilopterus (Luzon, E coast)	CATACATGACTACGCTTCTAAATTCTCCTGGCTCTGCCACAGCATCCATA
spilopterus (Polillo)	CATACATGACTACGCTTCTAAACTCTCCTGGCTCTGCCACAGCACCAATA
spilopterus (Negros)	TATACATAACCACACTTCTTAATTCTCCTGGCTCTGCCACAACATCCATA
spilopterus (Panay)	TGTACATAACCACACTTCTTAATTCTCCTGGCTCTGCCACAACATCCATA
spilopterus (Cebu)	TGTACATGACCACACTTCTTAATTCTCCTGGCTCTGCCACAACAGCCATA
spilopterus (Siquijor)	TGTACATGACCACACTTCTTAATTCTCCTGGCTCTGCCACAACATCCATA
bimaculatus	CATACATAACCACACTTCTTAATTCTCCTGGCTCTGCCACATCATCAATA
blanfordi	CATACATAACCACCCTCCTTACTTCTCCGGGCTCTGCCACATCATCCATA
indochinensis	CATATATAACTACGCTCCTTACTGCCCCTGGCTCTGCCACATCATCAATA
cornutus	TGTACGTAACAACACTTCTTAATTCTCCTGACTCTGCCACAGCATCCATA
cyanopterus (Mindanao)	TGTATATAACCGCGCTCCTTAACCCCCCTGCTTCTACCACATCAGCCATA
reticulatus (Samar)	TATATATAACCACACTTCTTAACCCCCCTGCTTCTACCACATCCGCCACA
reticulatus (Bohol)	TATACATAACCACACTTCTTAACCCCCCTGCTTCTACCACATCAACCGCA
maculatus	CGTACATAACTGCACTTCTAAACACCCCAGGCTCTACCACATTATCTATA
mindanensis	CGTACATAACTACGCTTCTAACCTCCCCTGGCTCTGCCACATCATCCATG
obscurus	CGTACATAACCACGCTTCTTACTTCTCCTGGCTCTGCCACAGCATCCATA
taeniopterus	CGTATATAACTACGCTTCTTACTTTTCCGGGCTCTGCCACGGCATCCATA
ornatus (Samar)	TGTACATAACCACACTTCTTAATTCTCCTGCCTCTGCCACAGCGCCTATA
ornatus (Bohol)	TGTACATAACCACGCTTCTTAATTCTCCTGGCTCTGCCACAGCATCCATG
fimbriatus (Borneo)	CGTATATGACTACACTTCTTAATTCTCCTGGCTCTGCCACATCAGCCATA
cristatellus (Borneo)	CATATATGACTACACTTCTTAATTCTCCTGGCTCCGCCACTTCAACCATG
fimbriatus (Malay Pen.)	CCTACATGACTACGCTTCTAAATTCTCCTGGCTCTGCCACATCAACTATG
fimbriatus (Java)	CCTACATAACCACGCTGCTAAATTCTCCTGGCTCTGCCACATCAACCATG
melanopogon	CATACATAACCACACTTATCACCTCTCCTGCCTCTACTACATCATCCATG
haematopogon	CGTACATAACCACACTACTCACCTCTCCTGGCTCTGCCACATCATCCATG
guentheri	TATACATGACTACGCTTCTTAATTCTCCTGCCTCTGCCACAGCATCCATG
quadrasi (Mindoro)	TGTACATGACAACCCTTCTTAATTCCCCTGGCTCTGCCACAGCATCCATA
palawanensis	TGTACATGACCACACTTCTTAATTCTCCTGGCTCTGCCACAGCATCCATA
formosus	CGTACATAACCACACTTCTTACTTCTCCTGGCTCTGCCACAGCACCCATT
sumatranus (Borneo)	CATACATAACTTCACTTCTTAACTCTCCTGGCTCTGCCACAGCATCCATA
sumatranus (Malay Pen.)	CATACATAACTTCACTTCTTAACTCTCCTGGCTCTGCCACAGCATCCATA
sumatranus (Sumatra)	CATACATAACCTCACTTCTTAATTCTCCTGCCTCTGCCACAGCATCCATA
volans (Java)	CATACATAACAACACTTCTTAACTCGCCTGACTCTGCCACAGCATCCATA
quadrasi (Sibuyan)	TATACATAACTACACTTCTTAATTCCCCTGGCTCTGCCACAACATCCATA
boschmai (Flores)	TATACATAACTACACTTCTTAATTCACCTGACTCTGCCACAGCATCCATA
boschmai (Sumba)	TATACATAACTACACTTCTTAATTCACCTGACTCTGCCACAGCATCCATA
boschmai (Lembata 1)	TGTACATAACTACACTTCTTAGTTCACCTGACTCTGCCACAGCATCCATA
boschmai (Lembata 2)	??
boschmai (Sumbawa)	TATACATGACTACACTTCTTAATTCTCCTGACTCTGCCACAGCATCCATA
timoriensis (Roti)	TATACATAACTACACTTCTTAATTCACCTGACTCTGCCACAACATCCATA
timoriensis (Timor)	TATACATAACTACACTCCTTAATTCACCTAACTCTGTCACAGCATCCATA
beccarii	CATATATAACTGCGCTCCTTAATTCCCCTGGCTCTGCCACAGCATCCATA
biaro	CGTACATAACTACAATTCTTAATTCCCCTGGCTCTGCCACGGCATCCATA
"Tahulandang"	CGTACATAACTACAATTCTTAATTCCCCTGGCTCTGCCACGGCATCCATA
bourouniensis	CATACATAACTGCACTCCTTAGTCCTCCTAGCTCTACCACAACATCAATA
caerhulians	CATACATAACTACAATTCTTAATTCCCCTGGCTCTGCCACAGCATCCATG
spilonotus	CATACATAACTACGATTCTTAATTCCCCTGGCTCTGCCACAGCAGCCATG

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                                           960       970       980       990      1000
                                             .         .         .         .         .
