Journal of Mammalogy, 88(2):302–318, 2007

TAXONOMY AND NATURAL HISTORY OF THE SOUTHEAST ASIAN FRUIT-BAT GENUS *DYACOPTERUS*

KRISTOFER M. HELGEN,* DIETER KOCK, RAI KRISTIE SALVE C. GOMEZ, NINA R. INGLE, AND MARTUA H. SINAGA

Division of Mammals, National Museum of Natural History (NHB 390, MRC 108), Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012, USA (KMH)
Forschungsinstitut Senckenberg, Senckenberganlage 25, Frankfurt, D-60325, Germany (DK)
Philippine Eagle Foundation, VAL Learning Village, Ruby Street, Marfori Heights, Davao City, 8000, Philippines (RKSCG)
Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA (NRI)
Division of Mammals, Field Museum of Natural History, Chicago, IL 60605, USA (NRI)
Museum Zoologicum Bogoriense, Jl. Raya Cibinong Km 46, Cibinong 16911, Indonesia (MHS)

The pteropodid genus *Dyacopterus* Andersen, 1912, comprises several medium-sized fruit-bat species endemic to forested areas of Sundaland and the Philippines. Specimens of *Dyacopterus* are sparsely represented in collections of world museums, which has hindered resolution of species limits within the genus. Based on our studies of most available museum material, we review the infrageneric taxonomy of *Dyacopterus* using craniometric and other comparisons. In the past, 2 species have been described—*D. spadiceus* (Thomas, 1890), described from Borneo and later recorded from the Malay Peninsula, and *D. brooksi* Thomas, 1920, described from Sumatra. These 2 nominal taxa are often recognized as species or conspecific subspecies representing these respective populations. Our examinations instead suggest that both previously described species of *Dyacopterus* co-occur on the Sunda Shelf—the smaller-skulled *D. spadiceus* in peninsular Malaysia, Sumatra, and Borneo, and the larger-skulled *D. brooksi* in Sumatra and Borneo. We further identify specimens of *Dyacopterus* from the large islands of Luzon and Mindanao in the Philippines as representatives of a distinctive new species, *Dyacopterus rickarti*. This new species differs from the Sundaic taxa in its much larger size, unique palatal ridge formula, and in qualitative craniodental features. The natural history of each species, so far as it is known, is briefly reviewed.

Key words: biogeography, *Dyacopterus*, Indonesia, Malaysia, morphology, new species, Philippines, Pteropodidae, taxonomy, Thailand

In 1889, Oldfield Thomas, a mammalogist at the British Museum of Natural History (today the Natural History Museum, London), received a shipment of mammals sent to him by Dr. Charles Hose, a government official, physician, and naturalist living in Sarawak, northern Borneo. Included in the shipment was a skin and partial skull of a craniodentally distinctive new species of pteropodid bat, which Thomas named as a species of *Cynopterus*, *C. spadiceus* (Thomas 1890). After examining this sole available specimen of *spadiceus*, the American mammalogist Gerrit S. Miller, Jr., transferred the species instead to the genus *Thoopterus*, based on his impressions of morphological similiarity between *spadiceus* and *Thoopterus nigrescens*, previously the only recognized species in that genus (Miller 1907). Several years later in his signal treatise on megachiropteran classification, the Danish bat systematist Knud Andersen erected a new genus for *spadiceus* (*Dyacopterus*—"a winged Dayak") and reviewed in detail its morphological isolation relative to all other fruit bats. At the time of Andersen's monograph, the holotype of *D. spadiceus* remained the only specimen known to science.

The 2nd specimen of *Dyacopterus* to come to light, collected in southern Sumatra, was reported by Thomas (1920). Considerably larger than the holotype of *spadiceus*, Thomas (1920) considered this 2nd specimen to represent a distinct taxon, introduced under the name *Dyacopterus brooksi*. In 1961 John Edward Hill of the British Museum reported the 3rd known specimen of the genus, referred to *D. spadiceus* and collected in peninsular Malaysia at Ulu Langat Forest Reserve (Hill 1961). Harrisson (1967) and Hill (1967) later discussed the collection of several additional specimens in Borneo and

* *Correspondent: helgen@post.harvard.edu*

mainland Malaysia, respectively, all of which were identified as *D. spadiceus* (although see Start 1974). Kock (1969) reviewed these previous accounts and reported the 1st record of the genus from the Philippines, based on a single very large-bodied specimen collected in northern Luzon, which he tentatively referred to *D. spadiceus*.

Subsequent to Kock's (1969) paper, infrageneric taxonomy of *Dyacopterus* has never been critically reviewed. Mainly because of the very small samples of *Dyacopterus* that have been discussed in detail in the literature, bat systematists have been unable to satisfactorily determine the number of species of *Dyacopterus* (or their geographic boundaries) currently represented by specimens stored in world museums (Heaney et al. 1998; Hill 1992; Koopman 1994; Simmons 2005). Still, in recent decades, additional records of *Dyacopterus* have accrued in the literature, and many additional specimens have accumulated in museum collections, primarily from northern Borneo and the Malay Peninsula, but also from Sumatra, southern Borneo, and the Philippines (e.g., Abdullah and Hall 1997; Abdullah et al. 1997; Francis 1990, 1994, 1995; Francis et al. 1994; Gomez et al. 2005; Heaney et al., in press; Hodgkison et al. 2004a, 2004b; Payne and Francis 1985; Peterson 1969; Start 1974, 1976; Studier et al. 1995; Utzurrum 1992; Zubaid 1993). Here we review patterns of morphological variation within *Dyacopterus* and their taxonomic significance. The results derive from study of most of the currently available material stored in museum collections.

Materials and Methods

Specimens discussed herein are deposited in the collections of the Natural History Museum, London (BMNH); the Delaware Museum of Natural History, Wilmington (DMNH); the Field Museum of Natural History, Chicago (FMNH); the Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB); the Royal Ontario Museum, Toronto (ROM); the Senckenberg Museum, Frankfurt (SMF); the United States National Museum of Natural History, Washington, D.C. (USNM); and the University of the Philippines in Mindanao, Davao (UPMIN). Collection of newly reported Philippine material of *Dyacopterus* followed guidelines established for animal capture and handling established by the American Society of Mammalogists (Animal Care and Use Committee 1998). Standard external measurements for the majority of museum specimens were recorded by the original collectors in the field; in other cases KMH measured these variables from specimens preserved in alcohol. Craniodental variables were measured by the authors with handheld calipers to the nearest 0.1 mm. Single-tooth measurements are measured on the crown. All measurements of length are in millimeters, and measurements of mass are given in grams.

Terminology for cranial and dental features follows Giannini et al. (2006). Measurements are abbreviated (and, where necessary, defined) as follows: FA (forearm length); CBL (condylobasal length); ONL (orbitonasal length, the distance from anterior margin of the orbit to the anterior midpoint of the premaxillae); ZYG (greatest bizygomatic width); MTR (length of maxillary toothrow, C–M1); BBC (breadth of braincase at intersection with zygomata); MH (coronoid height of mandible); CC (external width across alveoli of upper canines); IOB (least width of interorbital constriction); POB (least width of postorbital constriction). For wing measurements (arc lengths in the case of phalangeal measurements), digit is abbreviated as D, metacarpal as M, and phalanx as P; thus, D2P2 refers to the 2nd phalanx of the 2nd digit, and so on. For more details on features of soft palate anatomy referred to here, see Andersen (1912).

In the principal component analysis featured in this paper, components were extracted from a covariance matrix of natural-log–transformed craniodental variables, selected to sample cranial size and shape and to maximize sample size.

Results

During research visits to world museums in 2004, KMH compiled a large number of craniodental measurements for all 21 skulls of adult *Dyacopterus* encountered in American and European museums and at MZB. These include all key specimens previously discussed in the literature (especially Andersen 1912; Hill 1961, 1967; Kock 1969; Peterson 1969; Thomas 1890, 1920), but also additional material never before discussed, including specimens from Kalimantan (at MZB and ROM), specimens from various localities in Sumatra (at MZB), the 1st definitive voucher recorded from Thailand (at SMF), and newly collected material from Mindanao (at FMNH and elsewhere, see below). Armed with this data, we set out to evaluate the taxonomic status of Philippine *Dyacopterus* (cf. Hill 1992) and to clarify the nature of supposed distinctions between *D. spadiceus* and *D. brooksi*, the 2 nominal forms of *Dyacopterus* from the Sunda Shelf.

Only 2 museum specimens of *Dyacopterus* from the Philippines have previously been reported in the literature—1 from Luzon, the other from Mindanao (Heaney et al. 1987, 1998; Kock 1969; Utzurrum 1992). Previous authors disagree in their taxonomic assignment of these specimens; Kock (1969) and Heaney et al. (1998) tentatively identified Philippine specimens as *D. spadiceus*, whereas Hill (1992) tentatively assigned them to *D. brooksi*, citing their large size. More recently, Gomez et al. (2005) referred to newly captured animals from Mindanao as "*Dyacopterus* sp." We examined 3 skulls of Philippine Dyacopterus—1 from Luzon and 2 from Mindanao (see below). On the basis of pronounced differences in craniodental dimensions, specimens of *Dyacopterus* from the Philippines can be immediately distinguished from all available material collected on the Sunda Shelf (e.g., Figs. 1–3). Philippine specimens are absolutely larger than all other *Dyacopterus* in most craniometric variables sampled, including condylobasal length, maxillary toothrow length, interorbital width, and mandible height (e.g., Table 1; Figs. 1–3). This profound size distinction is complemented by absolute differences in external measurements (e.g., Table 2) in addition to other proportional and qualitative morphological distinctions, as described below. We suggest that these differences indicate that the Philippine representative of *Dyacopterus* represents an undescribed

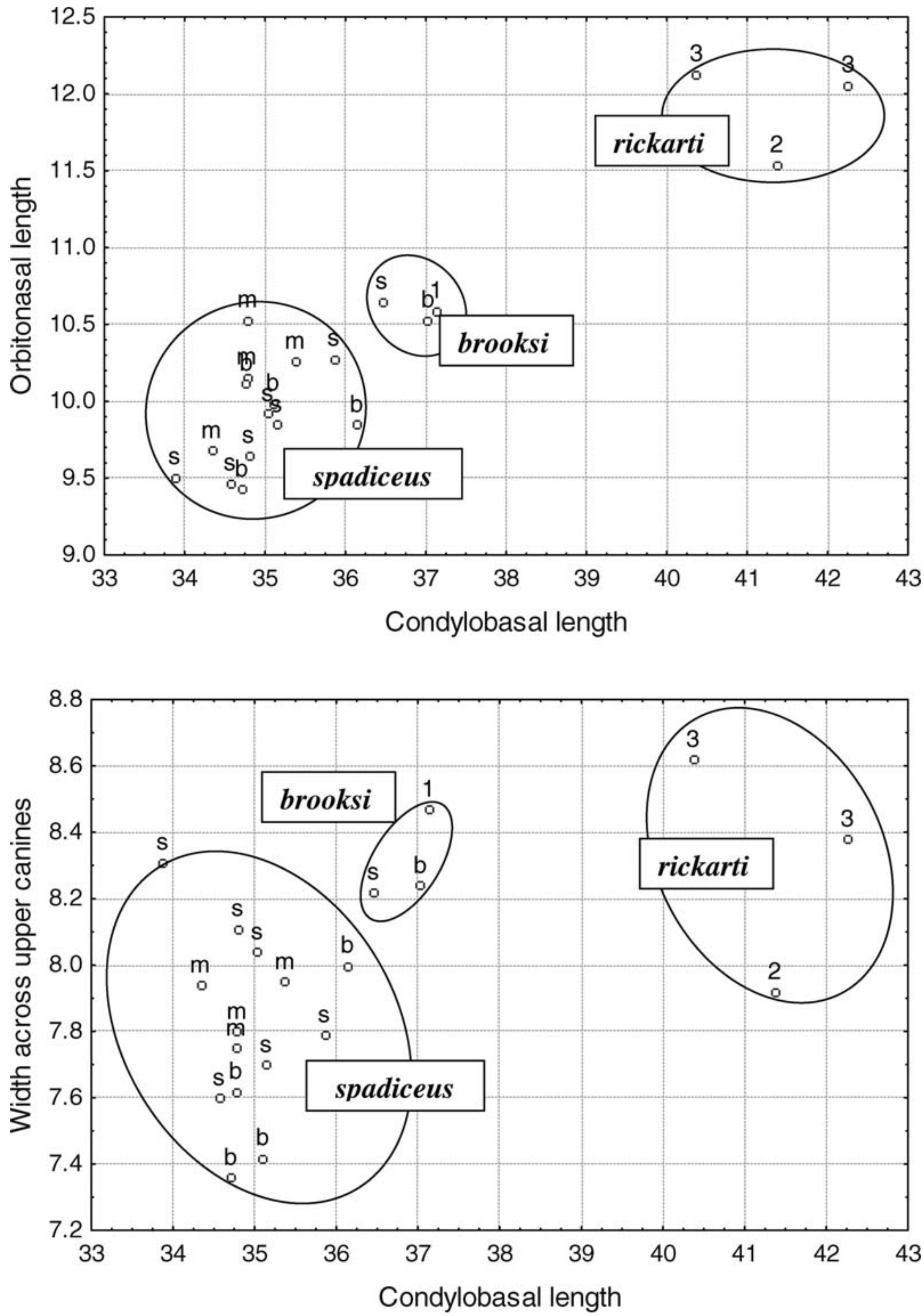

Fig. 1.—Bivariate contrasts in Sundaic and Philippine *Dyacopterus*. Top) Rostrum length (ONL) versus skull length (CBL). Bottom) A selected cranial width (CC) plotted against skull length (CBL). m = Peninsular Malaysia, s = Sumatra, b = Borneo, 1 = type of *D. brooksi* (Sumatra); 2 = type of *D. rickarti* (from Luzon), 3 = specimens from Mindanao.

species distinct from Sundaland *Dyacopterus*. Sample sizes are too small to assess whether consistent morphological distinctions characterize specimens of *Dyacopterus* from Luzon and from Mindanao, but direct comparisons of currently available material suggest their morphological and taxonomic equivalence (see below).

