Karl-L. Schuchmann (editor)

TROPICAL VERTEBRATES IN A CHANGING WORLD

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PREFACE

During May 3 – 8, 2009, the Alexander Koenig Zoological Research Museum (ZFMK) hosted the 6th International Tropical Zoology Symposium. This series of symposia was established in 1984 with the intention of bringing together specialists from various fields of tropical research to contribute to a better understanding of the organisms found in the most complex ecosystems, those spanning the Earth around the equator.

The 6th symposium in 2009 was organized by the curators of the Vertebrate Department. The topic "Tropical Vertebrates in a Changing World" was chosen to draw attention to the stochastic impacts of climate change and direct man-made habitat alterations on various levels of vertebrate communities.

Symposium sessions were arranged geographically (Africa and Madagascar, Central and South America, South-East Asia), and opened by six plenary talks.

The meeting was attended by over 150 colleagues from 16 nations: Australia, Ecuador, Kenya, Madagascar, South Africa, Thailand, USA, Vietnam, and eight European countries. A total of 50 oral presentations and 23 posters were featured.

The papers published in this proceedings issue are arranged in taxonomic order, ranging from fishes, amphibians, and reptiles to birds and mammals. All contributions were peer-reviewed.

I wish to express my special thanks to my colleagues from the ZFMK Vertebrate Department for the excellent organization of the symposium, and to the many student helpers. Jobst Pfaender, however, stands out for his painstaking efforts to keep all administrative matters under control.

Last but of course not least, I thank the authors and reviewers for their excellent cooperation and patience throughout the process of editing this volume. Superb editorial help was provided by Alexandra Schuh and Brian Hillcoat.

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Karl-L. Schuchmann, Editor.
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ON THE PHYLOGENETIC AFFINITY OF THE EXTINCT ACRODONTAN LIZARD *TINOSAURUS*

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ABSTRACT

North American species of the fossil lizard taxon *Tinosaurus* have been considered as indeterminate agamids or acrodontans for nearly a century. New material from the late Eocene Chadron Formation of North Dakota, USA, may provide the first glimpse of non-dental cranial elements of this taxon and so new information on the affinity of North American *Tinosaurus*. The ectopterygoid is most securely referred and shows a unique apomorphy of extant *Leiolepis* (butterfly lizards): a dual articulation of the pterygoid on the ectopterygoid. Other elements show a mosaic of sometimes conflicting apomorphies. Ultimately, the evidence provided by the new elements on the phylogenetic position of North American *Tinosaurus* is not strong, and some of them might pertain to a co-occurring iguanid lizard, *Cypressaurus* sp. MPH. Even if further work were to turn up more support for a union of *Leiolepis* and North American *Tinosaurus*, this would not necessarily apply to any nominal species of *Tinosaurus* outside of that continent. If *Tinosaurus* actually is related to *Leiolepis*, it constitutes another example of a modern tropical taxon with extratropical stem representatives in the greenhouse world of the Eocene.

Key words: Squamata, Iguania, Agamidae, Eocene, dispersal, climate change, North America, Asia.

INTRODUCTION

Acrodonta, comprising the possibly paraphyletic taxon Agamidae* (agamas, dragons, mastigures, etc.) and Chamaeleonidae, is today an exclusively Old World clade of lizards (e.g., Moody 1980). Leidy (1872), however, recognized that a species represented by a jaw fragment from the Eocene Bridger Formation of Wyoming, USA, is also referable to the group. He erected the name *Chamaeleo pristinus* for it and later (1873) gave the specimen a fuller description. He did not realize, however, that Marsh (1872) had previously named (but not figured) a new "carnivorous lizard," *Tinosaurus stenodon*, also from the Bridger, which likely pertained to the same lineage. Estes (1983) questioned the distinction of the two species but did not formally synonymize the former with the latter. Camp (1923) concluded that *Tinosaurus* could not be distinguished from either *Chamaeleo* (Chamaeleonidae) or *Calotes* (Agamidae*), implicitly questioning the diagnostic value of the type material. *Tinosaurus* has subsequently been recognized throughout the Eocene of North America (Gunnell & Bartels 1999; Gunnell & Bartels 2001; Hirsch *et al.* 1987; Kelly *et al.* 1991; McGrew *et al.* 1959; Moody 1980; Pearson 1998; Schatzinger 1975; Smith 2006a, b), although no new species have formally been named. On the other hand, a host of new nominal species has been referred to the genus from the Old World (Augé & Smith 1997; Averianov 2001; Dong 1965; Hou 1974; Li 1991; Li & Xue 2002; Prasad & Bajpai 2008), primarily on the basis of tricuspid, acrodont cheek teeth and early Tertiary age (Estes, 1983).