Aphaniotis fuscus                   AAATGACGACAAAAAATTAACGGCACAAAAATAGTAATTTTCTCACCAAC
Bronchocoela cristatella            AAATGACGACAAAACATAAACAACCTAAAAATAACCCAAATAGCACCAAC
Japalura splendida                  AAGTGACGACAAAAAATTG---AAACCAAAACAACAATCCTAACACCAAC
Japalura tricarinata                AAATGACGACAGAACCCTAATAAAATCAAACCAACAATACTAGCCCCAAC
maximus                             AAATGGCGACACCCAATTACCAAAACCAAAGCAACAATATTCGCACCAAC
quinquefasciatus                    AAATGGCGCTACCCAATCACCAAAACCAAAGCAACCCTACTCACCCCAGC
spilopterus (Luzon, SE Bicol Pen.)  AAATGACGTTGCCCAACTCCAAAAACCAACTCAACAATATTAGCACCTAC
spilopterus (Luzon, C Bicol Pen.)   AAATGACGTTGCCCAACTCCAAAAACCAACTCAACAATGTTAGCACCTAC
spilopterus (Luzon, E coast)        AAGTGGCGCCACCCAATTCAAAAAACAAGCTCAATGATACTCACTCCCAC
spilopterus (Polillo)               AAATGACGCCACCCAAT??AAAAAACTCACTCAATAGTACTCGCACCCAC
spilopterus (Negros)                AAATGACGTTGCCCGACCCCAAAAACCAACTCAACTATATTTGCACCTAC
spilopterus (Panay)                 AAATGACGTTGCCCGACCCCAAAAACCAACTCAACTATATTTGCACCTAC
spilopterus (Cebu)                  AAATGACGTTGCCCAACTCCAAAAACCAACTCAACAGTACTTGCACCCAC
spilopterus (Siquijor)              AAATGACGTTGCCCAACCCCAAAAACCAACTCAACAATATTTGCACCCAC
bimaculatus                         AAATGGCGATTCCCAATCACCAAGACTAACTCAACAATACTTATACCTAC
blanfordi                           AAATGGCGTCGCCCAATCACCAAGACCAAGGCAACAATACTCGCACCAAC
indochinensis                       AAGTGGCGCCACCCAATCACCAAAACCAAAACAACCATACTGGCACCAAC
cornutus                            AAATGACGTTGGCCAACTCCAAAAACCAACTCAACAATACTCGCACCCAC
cyanopterus (Mindanao)              AAATGACGCTGGCCCGTCACAAAAACTAACTCAACAGTACTCGCCCCCCT
reticulatus (Samar)                 AAATGACGCTGACCCCTCACAAAAACTAATTCAACAATGCTCGCCCCCCT
reticulatus (Bohol)                 AAATGACGCTGACCCCCCACAAAGACTAATTCAACAATGCTCGCCCCCCT
maculatus                           AAATGACGCCAGCCAGCCACCAAAACTCAAACGACAACGCTTGCACCCAC
mindanensis                         AAATGACGACACCCGATTGCTAAAACAAAAGCAACGATACTAGCACCAAC
obscurus                            AAATGGCGACGCCCCCTCATCAAAAC------GACAACACTCACACCCAC
taeniopterus                        AAATGACGACACCCTCTCACTAAAAC------AACAACACTCACACCCAC
ornatus (Samar)                     AAATGACGTTGGCCAACTCCAAAAACCAACTCGACAATACTCGCACCTGC
ornatus (Bohol)                     AAATGGCGTTGGCCGATTCCAAAAACCAACTCAGCAATACTCACACCCAC
fimbriatus (Borneo)                 AAATGGCGATCCCCTATCACCAAAACCAAAACTACAATACTCGCACCAAC
cristatellus (Borneo)               AAATGGCGTCACCCAATCATCAAAACCAAAACAACATCACTCGCACCAAC
fimbriatus (Malay Pen.)             AAATGGCGATGCCCAATTACCAAAACCAAAACAACAACACTTGCACCAAC
fimbriatus (Java)                   AAATGGCGATGCCCAATCACCAAAACCAAAACAACAGCACTCGCACCACC
melanopogon                         AAATGGCGACACCCAATCGCCAAAACTAAGGCAATAACACTCGCACCAAC
haematopogon                        AAGTGACGCTGCCCAATTGCTAAAACCAAAGCAACAATACTCGCACCAAC
guentheri                           AAGTGGCGTTGACCAATCTCAAAAACCAACTCAACGATATTTGCACCCAC
quadrasi (Mindoro)                  AAATGACGTTGGCCAATTCCAAAAACCAACTCGACAATACTTGCACCCAC
palawanensis                        AAGTGACGTTTCCCAGTCCCAAAGACCAACTCAATAATACTTACTCCCCC
formosus                            AAATGACGACACCCCCTCACCAAAAC------GACAACACTCACACCTGC
sumatranus (Borneo)                 AAATGACGGTGGCCAATTCCAAAAACCAGCTCATCAATACTAACACCAAC
sumatranus (Malay Pen.)             AAATGACGATGGCCTGTTCCAAAAACCAGCTCATCAATACTGACACCAAC
sumatranus (Sumatra)                AAATGACGATGGCCAATTCCAAAAACCAGCTCATCAATACTAGCACCAAC
volans (Java)                       AAATGACGATGGCCAATCCCAAAAACCAACTCAAC---ACTAGCGCCAAC
quadrasi (Sibuyan)                  AAATGACGTTGGCCAATTCCAAAAACCAACTCAACAATATTCGCACCCAC
boschmai (Flores)                   AAATGACGATCCTCAACTCAAAATCCCAGCTTAACAATACTGACCCCAAC
boschmai (Sumba)                    AAATGACGATCCTTAACTCAAAATCCCAGCTTAACAATACTGACCCCAAC
boschmai (Lembata 1)                AAATGACGGTCCTCAACTCAAAATTCCAGCTTAACAATACTCACCCCAGC
boschmai (Lembata 2)                ??????????????????????????????????????????????????