More challenging to establish is the identity of specimens from the Sunda Shelf. Previous authors have either regarded all specimens from Borneo, Sumatra, and peninsular Malaysia as representing a single species, *D. spadiceus* (e.g., Koopman 1994; Medway 1965), or have recognized 2 species—the smaller-skulled *D. spadiceus* of Borneo and peninsular

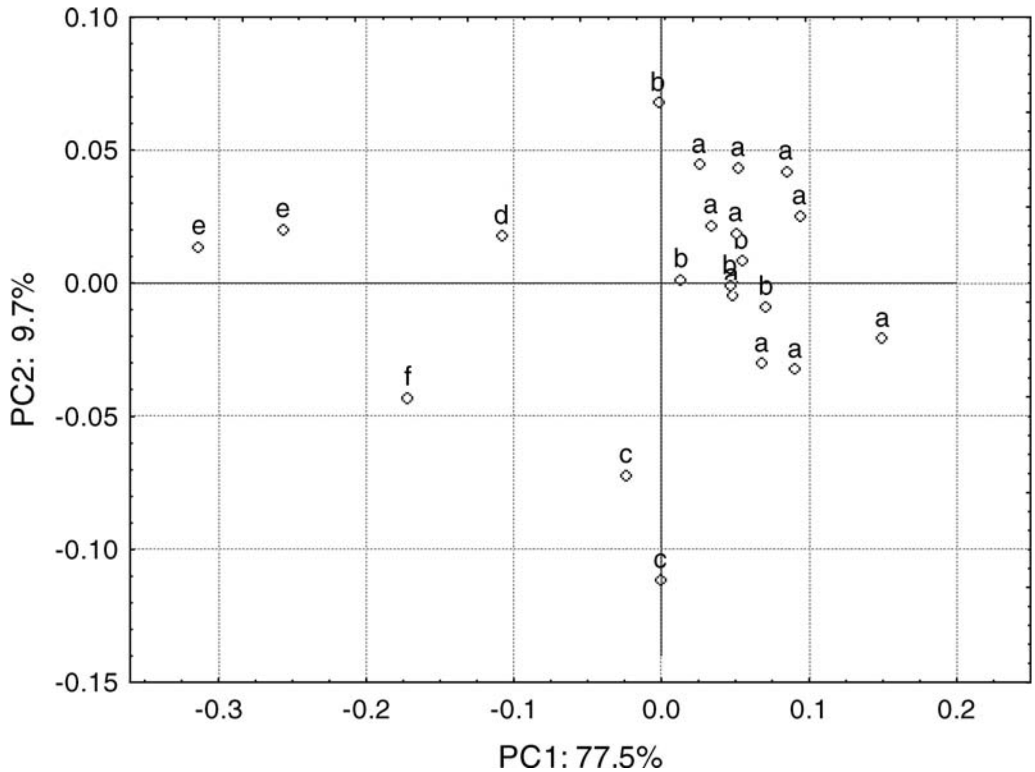

FIG. 2.—Morphometric separation (principal component analysis) of specimens identified as a, b = *D. spadiceus*, c, d = *D. brooksi*, and e, f = *D. rickarti*. Based on 6 measurements (ONL, ZYG, BBC, MTR, CC, MH). a = female *D. spadiceus*, b = male *D. spadiceus*, c = female *D. brooksi*, d = male *D. brooksi*, e = female *D. rickarti*, f = male *D. rickarti*. PC1 is an indication of overall cranial size (decreasing left to right), whereas PC2 largely reflects relative zygomatic and braincase breadths (decreasing from top to bottom). See Table 3.

Malaysia, and the larger-skulled *D. brooksi* from Sumatra (e.g., Peterson 1969; Simmons 2005). The only specimen unambiguously referred to *D. brooksi* in previous literature remains the holotype (Thomas 1920), heretofore the only specimen of *Dyacopterus* reported from Sumatra. Univariate, bivariate, and principal component analyses (Tables 1–3; Figs. 1–3) all demonstrate that the holotype of *brooksi* remains the largest specimen of *Dyacopterus* collected in Sundaland to date. (Because all craniodental variables loaded strongly and negatively on the 1st principal component [PC1], PC1 can be taken as a good indication of overall cranial size [Fig. 2; Table 3].) However, our sample includes 2 additional specimens (1 each from Borneo and Sumatra) that are both nearly as large as the holotype of *brooksi* (at least in condylobasal length [Fig. 1]), and replicate many of its distinctive attributes, such as its long rostrum and narrowed skull in proportional aspects (e.g., Figs. 1 and 3). These 2 additional specimens also agree with *brooksi* in their long forearms (all > 80 mm), large teeth (Table 4), and in dental proportions, particularly in having an anterolaterally enlarged m1 (see below). All 3 of these specimens are referred here to *D. brooksi*, which we regard as a Sundaic species distinct from *D. spadiceus*. Comparative dental wear and extent of ossification serve to demonstrate that putative distinctions between samples referred to *D. spadiceus* and *D. brooksi* are not simply age effects; we judge that these 3 large Sundaic specimens are equivalent in age to many smaller-skulled specimens from the Sunda Shelf referred to *D. spadiceus* (Table 1).

The remainder of specimens from Borneo, Sumatra, and the Malay Peninsula (peninsular Malaysia and Thailand), including the holotype of *Dyacopterus spadiceus* (Thomas 1890), comprise a fairly uniform morphometric cluster and are characterized by a distinctively shortened but proportionally wide skull relative to samples of *brooksi* and Philippine *Dyacopterus* (e.g., Figs. 1–3). Little geographic variation in these samples is evident (Table 5), and we suggest that these specimens can be unambiguously referred to a single species, *D. spadiceus*, by far the most commonly collected species in the genus (Appendix I).

Our taxonomic interpretations regarding Sundaland *Dyacopterus*, based on a larger number of museum specimens than previously available, thus differ considerably from previously published interpretations. Instead of regarding *spadiceus* and *brooksi* as separate subspecies or species endemic to Borneo and peninsular Malaysia on one hand and to Sumatra on the other, we regard them as separate species, both of which occur on Borneo and Sumatra, with at least 1 apparent example of sympatric interaction recorded for the 2 taxa (see below). Recognition of the taxonomic distinction and geographic overlap between *brooksi* and *spadiceus* demonstrates that the genus is not only more taxonomically diverse than previously estimated (e.g., Koopman 1994), but also more ecologically complex.

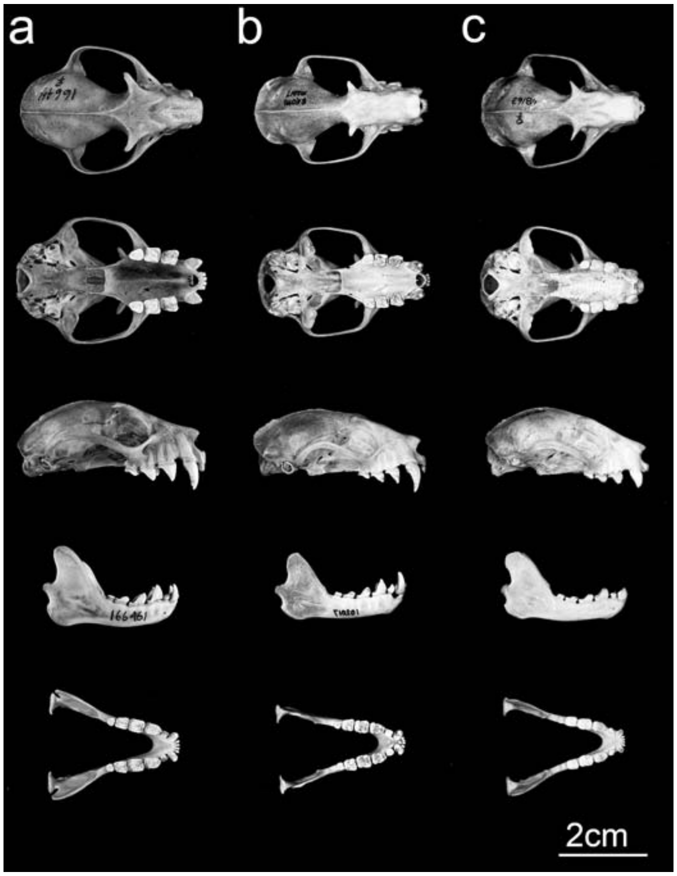

Fig. 3.—Representative skulls referred to a) *Dyacopterus rickarti* (left column: FMNH 166461, adult female, Mindanao), b) *D. brooksi* (middle column: ROM 102017, adult female, Borneo), and c) *D. spadiceus* (right column: ROM 48163, adult female, Borneo).

Table 1.—Selected craniodental measurements of adult specimens of *Dyacopterus spadiceus*, *D. brooksi*, and *D. rickarti*. "CBL M/F" = (average male CBL)/(average female CBL). "Palate" denotes the total number of palatal ridges, with the caveat that this trait has been verified for only 1 individual of each taxon. Based on all available skulls at BMNH, DMNH, FMNH, MZB, ROM, and SMF. Abbreviations are defined in the "Materials and Methods." Measurements of length are in millimeters.

	D. spadiceus (Sunda Shelf; $n = 15$)	*D. brooksi* (Sumatra, Borneo; $n = 3$)	*D. rickarti* (Philippines; $n = 3$)
CBL M/F	1.02	1.01	1.00
	(n = 5♂♂/8♀♀)	(n = 1♂/2♀♀)	(n = 1♂/2♀♀)
Palate	21 ridges	17–19 ridges	15–16 ridges
CBL	34.9 ± 0.58	36.8 ± 0.38	41.3 ± 0.95
	33.9–36.1	36.5–37.1	40.4–42.3
ZYG	25.5 ± 0.86	25.5 ± 1.33	28.0 ± 1.20
	23.9–27.6	24.3–27.0	26.7–28.8
MTR	13.0 ± 0.25	13.8 ± 0.12	15.0 ± 0.40
	12.5–13.4	13.7–13.9	14.6–15.4
BBC	15.4 ± 0.37	15.2 ± 1.07	17.0 ± 0.75
	14.9–16.1	14.5–16.4	16.1–17.6
ONL	9.9 ± 0.33	10.6 ± 0.06	11.9 ± 0.32
	9.4–10.5	10.5–10.7	11.5–12.1
IOB	7.5 ± 0.32	7.8 ± 0.70	9.1 ± 0.29
	6.8–8.1	7.3–8.6	8.8–9.4
POB	6.8 ± 0.48	6.3 ± 0.59	7.0 ± 0.33
	6.0–7.5	5.9–6.9	6.6–7.3
CC	7.8 ± 0.26	8.3 ± 0.14	8.3 ± 0.36
	7.4–8.3	8.2–8.5	7.9–8.6
MH	15.0 ± 0.29	15.8 ± 0.43	17.1 ± 0.78
	14.5–15.4	15.4–16.3	16.6–18.0

Systematics

Dyacopterus Andersen, 1912

Type species.—*Cynopterus spadiceus* (Thomas, 1890); see below.

Synonyms.—Full generic-level synonyms of *Dyacopterus* comprise only the lapses *Diacopterus* (Fain 1976) and *Dycopterus* (Abdullah and Hall 1997; Abdullah et al. 1997).