The chief difficulty in understanding "*Tinosaurus*" is that tricuspid teeth of a similar form are probably present in some 200 living species of Agamidae*, principally those species placed in Draconinae and *Leiolepis* (Smith *et al.* 2011), following the taxonomy of Macey *et al.* (2000). No other features of phylogenetic significance are known, which partly relates to the fact that the only described elements of *Tinosaurus* are from the jaws. At the present time, even polyphyly of "*Tinosaurus*" cannot be excluded. Although it is necessarily true that species of "*Tinosaurus*" have definite affinities with extant clades, no data are available that would link any nominal species of the genus to a particular clade.

In this paper I refer non-dental cranial remains of a species of *Tinosaurus*, in particular one from North America, for the first time. The material was discovered during recent examination of bone concentrate derived from screenwashing of the late Eocene Chadron Formation of North Dakota by crews of the Pioneer Trails Regional Museum under the direction of Dean Pearson. The material pertains to the Medicine Pole Hills local fauna, which was already known to preserve remains of a species of *Tinosaurus* (Pearson 1998; Smith 2006b). After describing the material, I present detailed comparative osteological observations on living acrodontan lizards (Appendix), and analyze the implications of the new character data for the relationships of North American *Tinosaurus* and their potential significance for biogeography and divergence times in Acrodonta.

For modern comparative specimens examined, see Appendix. Institutional abbreviations: CM: Carnegie Museum of Natural History – Herpetology, Pittsburgh, Pennsylvania, USA; PTRM: Pioneer Trails Regional Museum, Bowman, North Dakota, USA; SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; UF: University of Florida Museum of Natural History, Gainesville, Florida, USA.

SYSTEMATIC SECTION

Squamata Oppel 1811

Iguania Cope 1864

Agamidae Spix 1825

Genus *Tinosaurus* Marsh 1872

Tinosaurus sp. MPH
[after Pearson 1998, Smith 2006a]

Figs. 1, 3, 5, 7

Newly referred specimens. PTRM 19083 (jaw fragment), 19112 (partial frontal; Fig. 7d), 19113 (partial frontal; Fig. 7a–c), 19134 (partial right ectopterygoid; Fig. 5), 19203–19205 (jaw fragments), 19307 (partial premaxilla), 19340 (left maxilla fragment; Fig. 3), 19429 (partial premaxilla), 19467 (frontal fragment), 19515 (partial premaxilla; Fig. 1), 19533 (right maxilla fragment).

Comments. These specimens, like all those recovered by screenwashing, are isolated from one another and fragmentary. Smith (2009a) briefly reviews the reasons for the secondary association of such isolated vertebrate remains. In the case of the Medicine Pole Hills local fauna, the chief difficulty in associating the remains at hand is the existence of a second, not uncommon iguanian species in the locality, *Cypressaurus* sp. MPH (Smith 2011), to which they could also plausibly be attributed. In fact, the number of identified dentigerous elements of *Cypressaurus* sp. MPH markedly exceeds that of *Tinosaurus* sp. MPH; relative abundance, then, might even favor the former species. Many acrodontan isolated elements are scarcely distinguishable from their counterparts in Iguanidae. However, in each case there appear to be subtle features inconsistent with typical morphologies in Iguanidae but concordant with Acrodonta or some part thereof. Thus, I provisionally refer them to that taxon, recognizing that the study of more numerous or complete elements from this locality or specimens of *Tinosaurus* from other North American localities could necessitate a revision in which some of these elements are referred to *Cypressaurus* sp. MPH.

In the following, I have assumed that only a single species of acrodontan was present in the locality. It is true that many modern localities feature more than a single species of acrodontan. However, there is no evidence that North America was colonized by more than one species, and no evidence that the lineage it spawned (*Tinosaurus*) was ever represented by more than a single species in a locality. The size of the specimens does not contradict their pertaining to a single species, nor are distinct morphotypes apparent where more than one specimen of an element is known. The most parsimonious interpretation is that all acrodontan specimens represent a single species. It is referred to *Tinosaurus* under the assumption that only a single lineage of Acrodonta ever reached North America (see Smith 2006a), which is parsimonious but not clearly demonstrable at present. Informal nomenclature follows Smith (2006a), with "MPH" referring to the Medicine Pole Hills. Smith (2009a) notes that the common practice of writing "*Genus* sp." is informal and not governed by the ICZN. The "MPH" provides a convenient short-hand for specifying a population even if it is not well enough preserved to warrant a formal name.

Description of new elements. *Premaxilla.* Three premaxillae are associated here. They are considered to represent an iguanian because of the morphology, which compares well to Iguania but is inconsistent with the anguid *Peltosaurus*, the only other taxon known from the locality that is large enough and present in sufficient abundance to have produced this premaxillary morphotype. The apomorphic presence of a posterior shelf with dorsal facet (see below) supports referral to Acrodonta rather than to Iguanidae. Most of the description, except where otherwise indicated, comes from the more complete PTRM 19515.