boschmai (Sumbawa)                  AAATGACGGTGGCCAATTCAAAGCCCCAGCTCAGCAATACTAACCCCAAC
timoriensis (Roti)                  AAATGACGATCCTTAACTCAAAGCCCCAGCTTAACAATACTGACCCCAAC
timoriensis (Timor)                 AAATGACGATCCTTAACTCAAACCCCCAGCCTAACAACACTGACCCCAAC
beccarii                            AAATGACGATCCCCTATCACAAAAACCAGCTCCACGCTCCTTTCACCAAC
biaro                               AAATGACGACACCCAATCGTTAAAACTGGCCCAATCACACTCACACCTAC
"Tahulandang"                       AAATGACGACACCCAATCGTTAAAACTGGCCCAATCACACTCACACCTAC
bourouniensis                       AAATGACGATACCCGATCGCCAAGGCCAACTCAACTTTACTTACACCTAC
caerhulians                         AAATGACGACACCCAATCGCTAAAACTGGCCCAATCACACTCACACCTAC
spilonotus                          AAATGACGATACCCAATCGTTAAAACTGGCCCAATCACACTTACGCCCAC
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	1010 1020 1030 1040 1050
Aphaniotis fuscus	AGCCATAATAACTACACCTACACTACCAACCCTCATCCCATAGGAACTTG
Bronchocoela cristatella	AGCTGTAATAAGCACCACAGCACTTCCAACACTTTACTTATAGGAACTTA
Japalura splendida	AGCCCTTACAACCATAACAATACTCCCCGCAATAACCAAATAGGAACTTA
Japalura tricarinata	CGCTATTGCCAGCACGACAGCCCTACCAATAGTCATCCCATAGGAACTTA
maximus	CGCAATCTCCAGCACACCAACACTACCAACCATCACCCCTTAGAAGCTTA
quinquefasciatus	CGCAATTTCCACTACCCCAGCACTCCCAACCATCGCCCTCTAGAAGCTTA
spilopterus (Luzon, SE Bicol Pen.)	CGCTATCTTCAGTACTCCAGCACTACCTAATCTCCCAATCTAGAAGCTTA
spilopterus (Luzon, C Bicol Pen.)	CGCTATCTTTAGTACTCCAACACTACCTAATCTCCCACTCTAGAAGCTTA
spilopterus (Luzon, E coast)	TGCCATCTTTAGCACCCCCACACTACCAAACCTTCCAACTTAGAAACTTA
spilopterus (Polillo)	TGCCATCTTTAGCACCCCCACACTACCAAATCTTCCAACTTAGAAACTTA
spilopterus (Negros)	CGCCATTTTCAGCACCCCAACACTACCTAACCTGCCAATTTAGAAGCTTA
spilopterus (Panay)	CGCCATTTTCAGCACCCCAACACTACCTAACCTGCCAATTTAGAAGCTTA
spilopterus (Cebu)	CGCCATTTTCAGCACTCCAACATTACCTAACCTACCAATCTAGAAGCTTA
spilopterus (Siquijor)	CGCCATTTTCAGCACTCCAACATTGCCTAACCTATCAATTTAGAACCTTA
bimaculatus	CGCTATTTCAAGCACATCAGCACTACCAACAATTACCGCCTAGAAGCTTA
blanfordi	CGCAATCTTCAGTACATCAACATTACCCACCATTACTCCATAGAAGCTTA
indochinensis	CGCAATCTCCAGCACACCCGCACTACCAACTATTATCCCATAGAAGCTTA
cornutus	CGCTATCTTCAGCACCTTAACACTCCCGAACCTTCCAACCTAGAAGCTTA
cyanopterus (Mindanao)	CACCATTTTCAGCACCACAGCACTGCCAAACCTTCCACCCTAGAAGCTTA
reticulatus (Samar)	CGCCATTTTCAGCACCACAGCACTGCCGAACCTTCCAACCTAGAAGCTTA
reticulatus (Bohol)	CGCCATTTTCAGCACCACTGCACTACCAAACCTTCCAACCTAGAAGCTTA
maculatus	AGCAATCTTTTCCACCCCAGCACTACCAACCATTATCCCATAGAGACTTA