Generic diagnosis.—The species of *Dyacopterus* are small to medium-sized fruit bats (adult forearm length 74–97 mm, mass ≤ 150 g), gray-brown above and paler silvery gray below, with broad heads, short tails, short pelage, and wing membranes that attach to the 2nd toe. (Koopman [1994:34] stated that the tail is absent in *Dyacopterus*, but all 3 species have a short tail, 10–20% as long as the head and body.) The postorbital foramina are small to absent, the premaxillae are solidly fused anteriorly, P1 is absent, the cheek teeth are relatively massive and subquadrate in outline, and the foramen ovale is confluent with the caudal alar foramen (Andersen 1912; Giannini et al. 2006). The dental formula is i 2/2 (I1, I2, i1, i2), c 1/1 (C1, c1), p 2/3 (P3, P4, p1, p3, p4), m 1/2 (M1, m1, m2), total 28 (Andersen 1912; Giannini and Simmons, in press).

Specimens of *Dyacopterus* have sometimes been associated with *Thoopterus* in the past (Miller 1907; cf. Romagnoli and Springer 2000; possibly Elera 1895), which departs from *Dyacopterus* in typically retaining P1, in its sutured, less stout premaxillae (broader, lacking a clearly evident suture in *Dyacopterus*), in the profile of the nasal aperture (forming a deeply concave curve from the tip of nasals to the tip of the premaxillae in *Dyacopterus*, not so in *Thoopterus*), and in the shape and cuspidation of the cheek teeth (contrasts figured beautifully by Andersen [1912:663]).

Distribution and content.—The genus *Dyacopterus* is recorded in peninsular Malaysia and Thailand south of the Isthmus of Kra, on the largest islands of the Sunda Shelf (Borneo and Sumatra), and on the largest islands of the oceanic Philippines (Luzon and Mindanao; Fig. 4). Three species are recognized, as diagnosed and reviewed below.

Phylogenetics.—Essentially all authors have allied *Dyacopterus* as a member of a phyletic group of short-faced Asian bat genera, labeled taxonomically as the "Cynopterine section" (Andersen 1912) or the subfamily Cynopterinae, the latter now envisioned to encompass (in addition to *Dyacopterus*) the genera *Cynopterus*, *Ptenochirus*, *Megaerops*, *Balionycteris*, *Aethalops*, *Chironax*, *Otopteropus*, *Alionycteris*, *Haplonycteris*, *Penthetor*, *Latidens*, *Thoopterus*, and *Sphaerias* (Giannini and Simmons, in press). The more immediate phylogenetic relationships of *Dyacopterus* are not yet definitively established. Miller (1907) united *D. spadiceus* and *T. nigrescens* together in the genus *Thoopterus*. Andersen (1912:654) regarded the immediate relationships of *D. spadieus* as less

Table 2.—Selected linear and body mass measurements for adult specimens of the species of *Dyacopterus*. Shown are mean values ± *SD* above, with ranges given below. Based on all available specimens at BMNH, Central Mindanao University, DMNH, FMNH, MZB, ROM, SMF, and UPMIN, with additional external measurements from records reported by Start (1974, 1976), Abdullah and Hall (1997), Abdullah et al. (1997), and this paper. Measurements of length are in millimeters and of mass are in grams.

	D. spadiceus (Sunda Shelf)	*D. brooksi* (Sumatra, Borneo)	*D. rickarti* (Philippines)
Forearm	78.3 ± 1.71	81.8 ± 0.96	93.7 ± 2.13
	(74, 81.5)	(81, 83)	(91.0, 96.4)
	n = 21	*n* = 3	*n* = 6
Tibia	29.0 ± 1.42	29.3 ± 1.15	36.4 ± 2.42
	(27, 31)	(28, 30)	(35.0, 39.2)
	n = 15	*n* = 3	*n* = 3
Head−body	120.4 ± 7.76	118.0 ± 2.00	139.5 ± 5.30
	(106, 130)	(116, 120)	(130, 144)
	n = 7	*n* = 3	*n* = 6
Tail	19.1 ± 3.55	18.3 ± 1.53	21.7 ± 4.52
	(16, 26)	(17, 20)	(18, 29)
	n = 15	*n* = 3	*n* = 6
Ear	19.4 ± 1.12	20.3 ± 1.15	22.9 ± 2.01
	(18, 21)	(19, 21)	(21, 25)
	n = 12	*n* = 3	*n* = 5
Mass	84.2 ± 9.45	88.5	142 ± 5.29
	(70, 100)	(86, 91)	(138, 148)
	n = 9	*n* = 2	*n* = 3

certain, but noted that "it would seem to find its proper place in the vicinity of those genera (*Cynopterus*, *Ptenochirus*, *Megaerops*) in which the postorbital foramina are present and well-developed." Based largely on Andersen's (1912) data, morphological cladistic analyses presented by Romagnoli and Springer (2000) highlighted a potential phylogenetic link between *Dyacopterus* and *Thoopterus*, but with unsatisfactory resolution. *Dyacopterus* has not yet been sampled in published molecular phylogenetic studies (Alvarez et al. 1999; Colgan and Flannery 1995; Giannini and Simmons 2003, 2005; Hollar and Springer 1997; Kirsch et al. 1995; Romagnoli and Springer 2000; Springer et al. 1995).

Dyacopterus spadiceus (Thomas, 1890)

Cynopterus spadiceus Thomas, 1890:235.
T[*hoopterus*]. *spadiceus*: Miller, 1907:50.
Dyacopterus spadiceus: Andersen, 1912:651.
Dyacopterus spadiceus spadiceus: Medway, 1965:48.
Diacopterus [sic] *spadiceus*: Fain, 1976:51.
Dycopterus [sic] *spadiceus*: Abdullah and Hall, 1997:67.

Type material and type locality.—The holotype of *spadiceus* is BMNH 90.1.28.4, study skin and incomplete skull of an adult female, from "Baram, Sarawak" (Thomas 1890), collected by Charles Hose. The type locality, "Baram" could refer to the River, District, or Government Station that bore that name; Medway (1965:48) gave the locality as "Baram district." The settlement of Baram (= Claudeville), on the Baram River, was the historical seat of the Resident of Sarawak (e.g., Kükenthal 1896).

Table 3.—Principal component (PC) analysis factor loadings (Fig. 2). Abbreviations are defined in the "Materials and Methods."

	PC1	PC2	PC3
ONL	−0.9379	−0.1685	−0.0479
ZYG	−0.8411	0.4987	0.0545
BBC	−0.8003	0.5620	−0.0785
MTR	−0.9326	−0.2082	−0.1308
CC	−0.6540	−0.1008	0.7456
MH	−0.9260	−0.1831	−0.0833
Cumulative eigenvalue	0.0138	0.0156	0.0167
Cumulative % variance	77.4741	87.1790	93.3584

Referred material.—See Appendix I.

Revised diagnosis.—*Dyacopterus spadiceus* (Figs. 3, 5, and 6) is the smallest-bodied species of *Dyacopterus*, with condylobasal length (≤ 36.1 mm) measuring absolutely shorter than in *D. brooksi* or *D. rickarti* (Table 1). The skull is extremely robust, with the zygomata proportionately wider than in other *Dyacopterus* (the ratio of zygomatic width to condylobasal length averages 73% in *spadiceus*, compared to 69% and 71% in *brooksi* and *rickarti*, respectively). The 1st lower molar (m1) is proportionally narrowed relative to *D. brooksi* (ratio of m1 width to m1 averages 91% in *D. spadiceus*, compared to an average of 103% in *D. brooksi*). The soft palate bears 21 ridges (the central half of which are divided by a median ridge), more than in other *Dyacopterus* taxa (Peterson 1969; see below).

Distribution and natural history.—*Dyacopterus spadiceus* is restricted to the Sunda Shelf of southeast Asia (Fig. 4); its distribution includes the Malay Peninsula south of the Isthmus of Kra (peninsular southern Thailand and Malaysia) and the large islands of Sumatra and Borneo (the last including Kalimantan, Brunei, Sabah, and Sarawak). Thomas (1890) initially reported the discovery of the species in Borneo; its occurrence in the Malay Peninsula was 1st reported by Hill (1961). Subsequently, Hill (1992) queried its presence in peninsular Thailand, but a voucher specimen from a peat swamp forest in Narathiwat, southern Thailand (SMF 83778), confirms its occurrence there (Fig. 4). Here we report for the 1st time firm records of *D. spadiceus* from Sumatra (Table 5; Appendix I). Although it would presumably once have been a component of the chiropteran fauna of Singapore (Lane et al. 2006), *D. spadiceus* has never been recorded from there, and is quite likely to be locally extinct there today (cf. Brook et al. 2003; Corlett 1992; Lane et al. 2006; Pottie et al. 2005).

There is little evidence of consistent metric or qualitative morphological geographic variation among the currently allopatric populations of *D. spadiceus* found on the Malay Peninsula, on Sumatra, and on Borneo (Table 5); we do note that available skulls from mainland Malaysia and Thailand exhibit a trend toward slightly smaller lengths, but proportionally greater widths, relative to Bornean and Sumatran animals (cf. Table 5).

Vouchered records indicate that *D. spadiceus* inhabits lowland evergreen rain forest, with an elevational range extending from sea level to at least 1,190 m in Borneo (Bennett

Table 4.—Selected dental measurements (in mm) for the species of *Dyacopterus*, measured by the authors. w = width; l = length. r = *D. rickarti*, b = *D. brooksi*, s = *D. spadiceus*. Abbreviations are defined in the "Materials and Methods."

	r (SMF 33333, ♂, Luzon)	r (DMNH 5113, ♀, Mindanao)	r (FMNH 166461, ♀, Mindanao)	b (BMNH 20.1.15.1, ♂, Sumatra)	b (ROM 102017, ♀, Borneo)	b (MZB 13020, ♀, Sumatra)	s (BMNH 90.1.28.4, ♀, Borneo)	s (ROM 48163, ♀, Borneo)	s (MZB 13022, ♀, Borneo)	s (SMF 83778, ?, Thailand)
C1L	3.17	3.06	3.06	3.32	3.35	3.16	2.66	3.01	2.82	3.25
C1W	2.28	2.57	2.27	2.08	2.51	1.92	2.11	2.06	2.23	2.07
P3L	3.62	3.76	3.67	3.28	3.31	3.18	3.00	3.19	3.20	3.27
P3W	2.81	2.74	2.68	2.52	2.87	2.64	2.56	2.44	2.76	2.62
P4L	3.37	3.61	3.33	3.06	2.92	3.03	3.08	3.04	2.80	3.14
P4W	2.88	2.92	2.87	2.42	2.97	2.79	2.71	2.64	2.40	2.73
M1L	2.97	2.89	3.02	2.43	2.76	2.64	2.68	2.38	2.40	3.32
M1W	2.51	2.48	2.40	2.11	2.40	2.11	2.32	2.09	1.89	2.26
p1L	1.44	1.59	—	—	—	1.60	—	—	1.40	1.64
p1W	1.68	1.64	1.60	1.63	1.60	1.63	1.49	1.46	1.53	1.65
p3L	3.71	4.15	4.00	3.53	3.56	3.53	3.58	3.50	3.53	3.35
p3W	2.62	2.59	2.65	2.54	2.60	2.46	2.51	2.29	2.32	2.39
p4L	3.53	3.85	3.88	3.33	3.10	3.35	3.20	3.25	3.25	3.60
p4W	3.13	3.09	2.96	2.65	2.92	2.52	2.78	2.57	2.43	2.75
m1L	2.99	2.93	3.11	2.41	2.53	2.60	2.81	2.50	2.40	2.63
m1W	2.83	2.63	2.71	2.41	2.76	2.56	2.41	2.39	2.29	2.59
m2L	1.98	2.04	1.81	1.45	1.65	1.53	1.69	1.50	1.44	1.59
m2W	2.13	1.86	1.73	1.60	1.76	1.50	1.63	1.56	1.45	1.77
c1L	1.90	2.23	2.21	2.45	2.13	2.48	2.23	1.97	2.38	2.00
c1W	2.36	2.42	2.13	2.52	2.52	2.24	2.08	2.18	2.39	2.49
C1 height	—	5.89	5.90	6.85	6.61	6.54	5.35	—	5.95	—
c1 height	—	4.23	4.01	5.31	4.76	4.46	4.57	—	4.20	—

et al. 1987; Koffron 2002). Specimens have been collected in or near forested areas at fruiting trees, along rivers, over paddy fields, near caves, in open terrain, and in peat swamp forests (Abdullah et al. 1997; Harrisson 1967; Lim 1967; Payne and Francis 1985). Although individuals are occasionally collected in the forest understorey (e.g., Francis 1990), it is now clear that this species forages primarily in the canopy of mature forest (Francis 1994; Hodgkison 2004b). Often considered rare in the past (e.g., Lim 1967; Medway 1969, 1978; Mickleburgh et al. 1992), *D. spadiceus* is now known to be locally common in appropriate habitats (Francis 1994; Hodgkison et al. 2003, 2004a, 2004b). According to Francis (1994), during mistnetting at Krau in peninsular Malaysia, *D. spadiceus* accounted for 17% of all bats taken in subcanopy nets (set 11–30 m off the ground); and at Sepilok (in Sabah, northern Borneo), 45% (Francis 1994).