Description: The smallest specimen (PTRM 19429) is 2.2 mm across the main body, the largest (PTRM 19515) 4.4 mm. The anterior margin of the bone is distinctly curved in dorsal view (Fig. 1a). It extends nearly dorsally from just above its ventral edge (it is only weakly convex in sagittal cross-section), then curves abruptly toward the posterior (Fig. 1b). The nasal process (n.pr.), only the base of which is preserved, extends posterodorsally; its anterior surface is weakly convex in cross-section (Fig. 1b, c). A facet for the nasal is not present on the preserved portion of the nasal process (Fig. 1d). Lateral to the base of the nasal process on each side is a pair of tiny foramina, which presumably correspond to the posterior premaxillary foramina (p.pm.f.) of Bahl (1937); through them the maxillary artery and a portion of the ethmoidal nerve entered. On the left side of PTRM 19307 that foramen is single, not double. Lateral to these foramina is a rounded ridge that extends to the lateral-most margin of the bone and

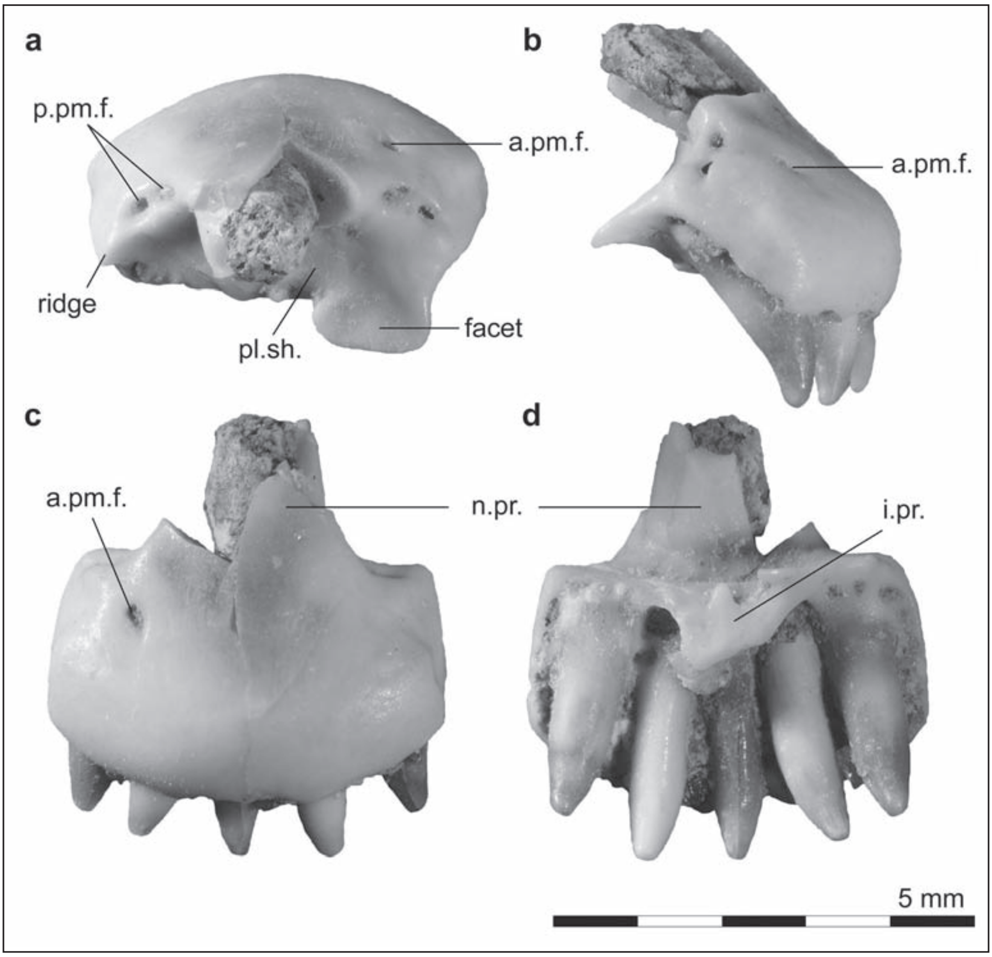

FIG. 1. Partial premaxilla of *Tinosaurus* sp. MPH, PTRM 19515, in (a) dorsal, (b) right lateral, (c) anterodorsal, and (d) posteroventral views. Abbreviations: a.pm.f., anterior premaxillary foramen; i.pr., incisive process; n.pr., nasal process; pl.sh., palatal shelf; p.pm.f., posterior premaxillary foramen.