mindanensis	CGCAATCTCTAGCACGCCAGCACTACCAATCATCACCCCATAAAAACTCA
obscurus	CGCAATCTTCAGCACACCAGCACTACCAACCTTCACCCCCTAGAAGCTTA
taeniopterus	TGCAATCTTCAGTACACCAGCACTACCAACCATTACCCCCTAGAAGCTTA
ornatus (Samar)	TGCCACCTTCAGCACTCCGGCACTCCCAAACTTTCCAATTTAGAGACTTA
ornatus (Bohol)	CGCCACCTTCAGCACTCCCGCACTACCAAATCTTCCAACTTAGAGACTTA
fimbriatus (Borneo)	CGCAATCTTCAGCACCCCAGCCCTACCAAGCATTATCCCATAGAGACTTA
cristatellus (Borneo)	CGCAATTTTCAGCACACCAGCCCTACCAACCATTATCCCATAGAAGCTTA
fimbriatus (Malay Pen.)	CGCAATCTTCAGCACCCCAGCCCTACCAACCCTTATCCCATAGAGACTTA
fimbriatus (Java)	CGCAATCTTCAGCACCCCCGCCCTACCAACCCTTATCCCATAGAGACTTA
melanopogon	ATCAATCTCAAGCGCTACAGCACTACCAACCATCATCCCCTAGAAGCTTA
haematopogon	CGCAATTTCCAGCACACCAGCACTGCCAACCATCATCCCATAGAAGCTTA
guentheri	CGCTACCTTCAGCACCCCAGCACTACCAAATCTGCCAATTTAGAGACTTA
quadrasi (Mindoro)	TGCCATCTTCAGCACCCCCACATTCCCAAATCTTCCAATCTAGAAGCTTA
palawanensis	CGCCATTTTCAGCACTACGATACTGCCGCATCTAACAGCTTAGAGATTTA
formosus	CGCAACCTTCAGCACACCAGCACTACCAACCATCACCCCCTAGAAGCTTA
sumatranus (Borneo)	CGCCATTTTCAGTACATCAACATTACCAAACCTGCCCACCTAGGAACTTA
sumatranus (Malay Pen.)	CGCCATTTTCAGCACATCAGCATTACCAAACCTACCCACCTAGGAACTTA
sumatranus (Sumatra)	CGCCATTTTCAGCACATCAGCATTACCAAACCTACCCACCTAGGAACTTA
volans (Java)	CGCCATTTTCAGTACACCAATACTACCAAACCTGCCCACCTAGAAGCTTA
quadrasi (Sibuyan)	TGCCATTTTCAGTACCCCCACATTACCGAACCTCCCAATCTAGAAGCTTA
boschmai (Flores)	CGCCAGCTTCAGTACATCAGCACTTCCTAATCTTCCAACCTAGAAGCTTA
boschmai (Sumba)	CGCCAGCTTTAGTACATCAGCACTTCCTAATCTTCCCATCTAGAAGCTTA
boschmai (Lembata 1)	CGCCAGCTTCAGTACATCAGCACTACCTAATCTTCCAACTTAGAAGCTTA
boschmai (Lembata 2)	??
boschmai (Sumbawa)	CGCCAGTTTCAGTACGTCAGCACTACCCAGTCTGCCAATTTAGAAACTTA
timoriensis (Roti)	CGCCAGCTTCAGTACATCAGCACTTCCTAACCTTCCAGTCTAGAAGCTTA
timoriensis (Timor)	CGCCAGCTTCAGTACATCAGCACTTCCTAATCTTCCCACCTAGAAGCTTA
beccarii	TGCTATCTCCAGCACACCAGCACTCCCAAGCATCACCCCCTAGAAACTTA
biaro	TGCCATCTCCAGCACACCTGCACTTCCAATTATCACCCCATAGAGGCTTA
"Tahulandang"	TGCCATCTCCAGCACACCTGCACTCCCAATTATCACCCCATAGAGGCTTA
bourouniensis	CGCCACCCTCAGCTTACCAACACTTCCAAGCATCTCCCCCTAGAGACTTA
caerhulians	TGCCACTTCCAGCACACCTGCACTCCCAATTATTGCCCCGTAAAGGCTTA
spilonotus	TGCCATCTCCAGCACACCTGCCCTTCCAATTATTACCCCATAGAGGCTTA

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                                          1060      1070      1080      1090      1100
                                             .         .         .         .         .