Little information has been compiled about the basic roosting and feeding habits of *D. spadiceus*. Two individuals were taken from a roost in a cracked tree trunk about 2.5 m off the ground in peninsular Malaysia (Lim 1967). Payne and Francis (1985) described a group of *D. spadiceus* feeding in a fig tree (*Ficus* sp.) alongside *Cynopterus horsfieldii*. On the basis of extensive mistnetting at various vertical heights in rain forest at Krau, Hodgkison et al. (2004b:672) noted that *D. spadiceus* is "mainly active in open airspaces above the forest canopy, where they fed on the fruits and flowers of large emergent trees and strangler figs." Francis (2001) suggested that the massive cheek teeth of this species may be used to feed also on large, hard fruits; in a skull from peninsular Thailand (SMF 83778), the outer part of the left upper 4th premolar was broken off in life, perhaps indicating that *D. spadiceus* does indeed chew hard food particles. The massive teeth are likely also used to squeeze pulp and juice from soft fruit (Hodgkison et al. 2003).

Examination of data derived from museum specimens suggests that both sexes weigh approximately 70 g at sexual maturity (cf. Koffron 2002). Testis length ranges from 5.1 to 9.3 mm in mature males (Koffron 2002). In Brunei, 2 adult females each carried minute embryos (< 0.1 g, total length 1.1–1.6 mm) when collected on 10 June; 1 of the 2 was lactating (Koffron 2002). Pregnant and lactating females also have been collected in August on the Malay Peninsula and in September in Kalimantan (Abdullah et al. 1997; Francis et al. 1994). Studier et al. (1995) reported concentrations of milk minerals in lactating mothers. This species exhibits little or no sexual size dimorphism (e.g., Table 1), and lactation has been recorded in both sexes (Francis et al. 1994). (Among all mammals, male lactation is singularly unique in *Dyacopterus* under natural conditions [Francis et al. 1994].) Although these traits strongly suggest that *D. spadiceus* is obligately monogamous (Francis et al. 1994), no studies of socioecology have been reported.

Maa (1968) speculated that the batfly *Leptocyclopodia brachythrinax* Theodor, 1959, of northern Borneo, the host of which was unknown, in fact parasitized *D. spadiceus*. Fain (1976) recorded an astigmatic mite (*Ladibocarpellus selangorensis*) as a parasite of *D. spadiceus* in peninsular Malaysia.

Dyacopterus brooksi Thomas, 1920

Dyacopterus brooksi Thomas, 1920:284.
Dyacopterus spadiceus: Medway, 1965:48.
D[*yacopterus*]. *s*[*padiceus*]. *brooksi*: Koopman, 1994:34.

TABLE 5.—Forearm and selected craniodental measurements (in mm) for regional populations of *Dyacopterus spadiceus*. Shown are mean values ± *SD* above, with minimum and maximum values and sample size (*n*) given below. Based on all available adult specimens at BMNH, MZB, ROM, and SMF, with additional external measurements from records reported by Start (1974, 1976), Abdullah and Hall (1997), and Abdullah et al. (1997), who deposited their specimens in Malaysian museum collections. Abbreviations are defined in the ''Materials and Methods.''

	D. spadiceus (Borneo)	*D. spadiceus* (Sumatra)	*D. spadiceus* (Malay Peninsula)
FA	78.3 ± 1.10	78.8 ± 1.30	77.5 ± 3.41
	(76, 80)	(77, 80)	(74, 81.5)
	n = 12	*n* = 5	*n* = 4
CBL	35.2 ± 0.66	34.9 ± 0.65	34.8 ± 0.43
	(34.7, 36.1)	(33.9, 35.9)	(34.3, 35.4)
	n = 4	*n* = 6	*n* = 4
ZYG	25.2 ± 0.57	25.3 ± 0.83	26.1 ± 1.06
	(24.6, 26.0)	(23.9, 26.0)	(25.0, 27.6)
	n = 5	*n* = 6	*n* = 4
MTR	13.0 ± 0.10	12.9 ± 0.26	12.9 ± 0.38
	(12.9, 13.2)	(12.5, 13.2)	(12.6, 13.4)
	n = 5	*n* = 6	*n* = 4
BBC	15.4 ± 0.35	15.4 ± 0.36	15.6 ± 0.33
	(14.9, 15.8)	(14.9, 16.1)	(15.2, 16.0)
	n = 5	*n* = 6	*n* = 4
ONL	9.8 ± 0.28	9.8 ± 0.30	10.2 ± 0.35
	(9.4, 10.1)	(9.5, 10.3)	(9.7, 10.5)
	n = 5	*n* = 6	*n* = 4
IOB	7.7 ± 0.28	7.3 ± 0.31	7.5 ± 0.28
	(7.3, 8.1)	(6.8, 7.6)	(7.3, 7.9)
	n = 5	*n* = 6	*n* = 4
CC	7.6 ± 0.26	7.9 ± 0.27	7.9 ± 0.10
	(7.4, 8.0)	(7.6, 8.3)	(7.8, 8.0)
	n = 5	*n* = 6	*n* = 4

Type material and locality.—The holotype of *brooksi* is BMNH 20.1.15.1, an adult male represented by a body in alcohol, with the skull extracted and cleaned, from Lebong Tandai (= Lebongtandai, 03°01′S, 101°54′E), on the Upper Ketuan River, ''about 100 miles north of Bencoolen,'' Sumatra, Indonesia, collected by C. J. Brooks, probably in 1920.

Referred material.—Two specimens in addition to the holotype are tentatively referred here to *D. brooksi*: ROM 102017, an adult female from Kayan Mentareng National Park in East Kalimantan (southeastern Borneo), and MZB 13020, an adult female from Gunung Leuser National Park in Aceh (northern Sumatra; Appendix I). In overall dimensions, these 2 specimens, both fully adult females, are not quite as large as the type of *D. brooksi*, and depart from the holotype in their relatively less expansive zygomata and braincase widths (Fig. 2). Additional specimens will be needed to determine whether these differences reflect consistent sex-related size and shape distinctions or normal individual variation within *D. brooksi*.

Revised diagnosis.—We regard the adult male type specimen of *D. brooksi* as undoubtedly taxonomically distinct from *D. spadiceus*, and more tentatively associate 2 additional *Dyacopterus* specimens with *brooksi* as well (see above). Our revised diagnosis of the species is thus based on examinations of all three specimens.

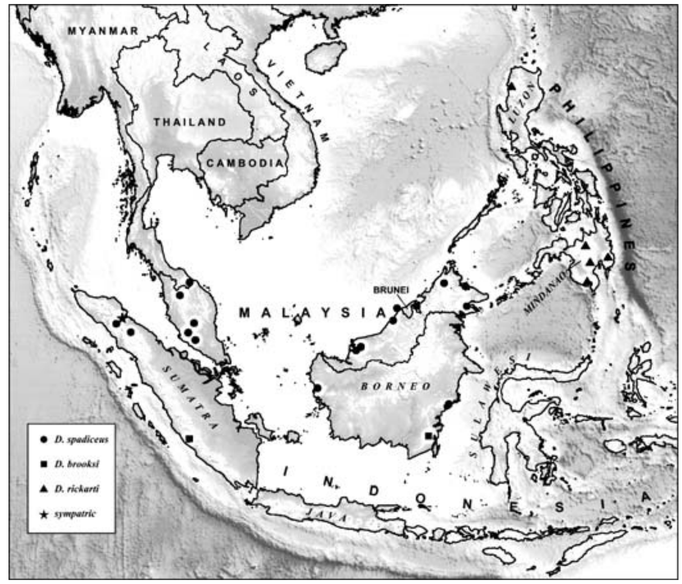

FIG. 4.—Distribution of *Dyacopterus*, showing all vouchered records of specimens referred here to *D. spadiceus* (circles), *D. brooksi* (squares), and *D. rickarti* (triangles). The area of recorded syntopy for *D. spadiceus* and *D. brooksi* is indicated with a star.

Dyacopterus brooksi (Figs. 3 and 7) is similar in overall size to *D. spadiceus*, but the forearm averages slightly longer (Tables 1 and 2). The cranium and mandible are longer than in *D. spadiceus* (Table 1), the rostrum is long and the braincase is proportionately more elongate (Fig. 3); the lateral frontal sinus is less conspicuously inflated; many teeth are more massive on average (Table 4), with the posterior basal ledges of postcanine teeth undeveloped; m1 is proportionately widened relative to both other species in the genus, because of an expanded anterolateral cusp (width of m1 measuring ≥ 98.5% of m1 length compared to ≤ 98.5% in *D. spadiceus* and *D. rickarti*); and the canines are proportionately longer and wider than other *Dyacopterus*, with well-developed posterointernal cingula. Despite the larger size of *D. brooksi*, the skull is not as robust as that of the smaller-skulled *D. spadiceus*, which has wider zygomata on average (averaging 73% of condylobasal length) than *D. brooksi* (averaging 69%; see Fig. 3). Likewise, the braincase is not as laterally expansive as in *D. spadiceus*. Postorbital processes of the specimen of *D. brooksi* from northern Sumatra are longer and heavier than other specimens taken sympatrically that we identify as *D. spadiceus* (cf. Thomas 1920), but this difference is apparently not entirely consistent (cf. Fig. 3). The soft palate of *D. brooksi*, as described by Thomas (1920), bears 17–19 ridges in an arrangement different from other *Dyacopterus* (Table 1), with the posterior half of these ridges divided by a median cleft.

Dyacopterus brooksi and *D. spadiceus* are extremely similar in external appearance, both in overall size and in coloration. Judging from the holotype (see Thomas 1920), the pale yellowish area of the shoulders may be more extensive in *D. brooksi* than in *D. spadiceus*, although we consider this difficult to definitively assess in the specimens that we have examined. Thomas (1920) and other authors have emphasized

FIG. 5.—*Dyacopterus spadiceus* in life (with eyes closed). Photograph by Tigga Kingston, from Krau Wildlife Reserve, Peninsular Malaysia.

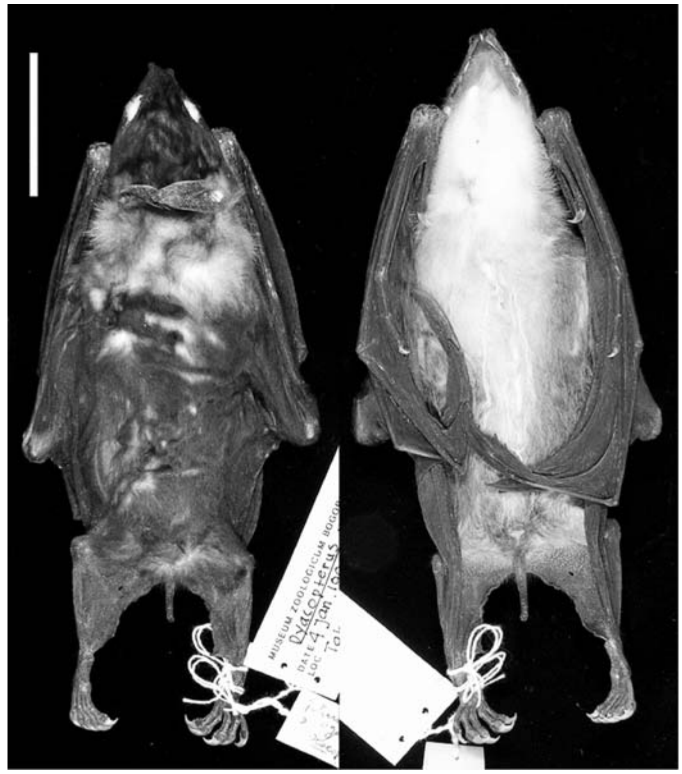

FIG. 6.—Representative study skin of *Dyacopterus spadiceus* (MZB 15374, adult male, Sumatra). Bar = 50 mm.

the ''prominent warts'' on the edge of the lips in the holotype of *brooksi*; these protuberances appear to likewise characterize the 2nd Sumatran specimen referred here to *D. brooksi* (MZB 13020), but we have not examined the skin of the Kalimantan skull tentatively referred to *D. brooksi*.

This species can be immediately distinguished from *D. rickarti* by its absolutely smaller skull, absolutely shorter forearm, much smaller body weight, proportionally wider molars, and different arrangement of palatal ridges (see below).

Distribution and natural history.—According to our identifications, specimens of *D. brooksi* are recorded from 3 forested localities in lowland Sumatra and Borneo—the type locality in southern Sumatra, 1 other locality in northern Sumatra (Sekunder, near Besitang in the vicinity of Gunung Leuser), and Lalat Barai Reserve Station in Kayan Mentareng Nature Reserve in East Kalimantan, Indonesian Borneo (Fig. 4).

The series from Sekunder also includes specimens referred here to *D. spadiceus* (Appendix I), suggesting that the 2 species occur sympatrically. MZB holds an additional small series of *Dyacopterus* from the vicinity of Gunung Leuser in Sumatra; these specimens are stored whole in alcohol and have not had their skulls extracted for craniometric examinations. Further study is needed to determine whether any of these specimens represent *D. brooksi*.

Essentially nothing is known of the natural history of *D. brooksi*. The few known localities indicate an association with mature lowland forests. The tag on the Kalimantan specimen (collected 30 May 1993 by M. Engstrom and B. Lim) bears the

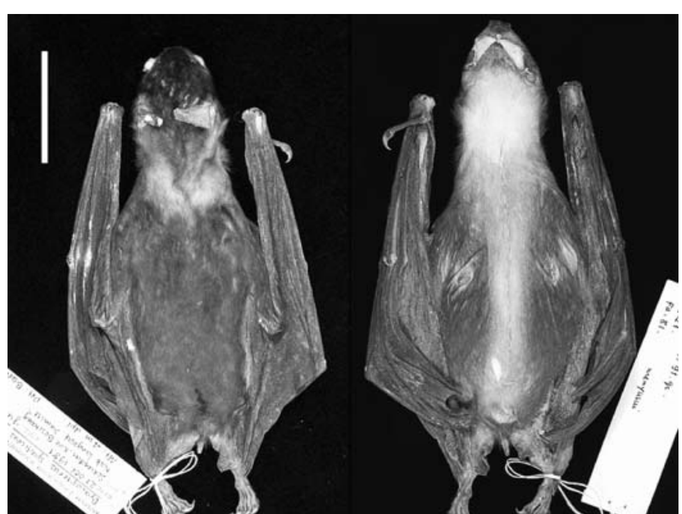

FIG. 7.—Representative study skin of *Dyacopterus brooksi* (MZB 13020, adult female, Sumatra). Bar = 50 mm.

Fig. 8.—Representative study skin of *Dyacopterus rickarti* (DMNH 5113, adult female, Mindanao). Bar = 50 mm.

phrase ''no embryos''; the Sekunder specimen (collected by Sugardjito) was lactating when collected on 21 October 1981. Judging from the number of specimens available in museum collections, *D. brooksi* would seem to be considerably rarer than *D. spadiceus*. Indeed, it is known from fewer museum specimens than is any other pteropodid from Sundaland.

Dyacopterus rickarti Helgen, Kock, Gomez, and Ingle, new species

(?) *Cynopterus latidens*: Elera, 1895:7.
Dyacopterus spadiceus: Kock, 1969:2.
Dyacopterus [?] *brooksi*: Hill, 1992:74.
Dyacopterus sp. Gomez, Ibañez, and Bastian, 2005:87.

Holotype.—SMF 33333, young adult male, skin, skull, and postcranial skeleton, in good condition, from San Isidro (17°27′N, 120°37′E), Luzon (Abra Province), Philippines, collected in April 1966 by Heinrich Bregulla (field number 4322). The altitude of collection is unrecorded, but Kock (1969) indicated that it originated from a mountainous region (i.e., the Cordillera Range of northern Luzon).

Referred specimens.—Six specimens, all from Mindanao:

DMNH 5113, adult female, skin and skull, from [Mt.] Malibato (06°06′N, 125°01′E), Mindanao (Opol, Misamis Oriental Province), altitude unrecorded, collected 28 June 1968 by D. S. Rabor.

FMNH 166461, adult female, body fixed in formalin and stored in 70% ethanol with skull extracted and cleaned, taken on Mt. Kitanglad at Barangay Lupiagan (08°11′20″N, 124°55′20″E), 1,450 m, Mindanao (Sumilao Municipality, Bukidnon Province), collected 29 November 1998 by N.,R. Ingle. See Ingle (2001, 2003) and Heaney et al. (in press) for further details regarding this locality.

UPMIN 20, adult male, stored intact in 70% ethanol, from Mt. Mahuson (07°13′5.3″N, 125°11′40.7″E), 1,260 m, Arakan Valley Conservation Area, Mindanao (Arakan Municipality, Cotabato Province), collected 18 May 2004 by J. C. Ibañez. See Gomez et al. (2005) for further details regarding this locality.

Three specimens from Purok Uduan (7°31′12.36″N, 126°13′47.1″E), 1,680 m, Barangay Andap, Mindanao (New Bataan Municipality, Compostela Valley Province), collected 1 May 2006 by R.K.S.C. Gomez (field numbers RKSG 47, 48, and 49, a subadult female, pregnant female, and adult male, respectively). These specimens will be deposited in the zoological collections of Central Mindanao University (Bukidnon, Philippines).

Diagnosis.—*Dyacopterus rickarti* (Figs. 3 and 8–10) is the largest-bodied species of *Dyacopterus*, with the skull (CBL > 40 mm) and forearm (> 90 mm) both measuring absolutely longer than in other species in the genus (Table 2; Figs. 1–3), and body mass measuring much larger (>135 g in *D. rickarti*, compared to ≤100 g in Sundaic *Dyacopterus*). The soft palate has 15 or 16 ridges, with the distal and proximal ones divided.

Etymology.—For Eric A. Rickart, Curator of Vertebrates at the Utah Museum of Natural History in Salt Lake City, and authority on Philippine mammals. We recommend ''Philippine Large-Headed Fruit Bat'' as an appropriate common name.

Distribution and natural history.—*Dyacopterus rickarti* is recorded to date only from Luzon and Mindanao, the 2 largest islands in the Philippines. As noted above, vouchered localities for the species include the type locality in northern Luzon (Abra Province) and 4 sites in Mindanao (Misamis Oriental, Bukidon, Cotabato, and Compostela Valley provinces). Together, these available records document its occurrence in lower montane to mossy rain-forest formations (1,260–1,680 m; Fig. 11). This appears to reflect a different pattern of habitat association in *D. rickarti* compared to *D. brooksi* and *D. spadiceus*, both of which are only known from lowland evergreen forests on the Sunda Shelf (<1,200 m). The altitude of the Malibato specimen is unrecorded, but Rabor's collections from June 1968 also include the owl *Mimizuku gurneyi* and the leafbird *Chloropsis flavipennis* (Collar et al. 2001), both of which are primarily lowland species with upper elevational limits at approximately 1,500 m (Collar et al. 2001; Kennedy et al. 2000).

Apart from habitat association, little information is yet available about the natural history of *D. rickarti*. The specimen from Mt. Kitanglad was captured 4 m above the ground in a net on a pulley system (Ingle 1993) set across a 6-m-wide dirt road through montane forest (1,450 m), about 400 m from the forest edge. It was the only *Dyacopterus* out of 909 fruit bats captured at the site by monthly mistnetting from August 1998 to November 1999 (Heaney et al., in press). The forested site where it was captured is contiguous with Mt. Kitanglad Range Natural Park. Oaks (*Lithocarpus* spp.) and oil-fruit trees (*Elaeocarpus* spp.) dominated the canopy, which was 20–25 m high. Fruiting trees in the general area that might be utilized by bats included *Elaeocarpus* spp., *Syzygium* spp., *Actinodaphne diversifolia*, and *Prunus grisea* (Ingle 2001). *Ficus* spp. were rare and all

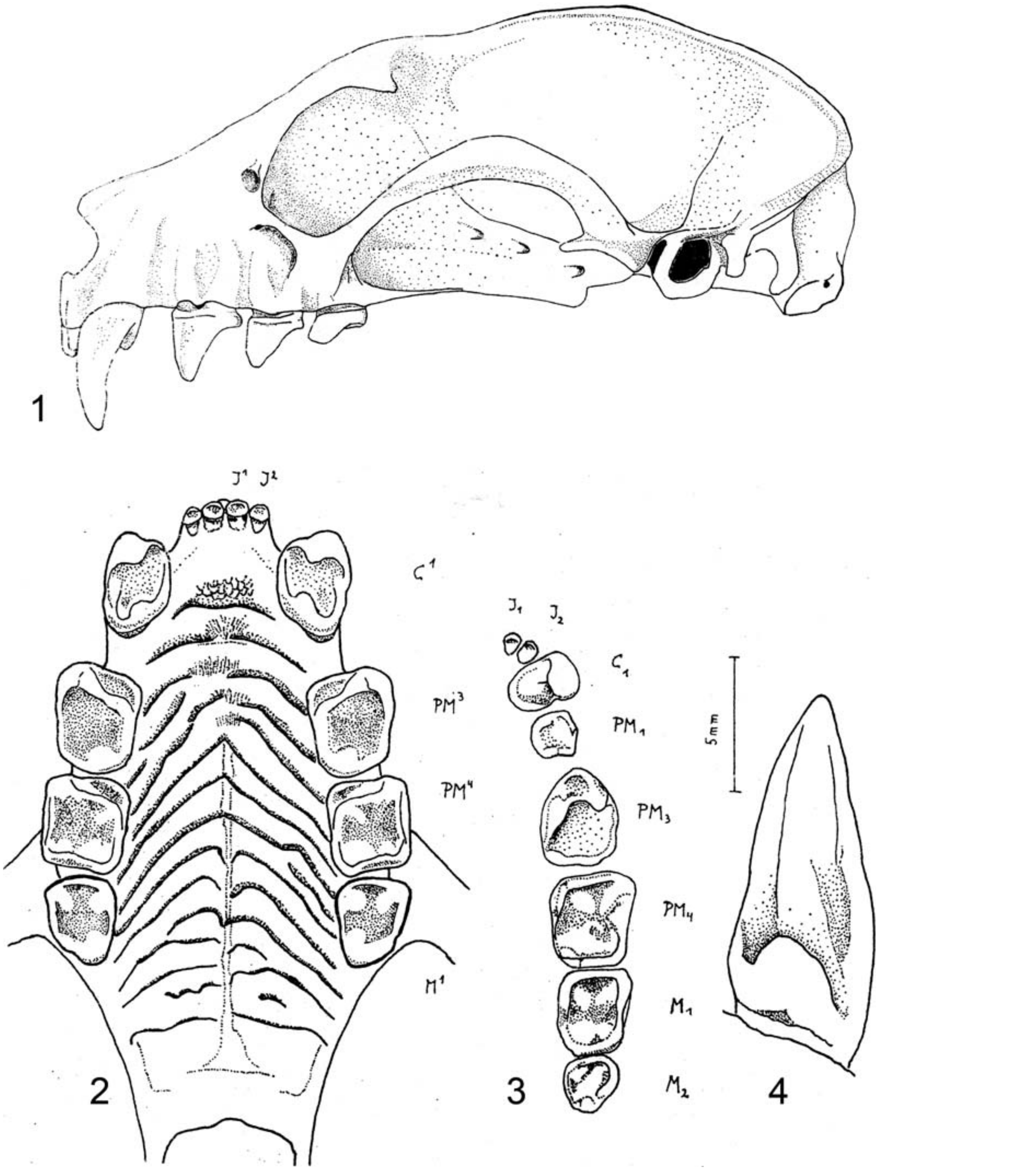

FIG. 9.—Craniodental attributes of *Dyacopterus rickarti*, based on the holotype, reprinted with permission from Kock (1969): 1) Cranium in lateral view. 2) Soft palate and maxillary dentition in ventral view. 3) Right mandibular dentition. 4) Posteroventral view of left upper canine.

were shrubs or free-standing trees; no strangler figs were present. Climbing pandans (*Freycinetia* spp.) were relatively abundant.

The specimen from Mt. Mahuson in the Arakan Conservation Valley was captured in a high net set at the edge of lower montane forest (1,260 m), and was the only *Dyacopterus* among 845 bats captured between 1,260 and 1,430 m during 1,150 net nights (Gomez et al. 2005). According to Gomez et al. (2005:90), the area is:

> . . .montane habitat with some areas of parang vegetation due to clearings in the past. These areas are now dominated by grasses and shrubs, especially buyo-buyo or *Piper aduncum*, ferns, baho-baho or *Lantana camara*, and Melastomaceae. Tree species locally known as walking and basikong (*Ficus* sp.) [were] common. Trees were also observed to have small diameter at breast height of 10–20 cm for the canopy trees and 30–40 cm for the emergent trees. Fruiting trees were also abundant and many fallen fruits were seen along the trail. Canopy trees reached 10–15 m in height with emergents reaching 20 m. . . . Emergent trees were mostly *Agathis philippinensis* . . . a few epiphytes were also seen growing on trees as well as vines. *Pandanus* sp. was also observed in the area as well as *Freycinetia* sp. There were also a few pitcher plants [*Nepenthes*]

Fig. 10.—*Dyacopterus rickarti* in life (pregnant female). Photograph courtesy of the Philippine Eagle Foundation, from Compostela Valley, Mindanao.