Aphaniotis fuscus                   GGAACTTAGGATGATCAAACCATAAACCTTCAAAGTTTAAAACAAGAGTA
Bronchocoela cristatella            GGATTACACCTA-----AACCAGAGACCTTCAAAGTCTCAAACAAGAGTA
Japalura splendida                  GGAATAACATTA-----AACCAGAGACCTTCAAAGTCACAAATAAGAGTC
Japalura tricarinata                GGACTAATATA------AACCAAAGGCCTTCAAAGCCTTAAACAAGAGAT
maximus                             GGATAATTTA-------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGTA
quinquefasciatus                    GGATAAACTA-------AACCAAAGGCCTTCAAAGCCCTAAACAAGAGTA
spilopterus (Luzon, SE Bicol Pen.)  GGATAAATCA-------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGTA
spilopterus (Luzon, C Bicol Pen.)   GGATAAATCA-------AACCAAGGGCCTTCAAAGCTCTAAACAAGAGTA
spilopterus (Luzon, E coast)        GGATAAACA--------AACCAAGAGCCTTCAAAGCCCTAAATAAGAACA
spilopterus (Polillo)               GGATAAGCA--------AACCAAGAGCCTTCAAAGCCCTAAATAAGAACA
spilopterus (Negros)                GGATAAACA--------AACCGAGGGCCTTCAAAGCCCTAAACAAGAGTA
spilopterus (Panay)                 GGATAAACA--------AACCGAGGGCCTTCAAAGCCCTAAACAAGAATA
spilopterus (Cebu)                  GGATAAACA--------AACCGAGGGCCTTCAAAGCCCTAAACAAGAGTG
spilopterus (Siquijor)              GGATAAACA--------AACCGAGGGCCTTCAAAGCCCTAAACAAGGGTA
bimaculatus                         GGATCAAACAA------AACCAAAGGCCTTCAAAGCCTTAAACAAGA?TA
blanfordi                           GGATAAACTA-------AACCGGGGGCCTTCAAAGCCCTAAACAAGAGCA
indochinensis                       GGATAAATTA-------GACCGGGGGCCTTCAAAGCCCTAAGAAAGAGTA
cornutus                            GGATAAACA--------AACCAGGAGCCTTCAAAGCCCCAAACAAGAGCA
cyanopterus (Mindanao)              GGATGAACA--------AACCGAGGGCCTTCAAAGCCCTAGACAAGAGCA
reticulatus (Samar)                 GGATAGACA--------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
reticulatus (Bohol)                 GGATAGACA--------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
maculatus                           GGATCAACTA-------AACCAAAGGCCTTCAAAGCCTTAAACAAGAGCA
mindanensis                         GAATAATTA--------AACCAAA??????????????????????????
obscurus                            GGATAGACTA-------AACCGGAGGCCTTCAAAGCCCCAAACAAGAGTA
taeniopterus                        GGATAAATTA-------AACCGGGGGCCTTCAAAGCCTCAAACAAGAGTA
ornatus (Samar)                     GGATAAATA--------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
ornatus (Bohol)                     GGATAAACA--------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCG
fimbriatus (Borneo)                 GGATAGACTA-------AACCAAGAGCCTTCAAAGCCCTAAACAAGAGTA
cristatellus (Borneo)               GGATAAGACTA------AACCAAGGGCCTTCAAAGCCCTAAATAAGAGCA
fimbriatus (Malay Pen.)             GGATAGGACTAA-----AACCGGGGGCCTTCAAAGCCCTAAACAAGAGTA
fimbriatus (Java)                   GGATGATACTAA-----AACCGAGGGCCTTCAAAGCCCTAAACAAGAGCA
melanopogon                         GGATAAACTA-------AACCGGGAGCCTTCAAAGCCCCAAACAAGAGTA
haematopogon                        GGATAAACTA-------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGTA
guentheri                           GGATAAATTA-------AACCAAGGGCCTTCAAAGCTCTAAACAGGAGCA
quadrasi (Mindoro)                  GGATAAACA--------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGAC
palawanensis                        GGATAGACTA-------AACCAGGAGCCTTCAAAGCCCCAAACAAGAGCA
formosus                            GGATAAATTA-------AACCAAGGGCCTTCAAAGCCCCAAACAAGAGTA
sumatranus (Borneo)                 GGATAGCATA-------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
sumatranus (Malay Pen.)             GGATAGCATTTA-----AACCAAGGGCCTTCTAAGCCCTAAACAAGAGCA
sumatranus (Sumatra)                GGATAGCATTA------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
volans (Java)                       GGATAACACA-------AACCAAGAGCCTTCAAAGCTCTAAACAAGAGCA
quadrasi (Sibuyan)                  GGATAAACGA-------AACCAAGAGCCTTCAAAGCTCTAAACAAGAGAT
boschmai (Flores)                   GGATAAACATA------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
boschmai (Sumba)                    GGATAACATA-------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
boschmai (Lembata 1)                GGATAAACATA------AACCAAGAGCCTTCAAAGCCCTAAACAAGAGCA
boschmai (Lembata 2)                ???????????------?????????????????????????????????
boschmai (Sumbawa)                  GGATAAACATA------AACCAAGGGCCTTCAAAGCCCTAAACAAGAACA
timoriensis (Roti)                  GGATAACATA-------AACCAAGGGCCTTCAAAGCTCTAAACAAGAGCA
timoriensis (Timor)                 GGATAAACATA------AACCAAGGGCCTTCAAAGCCCTAAACAAGAGCA
beccarii                            GGTCAAAATTA------AACCAAGGGCCTTCAAAGCCCTAAACAAGGGTT
biaro                               GGTCAAGCTA-------AACCAATGGCCTTCAAAGCCTTGAATAAGAGTT
"Tahulandang"                       GGTTCAAGCTA------AACCAATGGCCTTCAAAGCCTTGAATAAGAGTT
bourouniensis                       CGTTAAAATCTA-----AACCAACAGCCTTCAAAGCCCTAAATAAGAGCC
caerhulians                         GGTCAAGCTA-------AACCAATGGCCTTCAAAGCCTTGAATAAGAGTT
spilonotus                          GGTTCAAGCTA------AACCAATGGCCTTCAAAGCCTTGAATAAGAGTT
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                                          1110      1120      1130      1140      1150
                                             .         .         .         .         .