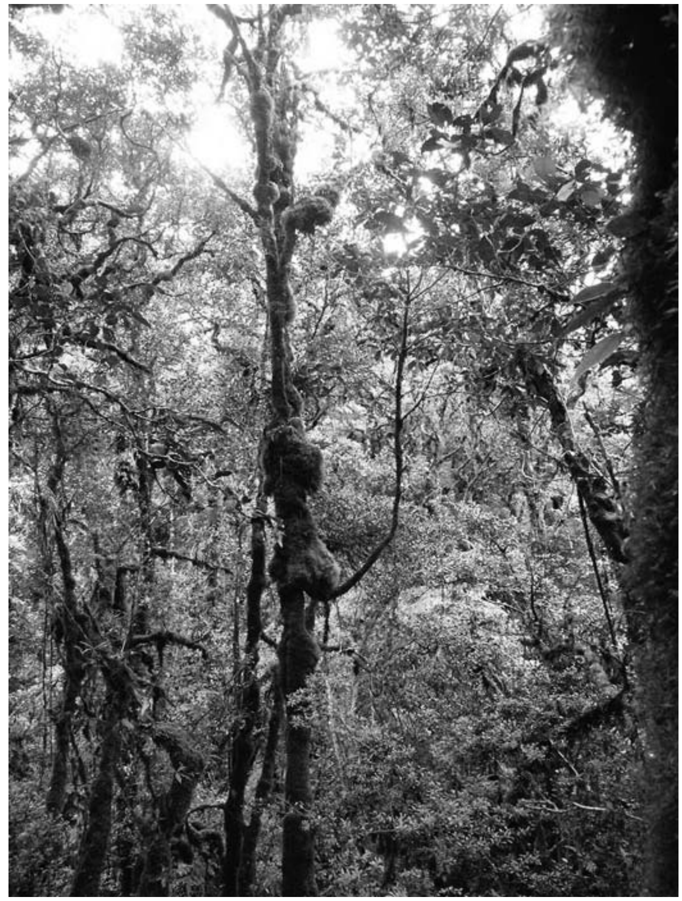

Fig. 11.—Habitat of *Dyacopterus rickarti*: mossy forest at 1,680 m at Purok Uduan, eastern Mindanao. Photograph courtesy of the Philippine Eagle Foundation.

seen growing in the area and the upper portion of some trees have moss. The area is about 2 km from a river.

The 3 specimens from Compostela Valley were taken in mist nets set along a high ridge in mossy forest (1,680 m). Pandanus and palms were fruiting in the vicinity, and the bats seemed to fly into the net from below the ridge. The latter captures include the only subadult and the only pregnant female recorded to date, both collected in May. Captures at Mt. Mahuson and in Compostela Valley both suggest that this species uses open areas or wide spaces as flyways, rather than flying through the forest understory (R. K. S. C. Gomez, pers. comm.).

More than a century ago, Elera (1895) reported records of *T. nigrescens* from the provinces of Laguna and Batangas in southern Luzon (then under the name combination "*Cynopterus latidens*," a perfect synonym of *Thoopterus nigrescens*). *T. nigrescens* is a fruit bat endemic to Wallacea (specifically to the Sulawesi subregion and the north Moluccas) that does not occur in the Philippines, but it closely resembles species of *Dyacopterus* phenetically, especially in its size, general external appearance, basic cranial conformation, and relatively massive cheek teeth (cf. Andersen 1912; Miller 1907). On this basis, we suspect that Elera's (1895) records may have been based on specimens of *D. rickarti* captured in southern Luzon. However, as far as we know, no modern museum material of *Dyacopterus* is associated with Elera's published identifications (indeed the holotype and earliest collected specimen of *D. rickarti* known to us dates from only 1966), although these earlier records could be based on specimens that are or were deposited in the museum of the University of Santo Tomás in Manila (cf. Elera 1915:78; Taylor 1934).

Description.—The holotype of *D. rickarti* has been described in detail elsewhere (Kock 1969). The following descriptive account emphasizes the most distinctive traits of *rickarti* as exemplified by all available specimens (2 specimens represented by skins and cleaned skulls, 1 fluid specimen with skull extracted and cleaned, and the remainder of specimens stored whole in fluid) and the ways in which these specimens together differ from *D. spadiceus* and *D. brooksi* of the Sunda Shelf.

Dyacopterus rickarti is a much larger bat than *D. spadiceus* and *D. brooksi* (Tables 1 and 2; Figs. 1–3), measuring absolutely larger than both of these species in forearm length, and averaging 70% and 60% larger in adult body mass compared to those species, respectively (Table 2). The pes measures 21–25 mm in length ($\bar{X} = 23.8$ mm $\pm$ 2.14 *SD*). As in the previously described members of the genus, and as is typical of cynopterine bats (Andersen 1912), there is little evidence of sexual size dimorphism (Table 1). Overall coloration of *D.*

TABLE 6.—Selected wing measurements (in mm) for the species of *Dyacopterus*. The type of *D. spadiceus* (BMNH 90.1.28.4) was measured by Andersen (1912:675), all others by the current authors. r = *D. rickarti*, b = *D. brooksi*, s = *D. spadiceus*. Abbreviations are defined in the "Materials and Methods."

	r (SMF 33333, ♂, Luzon)	r (UPMIN 20, ♂, Mindanao)	r (FMNH 166461, ♀, Mindanao)	r (DMNH 5113, ♀, Mindanao)	b (BMNH 20.1.15.1, ♂, Sumatra)	b (ROM 102017, ♀, Borneo)	b (MZB 13020, ♀, Sumatra)	s (MZB 15374, ♂, Sumatra)	s (MZB 12982, ♀, Sumatra)	s (BMNH 90.1.28.4, ♀, Borneo)
D2M	42.4	43	43.7	—	41.0	40.9	39.6	39.7	40.1	35.5
D2P1	12.3	12	10.6	—	10.9	9.8	9.3	9.6	8.5	8.5
D2P2	10.0	7	10.6	—	7.6	8.4	7.2	7.3	6.0	9.5
D3M	66.3	64	66.5	65.1	58.4	58.5	58.2	57.0	58.0	54.5
D3P1	43.4	43	45.5	43.5	39.3	37.2	39.6	36.8	37.4	35.0
D3P2	≈50	54	55.3	47.1	41.3	45.1	43.3	40.5	39.8	42.5
D4M	63.1	61	63.1	62.0	54.9	56.6	55.2	55.8	55.0	52.5
D4P1	37.0	40	38.6	35.3	34.2	32.7	32.4	32.6	31.6	30.5
D4P2	—	32	32.4	30.1	27.6	26.7	27.3	26.5	23.6	26.0
D5M	64.6	62	64.1	63.3	57.8	56.4	55.6	56.6	54.1	53.5
D5P1	28.5	31	31.1	30.1	27.8	25.5	24.0	26.2	23.0	23.5
D5P2	27.5	28	28.2	26.7	25.3	23.0	24.4	23.3	22.0	22.5

rickarti is similar to that of other *Dyacopterus*: warm brown dorsally, extending ventrally to the lower sides of the body, with paler gray fur covering the nape, throat, and midventer from breast to tail. The color of the crown is slightly darker than the dorsum, and a paler middorsal stripe is variably pronounced. A ring of light-colored hairs circumscribes the neck, with the hairs being somewhat lighter ventrally (on the sparsely furred throat) than dorsally (on the nape). A small hair tuft can be discerned on the shoulders, featuring longer hairs tipped with light-brownish tips. The ear is brown, relatively narrow, and pointed at the tip. No prominent "warts" can be discerned on the lips (cf. *D. brooksi*, see above). The wing membranes are blackish brown, sometimes with white spotting (wing measurements are provided in Table 6). Kock (1969) previously described the arrangement of soft palatal ridges in the holotype of *D. rickarti*, which bears 15 or 16 ridges, with the posterior and some of the anterior ridges divided (see Fig. 9). This differs notably from the palatal ridge arrangement described for *D. spadiceus* (21 ridges with the central half of the ridges divided—Peterson 1969) and is rather similar to that of *D. brooksi* (17–19 ridges with posterior ridges divided—Thomas 1920).

The skull of *Dyacopterus rickarti* differs from the 2 Sundaic species of the genus in its absolutely much larger size (Table 2; Figs. 1–3) as well as in proportional and qualitative aspects. The skull is long, the braincase and occiput are relatively very elongate, and the zygomata are robust and widely splayed in older animals (the holotype skull from Luzon is a young adult, the Mindanao skulls are from older animals), although not quite to the same extent as in series of the smaller-skulled *D. spadiceus* (see above). The sagittal and supraoccipital crests are well developed. The postorbital width is narrowed in comparison to other species, especially relative to the width of the interorbital region of the skull (ratio of POB to IOB < 0.80 in *D. rickarti*, compared to > 0.80 in other *Dyacopterus*). The infraorbital foramen is relatively large, broad, and clearly visible in lateral view. The nasal aperture is high relative to its width. The supraorbital foramina, minute in *D. spadiceus* and *D. brooksi*, are lacking.

The bases of the upper incisors are narrow, widening to their tips; the upper inner incisor pair (I1) is more vertically elongate than the outer pair (I2). The lower incisors are narrower than the uppers and are spaced slightly apart, with the outer pair slightly taller than the inner. A moderately developed vertical grove is evident on the anteromedial surface of the upper canines; the upper canines also bear a posterolateral basal cusp and an internal cingular ledge that is longer than broad. The canines are relatively very long. All of the premolars and molars are relatively high-crowned and bear prominent raised ridges around their edges, especially on the posterior borders. Cusps and ridges of postcanine teeth are as in *D. spadiceus* (Andersen 1912; Kock 1969). P4 bears a well-developed anteromedial cingular ledge. As in other *Dyacopterus*, P1 is lacking and p1 is relatively large compared to most fruit bats. The upper and lower 1st molars (M1 and m1) are longer than broad. The lower 2nd molar (m2) is relatively large and nearly rounded, only very slightly shorter than broad.

Dyacopterus rickarti shares a number of derived traits with *D. brooksi* to the exclusion of *D. spadiceus*, such as its larger body size, more elongate skull, and long canines, although all of these are likely linked to a single factor, size. Large size is assumed to be a derived trait because *D. rickarti* and *D. brooksi* are among the largest of the cynopterine bats (see below). Although larger size (especially larger cranial size) is shared between *D. rickarti* and *D. brooksi*, the overall phenetic resemblance between *D. brooksi* and *D. spadiceus* is striking and may reflect a close relationship. Phylogenetic relationships among the species of *Dyacopterus* can only be resolved by future phylogenetic analysis of additional data, particularly molecular sequence data.

DISCUSSION

Efforts aimed at inventorying mammalian biodiversity in the Philippines, as in many tropical areas worldwide, are still far from complete (Heaney et al. 1998; Heaney and Regalado

1998). New mammal species from the archipelago, especially murine rodents, are still regularly described in the literature, based both on new field discoveries and on new studies of older museum material (e.g., Heaney and Tabaranza 2006; Rickart et al. 2002, 2003, 2005). Although *D. rickarti* is the 1st new fruit-bat species from the Philippines to be named in nearly 3 decades (Yoshiyuki 1979), a number of additional unnamed pteropodid taxa from the archipelago are currently being described (e.g., Heaney et al. 1998).

Of all species recognized in the 14 megachiropteran genera currently classified in the subfamily Cynopterinae (see Giannini and Simmons, in press), *D. rickarti* is the largest. With the exception of the flying foxes (fruit bats of the genera *Pteropus* and *Acerodon*) and the Negros naked-backed fruit bat (*Dobsonia chapmani*), *D. rickarti* is the largest bat in the oceanic Philippines (Ingle and Heaney 1992). At an island scale, *D. rickarti* is the 3rd or 4th largest bat recorded from Mindanao (after *Acerodon jubatus* and *Pteropus vampyrus*; similar in body size to *Pteropus pumilus*) and the 4th or 5th largest bat recorded from Luzon (after *A. jubatus*, *P. vampyrus*, and *P. leucopterus*, again similar in size to *P. pumilus*—Heaney et al. 1998; Ingle and Heaney 1992). As a relatively larger-bodied and rarely recorded bat that is presumed to be dependent on forested habitats, *D. rickarti*, like other large Philippine fruit bats (e.g., Mildenstein et al. 2005), is considered a species of conservation concern (Mickleburgh et al. 1992; Utzurrum 1992). Although lowland forests in the Philippines have been extensively logged and converted to agricultural use in recent decades, if *D. rickarti* is primarily a species of montane forests, which are currently less accessible to human encroachment in many areas, it may be less threatened with extinction than those Philippine mammals that are obligate inhabitants of lower-elevation forests (Brooks et al. 1999; Heaney et al. 1998). On the basis of the few available captures and their associated ecological data, we suggest that insufficient information is available to satisfactorily categorize the conservation status of this new species, such that at present we recommend a formal ranking of "Data Deficient" under the current criteria of the World Conservation Union (Baillie et al. 2004).

Dyacopterus is 1 of a number of Asian pteropodid genera that extend to the oceanic Philippines but are more species-rich on the Sunda Shelf to the west (Fig. 4). Other examples include *Cynopterus* (1 species in the Philippines; up to 4 syntopic species on the Sunda Shelf), *Macroglossus* (1 species in the Philippines; 2 syntopic species on the Sunda Shelf), *Rousettus* (1 species in the Philippines; up to 3 syntopic species on the Sunda Shelf), and *Megaerops* (1 species in the Philippines; 2 syntopic species on the Sunda Shelf—Campbell et al. 2004; Heaney 1991; Hill 1992). This pattern of reduced diversity in the Philippines compared to Sundaland must ultimately be accountable to a complex combination of factors, likely reflecting especially the longer histories of these generic lineages in mainland Asia, oceanic barriers to dispersal from the Sunda Shelf to the Philippines, and the smaller land area of the Philippine archipelago (cf. Heaney 1991; Roberts 2006). Of all of these genera, it is the Philippine representative of *Dyacopterus* that exhibits the greatest amount of morphological divergence relative to its phylogenetic counterparts on the Sunda Shelf.

Sulawesi is a large island with dramatic relief and varied tropical forest formations. It is also the largest oceanic island immediately to the east of the Sunda Shelf. The majority of pteropodid genera represented in the fauna of the Sunda Shelf extend also to Sulawesi, including *Cynopterus*, *Chironax*, *Macroglossus*, *Eonycteris*, *Rousettus*, and *Pteropus*. Given the level of intensity with which the fruit-bat fauna of Sulawesi has been historically and recently sampled by collectors (cf. specimens at AMNH, BMNH, MZB, USNM, Dresden, Amsterdam, and Leiden—Bergmans and Rozendaal 1988), we suspect that the lack of records of *Dyacopterus* from Sulawesi reflects its legitimate absence from that island, rather than an artifact of insufficient study. Ancestors of extant taxa of *Dyacopterus* crossed major oceanic expanses to colonize the Philippines from the Sunda Shelf, or vice versa. We speculate that the failure of *Dyacopterus* to colonize Sulawesi is linked to the presence in Sulawesi of the cynopterine genus *Thoopterus*, an endemic Wallacean lineage of bats ecomorphologically similar to *Dyacopterus* (see above); 2 occasionally syntopic species of *Thoopterus* occur throughout much of Sulawesi (*T. nigrescens* and an unnamed species).

Dyacopterus rickarti is currently known only from the 2 largest islands in the Philippine archipelago—the island of Luzon in the north and Mindanao in the south (Fig. 4). Given this seeming disjunction, taxonomic differences might be expected between these 2 island populations, especially because Luzon and Mindanao have always been separated by deepwater boundaries (Steppan et al. 2003). However, given their close craniometric similarity (e.g., Table 1; Figs. 1–3), we recommend that on current evidence all specimens from the Philippines can be satisfactorily classified as a single species, *D. rickarti*. Many additional specimens will be needed to evaluate whether more complex patterns of morphological or genetic diversification, or both, characterize different insular populations of *D. rickarti*.

Although recorded to date from only a few sites, *D. rickarti* might be expected to occur in remaining montane forests throughout the large islands of Luzon and Mindanao, and perhaps also in similar habitats on intervening islands throughout the oceanic Philippines. The few records of the species may simply reflect inadequate sampling efforts: like *D. spadiceus*, this bat may rarely fly low. However, species of *Dyacopterus* are thus far known only from very large islands globally (Sumatra, Borneo, Luzon, and Mindanao, in addition to peninsular Thailand–Malaysia), all of which were formerly part of much larger Pleistocene landmasses (Heaney 1991; Heaney et al. 2005; Meijaard 2003; Roberts 2006; Steppan et al. 2003; Voris 2000). It seems possible that, as in certain other pteropodid genera dependent on old-growth habitats (particularly *Pteralopex*, the monkey-faced bats—see Helgen 2005), the long-term survival of populations of *Dyacopterus* may well require large islands, with extinction proceeding on smaller land-bridge islands following eustatic vicariance. If this is the case, then apart from the Malayan mainland, the genus could be truly restricted to the very largest islands in the broader Sundaic and Philippine regions. Continuing field surveys in appropriate forested habitats throughout the Philippines, especially those using methodologies appropriate to the detection of *Dyacopterus* (particularly canopy-netting), will undoubtedly shed additional light on the geographic distribution of this species.

Acknowledgments

For access to specimens and other assistance during museum visits, we especially thank P. D. Jenkins, R. Harbord, and D. Hills (BMNH); W. T. Stanley and L. R. Heaney (FMNH); A. Suyanto and I. Maryanto (MZB); G. Storch and K. Krohmann (SMF); and D. E. Wilson and L. K. Gordon (USNM). We also thank N. Giannini, N. Simmons, and D. Lunde, who provided us with access to the ROM specimens, currently on loan to the American Museum of Natural History (AMNH); G. Hess, who facilitated loan of specimens from DMNH; M. Kageyama, who photographed the ROM specimens at AMNH; L. E. Helgen, who prepared the photographic figures at USNM; and J. C. Ibanez, Jr., J. Eger, T. Kingston, and L. R. Heaney for advice and assistance with this manuscript. NRI was assisted in the field by R. Baylomo and A. Pepay, and thanks the Department of Environment and Natural Resources (Protected Areas and Wildlife Bureau), the Protected Areas and Management Board of the Mt. Kitanglad Range National Park, and the Kitanglad Council of Elders for permission to conduct her study. Fieldwork by RKSCG was supported by the Biodiversity Archiving and Assessment of the Philippine Eagle Foundation, funded by the Critical Ecosystem and Partnership Fund of Conservation International. Our taxonomic research has been supported by grants and fellowships to KMH from the United States National Science Foundation (Graduate Research Fellowship), the Australian–American Fulbright Commission, the American Society of Mammalogists (Fellowship in Mammalogy), the University of Adelaide, the Smithsonian Institution (Short-Term Visitor and Postdoctoral Fellowship Programs), and the South Australian Museum. Funding for NRI was provided by the Cornell International Institute for Food, Agriculture and Development; the Chicago Zoological Society; the Garden Club of America; Bat Conservation International; The Field Museum; the Sophie Danforth Conservation Biology Fund of the Rhode Island Zoological Society; and the Department of Natural Resources at Cornell University.

Literature Cited

Abdullah, M. T., and L. S. Hall. 1997. Abundance and distribution of fruit bats and other mammals in the tropical forest canopy in Borneo. Sarawak Museum Journal 51:63–74.

Abdullah, M. T., H. Siswanto, A. Widiyanto, A. Setiobudi, and Firmansyah. 1997. Abundance, diversity and distributional records of bats in disturbed habitats in Kalimantan Barat, Indonesia. Sarawak Museum Journal 51:75–84.

Alvarez, Y., J. Juste, E. Tabares, A. Garrido-Pertierra, C. Ibañez, and J. M. Bautista. 1999. Molecular phylogeny and morphological homoplasy in fruitbats. Molecular Biology and Evolution 16:1061–1067.

Andersen, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. 1: Megachiroptera. Trustees of the British Museum (Natural History), London, United Kingdom.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Baillie, J. E. M., C. Hilton-Taylor, and S. N. Stuart (eds.). 2004. 2004 IUCN red list of threatened species: a global species assessment. IUCN (World Conservation Union), Gland, Switzerland.

Bennett, E., J. O. Caldecott, and G. E. H. Davison. 1987. A wildlife survey of Ulu Temburong, Brunei. Brunei Museum Journal 6:121–169.

Bergmans, W., and F. G. Rozendaal. 1988. Notes on collections of fruit bats from Sulawesi and some off-lying islands (Mammalia: Megachiroptera). Zoologische Verhandelingen 248:1–74.

Brook, B. W., N. S. Sodhi, and P. K. L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424:420–426.

Brooks, T. M., S. L. Pimm, V. Kapos, and C. Ravilious. 1999. Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. Journal of Animal Ecology 68:1061–1078.

Campbell, P., C. J. Schneider, A. M. Adrian, A. Zubaid, and T. H. Kunz. 2004. Phylogeny and phylogeography of Old World fruit bats in the *Cynopterus brachyotis* complex. Molecular Phylogenetics and Evolution 33:764–781.

Colgan, D. J., and T. F. Flannery. 1995. A phylogeny of Indo-West Pacific Megachiroptera based on ribosomal DNA. Systematic Biology 44:209–220.

Collar, N. J., A. V. Andreev, S. Chan, M. J. Crosby, S. Subramanya, and J. A. Tobias. 2001. Threatened birds of Asia: the BirdLife International red data book. BirdLife International, Cambridge, United Kingdom.

Corlett, R. T. 1992. The ecological transformation of Singapore, 1819–1900. Journal of Biogeography 19:411–420.

Elera, C. de. 1895. Catálogo sistemático de toda la fauna de Filipinas conocido hasta el presente, y à la vez el de la colección zoológico del Museo de P.P. Dominicos del Colegio–Universidad de Santo Tomás de Manila, esrito con motivo de la exposición regional filipinas. Manila, Philippines.

Elera, C. de. 1915. Contribucion a la fauna Filipina. Universidad de Santo Tomás, Manila, Philippines.

Fain, A. 1976. Nouveaux acariens parasites de la superfamille Listrophoroidea (Astigmates). Acta Zoologica et Pathologica Antverpiensia 64:37–67.

Francis, C. M. 1990. Trophic structure of bat communities in the understorey of lowland dipterocarp rain forest in Malaysia. Journal of Tropical Ecology 6:421–431.

Francis, C. M. 1994. Vertical stratification of fruit bats (Pteropodidae) in lowland dipterocarp rainforest in Malaysia. Journal of Tropical Ecology 10:523–530.

Francis, C. M. 1995. The diversity of bats in Temengor Forest Reserve, Hulu Perak, Malaysia. Malayan Nature Journal 48:403–408.

Francis, C. M. 2001. A photographic guide to mammals of South-East Asia including Thailand, Malaysia, Singapore, Myanmar, Laos; Cambodia; Vietnam, Java, Sumatra, Bali and Borneo. Ralph Curtis Publishing, Sanibel, Florida.

Francis, C. M., E. L. P. Anthony, J. A. Brunton, and T. H. Kunz. 1994. Lactation in male fruit bats. Nature 367:691–692.

Gathorne-Hardy, F. J., Syaukani, R. G. Davies, P. Eggleton, and D. T. Jones. 2002. Quaternary rainforest refugia in south-east Asia: using termites (Isoptera) as indicators. Biological Journal of the Linnean Society 75:453–466.

Giannini, N. P., and N. B. Simmons. 2003. A phylogeny of megachiropteran bats (Mammalia: Chiroptera: Pteropodidae) based on direct optimization analysis of one nuclear and four mitochondrial genes. Cladistics 19:496–511.

Giannini, N. P., and N. B. Simmons. 2005. Conflict and congruence in a combined DNA–morphology analysis of megachiropteran bat relationships (Mammalia: Chiroptera: Pteropodidae). Cladistics 21:411–437.

Giannini, N. P., and N. B. Simmons. In press. Element homology and the evolution of dental formulae in megachiropteran bats (Mammalia: Chiroptera: Pteropodidae). American Museum Novitates.

Giannini, N. P., J. R. Wible, and N. B. Simmons. 2006. On the cranial osteology of Chiroptera. I. *Pteropus* (Megachiroptera: Pteropodidae). Bulletin of the American Museum of Natural History 295:1–134.

Gomez, R. K. S. C., J. C. Ibañez, and S. T. Bastian, Jr. 2005. Diversity and community similarity of pteropodids and notes on insectivorous bats in the Arakan Valley Conservation Area, Mindanao. Sylvatrop 15:87–102.

Harrisson, T. 1967. Bats netted in and around Niah Great Cave, 1965–6. Sarawak Museum Journal 14:229–233.

Heaney, L. R. 1991. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). Bulletin of the American Museum of Natural History 206:145–167.

Heaney, L. R., et al. 1998. A synopsis of the mammalian fauna of the Philippine Islands. Fieldiana: Zoology (New Series) 88:1–61.