Aphaniotis fuscus                    AAC---CTCTTAGTACCTG-AATAAAACCTGTAAAACT---AATACATCC
Bronchocoela cristatella             CAC-T-CTCTTAGTACCTG-A-TAAGACCTGAAAGACTCCACTTTCATCT
Japalura splendida                   ACCACCCTCTTAGTACCTGCAATAAAGACTGCGGGATCACCCT???????
Japalura tricarinata                 CCA-C-CTCTTAGTACCTG-ATTAAAACCTGTGAAATTTTACTCACATCA
maximus                              CTAAT-CTCTTAGCCTCTG-CCTAAAACCTGCAAGACTCCACTTACATCA
quinquefasciatus                     TAAAC-CTCTTAGCCTCTG-CCTAAAACCTGCAAGACTCCACTCACATCA
spilopterus (Luzon, SE Bicol Pen.)   CCAAC-CTCTTAGCCTCTG-CTTAAAACCTGTAAGACTTCACTCACATCA
spilopterus (Luzon, C Bicol Pen.)    CCAAC-CTCTTAGCCTCTG-CTTAAAACCTGTAAGACTTCACTCACATCA
spilopterus (Luzon, E coast)         TCGAC-TTCTTAGTTTCTG-CTTAAAACCTGTAAGACTCCACTTACATCA
spilopterus (Polillo)                TCAAC-TTCCTAGTTTCTG-CCTAAAACCTGTAAGACTTCACTCACATCA
spilopterus (Negros)                 CCAAC-CCCTTAGCCTCTG-TCTAAAACCTGTAAGACTCTACTCACATCA
spilopterus (Panay)                  CCAAC-CCCTTAGCCTCTG-TCTAAAACCTGTAAGACTCTACTCACATCA
spilopterus (Cebu)                   CCAAC-CTCTTAGCCTCTG-CCTAAAACCTATGAGACTCTACTCACATCA
spilopterus (Siquijor)               CCAAC-CCCTTAGCCTCTG-TCTAAAACCTGTAAGACTCTACTCACATCA
bimaculatus                          TAAAC-CTCTTAGCCTCTG-CCTAAAACCTGCAAGA?TTCACTCACATCA
blanfordi                            CTAAC-CTCTTAGCCTCTG-CCTAAAACCTGTGAGACTCCACTCACATCA
indochinensis                        TTAAC-CTCTTAGCCTCTG-CCTAAAACCTGCAAGACTCCACTTACATCG
cornutus                             CTGAC-CTCTTAGCCTCTG-CCTAAAACCTGCAAGATTTCACTCACATCA
cyanopterus (Mindanao)               ATGAT-CTCTTAGCCTCTG-CCTAAAACCTGTAAGAATTCACTCTTATCA
reticulatus (Samar)                  ATGAC-CTCTTAGCCTCTG-CCTAAAACCTGTAAGACTCCACTCACATCA
reticulatus (Bohol)                  ATGAC-CTCTTAGCCTCTG-CCTAAAACCTGTAAGACTCCACTCACATCA
maculatus                            TAAAC-CTCTTAGCCTCTG-TTTAAAGCCTGCAAGAATTCACTCACATCA
mindanensis                          ??????????????????????????????????????????????????
obscurus                             TTAAC-CTCTTAGCCTCTG-CCTAAAACCTGCAAGAACCCACTCACATCA
taeniopterus                         TTAAC-CTCTTAGCCTCTG-CCTAAAACCTGCAAGACTCCACTCACATCA
ornatus (Samar)                      CCAAC-CTCTTAGCCTCTG-CCTAAAACCTGTAAGACTCCACTCACATCA
ornatus (Bohol)                      CCAAT-CTCTTAGCCTCTG-CCTAAAACCTGCAAGACTCCACTTACATGA
fimbriatus (Borneo)                  TCAAC-CTCTTAGCCTCTG-ACTAAAACCTGCAAGACTCCACTCACATCA
cristatellus (Borneo)                CCAAC-CTCTTAGCCTCTGCATTAAAACCTGCAAGACTCCACTCACATCA
fimbriatus (Malay Pen.)              CCAAC-CTCTTAGCCTCTGCACTAAAACCTGCAAGACTCCACTCACATCA
fimbriatus (Java)                    CCAGC-CTCTTAGCCTCTGCACTAAAACCTGCAAGACTCCACTCACATCA
melanopogon                          CTAAC-CTCTTAGCCTCTG-CCTAAAACCTGCAAGACTTCACTCACATCA
haematopogon                         CCAAC-CTCTTAGCCTCTG-CCTAAAACCTGCGAGACTCTACTCACATCA
guentheri                            CCAAC-CTCTTAGCCTCTG-CCTATAACCTGTAAGAATCCACTCACATCA
quadrasi (Mindoro)                   AAC---CTCTTAGCCTCTG-CTTAAAACCTGTAAGACTTCACTCACATCA
palawanensis                         TCAAT-CTCTTAATCTCTG-CTTAAAACCTGCAAGATTCCACTTACATCA
formosus                             TTAAC-CTCTTAGCCTCTG-CCTAAAACCTGTAAGACTCCACTCACATCA
sumatranus (Borneo)                  CCAAC-CTCTTAGCTCCTG-GCTAAAACCTGTAAGGTTTCACTCACATCA
sumatranus (Malay Pen.)              CCAAC-CTCTTAGTTCCTG-CCTAAAACCTGTAAGGCTTCACTCACAT??
sumatranus (Sumatra)                 CCAAC-CTCTTAGCTCCTG-CCTAAAACCTGTAAGGCTTCACTCACATCA
volans (Java)                        CCAAC-CTCTTAGCTCCTG-CCTAAAACCTGTAAGCCTTCACTCACATCA
quadrasi (Sibuyan)                   GGC---CTCTTAGTTTCTG-C-TAAAACCTGTAAGACTTCACTCACATCA
boschmai (Flores)                    CAAAC-CTCTTAGCTTCTG-CCTAAAACCTGTGGGGGTTCACTCACATCA
boschmai (Sumba)                     CAAAC-CTCTTAGCTTCTG-CCTAAAACCTGTAAGAATTCACTCACATCA
boschmai (Lembata 1)                 CAA-C-CTCTTAGCTTCTG-CCTAAAGCCTGTAAGAATTCACTCACATCA
boschmai (Lembata 2)                 ?????-????????????????????????????????????????????
boschmai (Sumbawa)                   CTAAT-CTCTTAGCTTCTG-CCTAAAGCCTGTAAGAATTCACTCACATCA
timoriensis (Roti)                   CAAAC-CTCTTAGCTTCTG-CCTAAAACCTGTAAGAATTCACTCACATCA
timoriensis (Timor)                  CAAAC-CTCTTAGCTTCTG-CCTAAAACCTGTAAGAATTCACTCACATCA
beccarii                             AAC---CCCTTAGTCTCTG-ACTAAAACCTGCAAGACTCCACTTACATCA
biaro                                AAA-C-CTCTTAGCCTCTG-ACTAAAACCTGCAAGACTCCACTCACATCA
"Tahulandang"                        AAA-C-CTCTTAGCCTCTG-ACTAAAACCTGCAAGACTCCACTCACATCA
bourouniensis                        AGC-C-CTCTTAGTCTCTG-ACTAAAGCCTGCAAGACTCAACTCACATCA
caerhulians                          AAA-C-CTCTTAACCTCTG-ACTAAAACCTGCAAGACTTCACTCACATCA
spilonotus                           AAG-C-CTCTTAGCCTCTG-ACTAAAACCTGTAAGATTTCACTCACATCA
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	1160 .
Aphaniotis fuscus	TCCGAATGCAACTCA
Bronchocoela cristatella	TCCGAATGCAACTCA
Japalura splendida	???????????????
Japalura tricarinata	C??????????????
maximus	CCCGAATGCAACTCA
quinquefasciatus	CCCGAATGCAACTCA
spilopterus (Luzon, SE Bicol Pen.)	CCCGAATGCAACTCA
spilopterus (Luzon, C Bicol Pen.)	CCCGAATGCAACTCA
spilopterus (Luzon, E coast)	CCCGAATGCAACTCA
spilopterus (Polillo)	CCCGAATGCAACTCA
spilopterus (Negros)	CCCGAATGCAACTCA
spilopterus (Panay)	CCCGAATGCAACTCA
spilopterus (Cebu)	CCCGAATGCAACTCA
spilopterus (Siquijor)	CCTGAATGCAACTCA
bimaculatus	CCCGAATGCAACTCA
blanfordi	CCCGAATGCAACTCA
indochinensis	CCCGAATGCAACTCA
cornutus	CCCGAATGCAACTCA
cyanopterus (Mindanao)	CCCGAATGCAA????
reticulatus (Samar)	CCCGAATGCAACTCA
reticulatus (Bohol)	CCCGAATGCAACTCA
maculatus	CCCGAATGCAACTCA
mindanensis	???????????????
obscurus	CCCGAATGCAACTCA
taeniopterus	CCCGAATGCAACTCA
ornatus (Samar)	CCCGAATGCAACTCA
ornatus (Bohol)	C??????????????
fimbriatus (Borneo)	CCCGAATGCAACTCA
cristatellus (Borneo)	CCCGAATGCAACTCA
fimbriatus (Malay Pen.)	CCCGAATGCAACTCA
fimbriatus (Java)	TCCGAATGCAACTCA
melanopogon	CCCGAATGCAACTCA
haematopogon	CCCGAATGCAACTCA
guentheri	CCCGAATGCAACTCA
quadrasi (Mindoro)	CCCGAATGCAACTCA
palawanensis	CCCGAATGCAACTCA
formosus	CCCGAATGCAACTCA
sumatranus (Borneo)	CCCGAATGCAACTCA
sumatranus (Malay Pen.)	???????????????
sumatranus (Sumatra)	CCCGAATGCAACTCA
volans (Java)	CCCGAATGCAACTCA
quadrasi (Sibuyan)	CCCGAATGCAACTCA
boschmai (Flores)	TCCGAATGCAACTCA
boschmai (Sumba)	TCCGAATGCAACTCA
boschmai (Lembata 1)	CCCGAATGCAACTCA
boschmai (Lembata 2)	???????????????