Heaney, L. R., P. C. Gonzales, and A. C. Alcala. 1987. An annotated checklist of the taxonomic and conservation status of land mammals in the Philippines. Silliman Journal 34:32–66.

Heaney, L. R., and J. C. Regalado, Jr. 1998. Vanishing treasures of the Philippine rain forest. Field Museum of Natural History, Chicago, Illinois.

Heaney, L. R., and B. R. Tabaranza, Jr. 2006. A new species of forest mouse, genus *Apomys* (Mammalia: Rodentia: Muridae), from Camiguin Island, Philippines. Fieldiana: Zoology (New Series) 106:14–27.

Heaney, L. R., B. R. Tabaranza, Jr., D. S. Balete, E. A. Rickart, and N. R. Ingle. In press. The mammals of Mt. Kitanglad Nature Park, Mindanao, Philippines. Fieldiana: Zoology (New Series).

Heaney, L. R., J. S. Walsh, and A. T. Peterson. 2005. The roles of geological history and colonization abilities in genetic differentiation between mammalian populations in the Philippine archipelago. Journal of Biogeography 32:229–247.

Helgen, K. M. 2005. Systematics of the Pacific monkey-faced bats (Chiroptera: Pteropodidae), with a new species of *Pteralopex* and a new Fijian genus. Systematics and Biodiversity 3:433–453.

Hill, J. E. 1961. Fruit-bats from the Federation of Malaya. Proceedings of the Zoological Society of London 136:629–642.

Hill, J. E. 1967. Two unusual bats from Malaya. Federated Museum Journal (New Series) 11:58–60.

Hill, J. E. 1992. Order Chiroptera. Pp. 54–161 in Mammals of the Indomalayan region (G. B. Corbet and J. E. Hill, eds.). Oxford University Press, Oxford, United Kingdom.

Hodgkison, R., S. T. Balding, A. Zubaid, and T. H. Junz. 2003. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. Biotropica 35:491–502.

Hodgkison, R., S. T. Balding, A. Zubaid, and T. H. Junz. 2004a. Temporal variation in the relative abundance of fruit bats (Megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. Biotropica 36:522–533.

Hodgkison, R., S. T. Balding, A. Zubaid, and T. H. Junz. 2004b. Habitat structure, wing morphology, and the vertical stratification of Malaysian fruit bats (Megachiroptera: Pteropodidae). Journal of Tropical Ecology 20:667–673.

Hollar, L. J., and M. S. Springer. 1997. Old World fruitbat phylogeny: evidence for converegent evolution and an endemic African clade. Proceedings of the National Academy of Sciences 94:5716–5721.

Ingle, N. R. 1993. Vertical stratification of bats in a Philippine rainforest. Asia Life Sciences 2:215–222.

Ingle, N. R. 2001. Seed dispersal in Philippine montane rainforest and successional vegetation: role of birds, bats, and wind. Ph.D. dissertation, Cornell University, Ithaca, New York.

Ingle, N. R. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. Oecologia 134:251–261.

Ingle, N. R., and L. R. Heaney. 1992. A key to the bats of the Philippine Islands. Fieldiana: Zoology (New Series) 69:1–44.

Kennedy, R. S., P. C. Gonzales, E. C. Dickinson, H. C. Miranda, Jr., and T. H. Fisher. 2000. A guide to the birds of the Philippines. Oxford University Press, Oxford, United Kingdom.

Kirsch, J. A. W., T. F. Flannery, M. S. Springer, and F. J. Lapointe. 1995. Phylogeny of the Pteropodidae (Mammalia, Chiroptera) based on DNA hybridization, with evidence for bat monophyly. Australian Journal of Zoology 43:395–428.

Kock, D. 1969. *Dyacopterus spadiceus* (Thomas 1890) auf den Philippinen (Mammalia, Chiroptera). Senckenbergiana Biologica 50:1–7.

Koffron, C. P. 2002. The bats of Brunei Darussalam, Borneo. Mammalia 66:259–274.

Koopman, K. F. 1994. Chiroptera: systematics. Handbuch der Zoologie VIII Mammalia, Walter de Gruyter, Berlin, Germany.

Kükenthal, W. 1896. Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo, im Auftrage der Senckenbergischen naturforschenden Gesellschaft ausgeführt von Prof. Dr. W. Kükenthal. Erster Teil. Reisebericht. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 22:1–321.

Lane, D. J. W., T. Kingston, and B. P. H. Lee. 2006. Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia. Biological Conservation 131:584–593.

Lim Boo Liat. 1967. Abundance and distribution of Malaysian bats in different ecological habitats. Federation Museum Journal (New Series) 11:61–76.

Maa, T. C. 1968. Additions to the Cyclopodiinae. Part I etc. Pacific Insects 10:1–23.

Medway, L. 1965. Mammals of Borneo. Malaysian Branch of the Royal Asiatic Society, Singapore.

Medway, L. 1969. The wild mammals of Malaya and offshore islands including Singapore. Oxford University Press, London, United Kingdom.

Medway, L. 1978. The wild mammals of Malaya (Peninsular Malaysia) and Singapore. Oxford University Press, Kuala Lumpur, Malaysia.

Meijaard, E. 2003. Mammals of south-east Asian islands and their Late Pleistocene environments. Journal of Biogeography 30:1245–1257.

Mickleburgh, S. P., A. M. Hutson, and P. A. Racey. 1992. Old World fruit bats: an action plan for their conservation. IUCN, Gland, Swizerland.

Mildenstein, T. L., S. C. Stier, C. E. Nuevo-Diego, and L. S. Mills. 2005. Habitat selection of endangered and endemic large flying-foxes in Subic Bay, Philippines. Biological Conservation 126:93–102.

Miller, G. S., Jr. 1907. The families and genera of bats. Bulletin of the United States National Museum 57:1–282.

Payne, J., and C. M. Francis. 1985. A field guide to the mammals of Borneo. Sabah Society, Kota Kinabalu, Malaysia.

Peterson, R. L. 1969. Notes on the Malaysian fruit bats of the genus *Dyacopterus*. Life Sciences Occasional Papers of the Royal Ontario Museum 13:1–4.

Pottie, S. A., D. J. W. Lane, T. Kingston, and B. P. Y.-H. Lee. 2005. The microchiropteran bat fauna of Singapore. Acta Chiropterologica 7:237–247.

Rickart, E. A., L. R. Heaney, S. M. Goodman, and S. Jansa. 2005. Review of the Philippine genera *Chrotomys* and *Celaenomys* (Murinae) and description of a new species. Journal of Mammalogy 86:415–428.

Rickart, E. A., L. R. Heaney, and B. R. Tabaranza. 2002. Review of *Bullimus* (Muridae: Murinae) and description of a new species from Camiguin Island, Philippines. Journal of Mammalogy 83: 421–436.

Rickart, E. A., L. R. Heaney, and B. R. Tabaranza. 2003. A new species of *Limnomys* (Rodentia: Muridae: Murinae) from Mindanao Island, Philippines. Journal of Mammalogy 84:1443–1455.

Roberts, T. E. 2006. History, ocean channels, and distance determine phylogeographic patterns in three widespread Philippine fruit bats (Pteropodidae). Molecular Ecology 15:2183–2199.

Romagnoli, M. L., and M. S. Springer. 2000. Evolutionary relationships among Old World fruitbats (Megachiroptera: Pteropodidae) based on 12S rRNA, tRNA, valine and 16S rRNA gene sequences. Journal of Mammalian Evolution 7:259–284.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.

Springer, M. S., L. J. Hollar, and J. A. W. Kirsch. 1995. Phylogeny, molecules versus morphology, and rates of character evolution among fruitbats (Chiroptera: Megachiroptera). Australian Journal of Zoology 43:557–582.

Start, A. 1974. Notes on *Dyacopterus spadiceus* from Sarawak. Sarawak Museum Journal (New Series) 20:367–369.

Start, A. 1976. Another specimen of *Dyacopterus spadiceus* from Sarawak. Sarawak Museum Journal (New Series) 23:267.

Steppan, S. J., C. Zawadzki, and L. R. Heaney. 2003. Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. Biological Journal of the Linnean Society 80:699–715.

Studier, E. H., S. H. Sevick, D. E. Wilson, and A. P. Brooke. 1995. Concentrations of minerals and nitrogen in milk of *Carollia* and other bats. Journal of Mammalogy 76:1186–1189.

Taylor, E. H. 1934. Philippine land mammals. Monograph of the Bureau of Science (Manila) 30:1–548.

Thomas, O. 1890. Diagnosis of a new *Cynopterus* from Borneo. Annals and Magazine of Natural History (Series 6) 5:235–236.

Thomas, O. 1920. Two new Asiatic bats of the genera *Tadarida* and *Dyacopterus*. Annals and Magazine of Natural History (Series 9) 5:283–285.

Utzurrum, R. C. B. 1992. Conservation status of Philippine fruit bats (Pteropodidae). Silliman Journal 36:27–45.

Voris, H. K. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. Journal of Biogeography 27:1153–1167.

Yoshiyuki, M. 1979. A new species of the genus *Ptenochirus* (Chiroptera, Pteropodidae) from the Philippine Islands. Bulletin of the National Science Museum (Tokyo), Series A, Zoology 5:75–81.

Zubaid, A. 1993. A comparison of the bat fauna between a primary and fragmented secondary forest in Peninsular Malaysia. Mammalia 57:201–206.

Submitted 15 August 2006. Accepted 31 October 2006.

Associate Editor was Carey W. Krajewski.

Appendix I

Gazetteer of vouchered localities for *Dyacopterus* on the Sunda Shelf, based on specimens examined and selected references. For vouchered localities and specimens examined of *D. rickarti*, see text.

Dyacopterus spadiceus.—BRUNEI: Batu Apoi National Park (Sungai Tembrong; summit of Bukit Tudal, 1,181 m), approximately 4°42′N, 115°06′E (Bennett et al. 1987; Koffron 2002). INDONESIA: Aceh (Sumatra); Gunung Leuser National Park (Ketambe Research Station, approximately 500 m fide Gathorne-Hardy et al. 2002), 03°41′N, 97°39′E (MZB 12982); Gunung Leuser National Park (Sekunder, 4 m), approximately 04°N, 98°E (MZB 13021, 13022). Kalimantan Timur (Borneo); Wanariset Semboja, 00°59′48″S, 116°58′37″E (MZB 12688–12693). Kalimantan Barat (Borneo); Pontianak (Universitas Tanjungpura Campus), 00°03′50″S, 109°20′29″E (Abdullah et al. 1997). Sumatra Utara (Sumatra); Tahura (= Bukit Barisan Forest Park, Tongkoh), approximately 03°11′N, 98°30′E (MZB 15374, 15403). MALAYSIA: Negri Sembilan (Peninsular Malaysia); Kuala Pilah, Bukit Tembusu, approximately 02°44′N, 102°15′E (BMNH 64.781—Hill 1967). Pahang (Peninsular Malaysia); Krau Wildlife Reserve, 03°43′N, 102°10′E (Francis 1994; Hodgkison et al. 2004a, 2004b; Studier et al. 2005; Zubaid 1993). Perak (Peninsular Malaysia); Temengor Forest Reserve (near Sungai Halong camp), approximately 05°20′N, 101°21′E (Francis 1995). Sabah (Borneo); Baturong Caves, 04°42′N, 118°01′E (Payne and Francis 1985); Kinabalu National Park (Poring, 579 m), 06°02′40″N, 116°42′17″E (Abdullah and Hall 1997); Sepilok Forest Reserve, 05°52′N, 117°56′E (Francis 1990). Sarawak (Borneo); "Baram District," approximately 04°35′N, 113°58′E (BMNH 90.1.28.4—Thomas 1890); Binatang, 02°10′N, 111°38′E (ROM 48163—Peterson 1969); Niah River (near Niah Cave), 03°52′N, 113°44′E (Harrisson 1967; Start 1974, 1976); Sibu, 02°18′N, 111°49′E (Payne and Francis 1985). Selangor (Peninsular Malaysia); Kajang District, Ulu Langat Forest Reserve, 03°10′N, 101°50′E (BMNH 60.738—Hill 1961). THAILAND: Narathiwat; Amphoe Sungai Padi, 06°05′N, 101°54′E (SMF 83778).

Dyacopterus brooksi.—INDONESIA: East Kalimantan (Borneo); Kayan Mentareng Nature Reserve (Lalat Birai Reserve Station), 02°51′N, 115°48′E (ROM 102017). Aceh (Sumatra); Gunung Leuser National Park (Sekunder, 4 m), approximately 04°N, 98°E (MZB 13020). Bengkulu (Sumatra); Lebong Tandai, Upper Ketuan River, 03°01′S, 101°54′E (BMNH 20.1.15.1—Thomas 1920).