boschmai (Sumbawa)	CCCGAATGCAACTCA
timoriensis (Roti)	TCCGAATGCAACTCA
timoriensis (Timor)	TCCGAATGCAACTCA
beccarii	CCCGAATGCAACTCA
biaro	ACCGAATGCAACTCA
"Tahulandang"	CCCGAATGCAACTCA
bourouniensis	CCCGAATGCAACTCA
caerhulians	CCGGAATGCAACTCA
spilonotus	CCCGAATGGAACTCA

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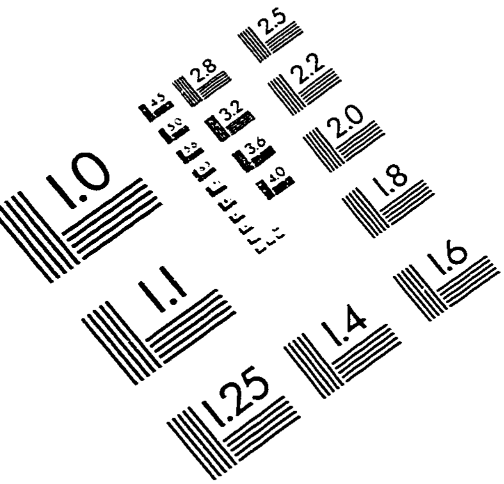
VITA

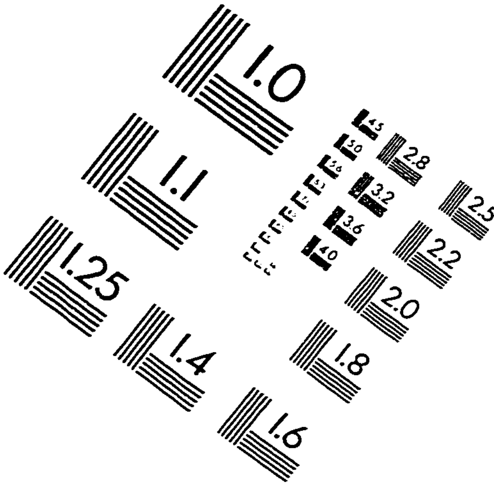
Jimmy Adair McGuire was born in La Mesa, California, on September 14, 1967, the son of Joan Glenda McGuire and Jimmy Iwan McGuire. After completing his work at Valhalla High School, El Cajon, California, in 1985, he entered San Diego State University in San Diego, California. He received the degree of Bachelor of Science in Business/Finance from San Diego State University in May 1989. In September 1989 he entered the Graduate School of San Diego State University, from which he received the degree of Master of Science in Biology in May 1994. He is the author or co-author of 10 scholarly articles. In September 1993 he entered the Graduate School of the University of Texas.

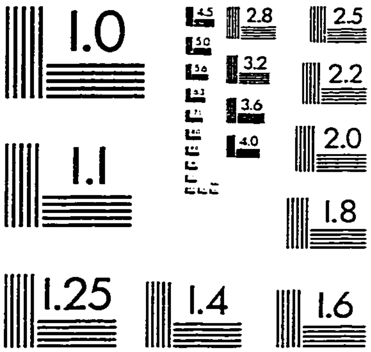
Permanent Address: 4412 Caswell Avenue, Austin, Texas 78751

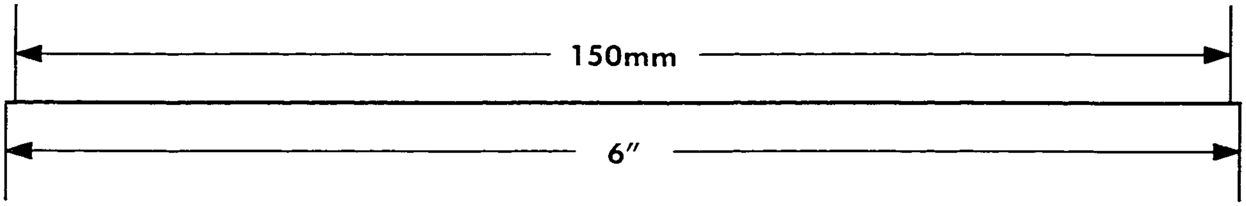
The dissertation was typed by the author.

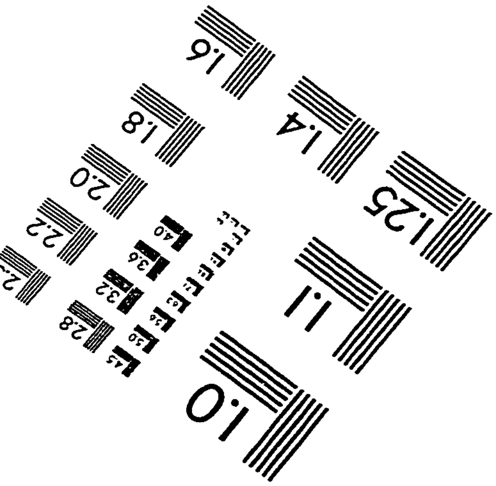
IMAGE EVALUATION TEST TARGET (QA-3)

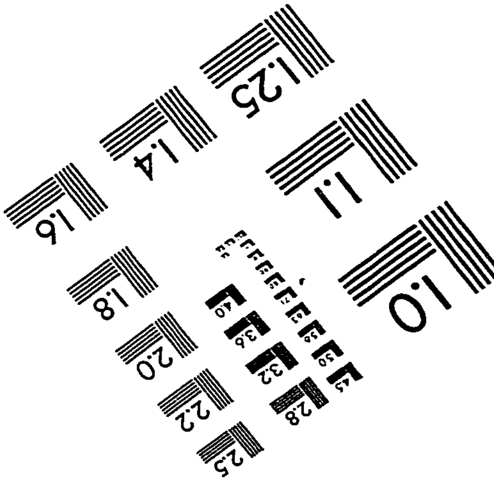












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