divides the maxillary articulation into a large labial portion and a small lingual one (Fig. 1a). The maxillary articulation does not appear to run up the lateral edge of the nasal process, which is somewhat surprising. All acrodontans have a strong dorsal projection at the anterior end of the premaxillary process of the maxilla which articulates on the lateral surface of the premaxilla (Evans *et al.* 2002). However, in most taxa the ethmoidal nerve exits the nasal capsule onto the snout through a dorsoventrally elongate foramen located between the premaxilla and the dorsal projection of the maxilla. Thus, the articulation between premaxilla and maxilla along the projection is not continuous (except in *Uromastyx*[1], in which the ethmoidal nerve penetrates the premaxilla and forms a pair of foramina on its anterior surface, and *Physignathus cocincinus* and perhaps a few other taxa, where the foramina appear to be greatly reduced or absent). The absence of a dorsal maxillary articulation in *Tinosaurus* sp. MPH suggests that these foramina were located low on the snout. On the right side of PTRM 19515 only there is a small anterior premaxillary foramen (a.pm.f.), which would have transmitted a branch of the ethmoidal nerve onto the snout.

Posterior to the nasal process is a shelf, weakly dorsally concave in transverse section (Fig. 1a, pl.sh.). Along the anterior margin of this shelf, at the base of the nasal process, is a curvilinear series of about five tiny foramina. Posteriorly the shelf is divided by a wide median cleft. On either side of the cleft is a posterior continuation of the palatal shelf whose dorsal surface is marked by a weak oval depression (facet) for articulation with the maxilla. A pair of struts projects ventromedially from the underside of the posterior continuation of the shelf (Fig. 1d). These struts fused on the midline to form a distinct, anteroposteriorly compressed, tabular incisive process (i.pr.). On the dorsal edge of this plate is a peg-like projection that extends as far dorsally as the dorsal surface of the palatal shelf. Anterior to this projection is a foramen that runs dorsoventrally through the palatal shelf.

Both of the more complete specimens had five simple, pleurodont teeth (Fig. 1c, d). These teeth are stocky. Their bases are circular in cross-section. Just below the jaw parapet they begin to taper, terminating in conical tips; the tips are distinctly posteriorly decurved, sometimes also with a distal component (e.g., first right tooth: Fig. 1d) which gives them a diverging appearance. No carinae or striae are evident. The base of the first right tooth appears to be eroded, indicating that tooth replacement was in progress.

Comparisons: The size of the lateral processes of the premaxilla varies significantly in Acrodonta (Siebenrock 1895). In *Leiolepis* these are relatively stronger (Fig. 2b, l.pr.) than many other acrodontans, including Agaminae (Fig. 2a) and *Uromastyx* (Fig. 2c). Consequently, it also possesses a greater number of teeth: four teeth are present in each available specimen of *L. belliana,* whereas most other examined acrodontans have no more than three (except *Japalura polygonatus*, also with five, and some *Uromastyx*). Siebenrock (1895) lists only a few other taxa with four or more premaxillary teeth: *Hydrosaurus*, several members of Amphibolurinae (one species each of *Ctenophorus, Amphibolurus, Pogona*), and one species of *Gonocephalus. Tinosaurus* sp. MPH is thus similar to *Leiolepis* and a few other living acrodontans in having >3 teeth. Outgroup comparisons with Iguanidae (Smith 2009b) and stem acrodontans from the Late Cretaceous of Mongolia (Alifanov 1989; Borsuk-Białynicka & Moody 1984; Gao & Norell 2000) suggest that the condition of having large lateral processes and a high tooth count is plesiomorphic. However, its interpretation in *Leiolepis* depends in part on the phylogenetic position of that taxon.

Uromastyx appears to be distinctive in Acrodonta in commonly having anterior premaxillary foramina (Fig. 2f). I may have erred in stating that these are also present in *Leiolepis* (Smith, 2009a), for they are absent in the three specimens currently available to me (Fig. 2e). They only occasionally occur in other agamids, such as unilaterally in one *Trapelus pallidus* (CM 41289). The unilateral presence of a foramen in one of three specimens of *Tinosaurus* sp. MPH provides some evidence that this taxon is related to *Uromastyx*, but under a frequency-coding scheme (e.g., Poe 2004) this support would be considerably less than one full step. Furthermore, the single foramen found in PTRM 19515 is relatively small in comparison with those seen in *Uromastyx* and most iguanids with such foramina.

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[1] Wilms *et al.* (2009) recently revised the generic taxonomy of *Uromastyx*, placing three species, *U. hardwickii, U. asmussi,* and *U. loricata,* which had been considered basal in the genus (Moody 1980, 1987) and which Wilms *et al.* determined to form a clade, in the genus *Saara* Gray (type species: *Saara hardwickii*). For the present I follow the TIGR Reptile Database (Uetz *et al.* 2007) in retaining those species in *Uromastyx*.

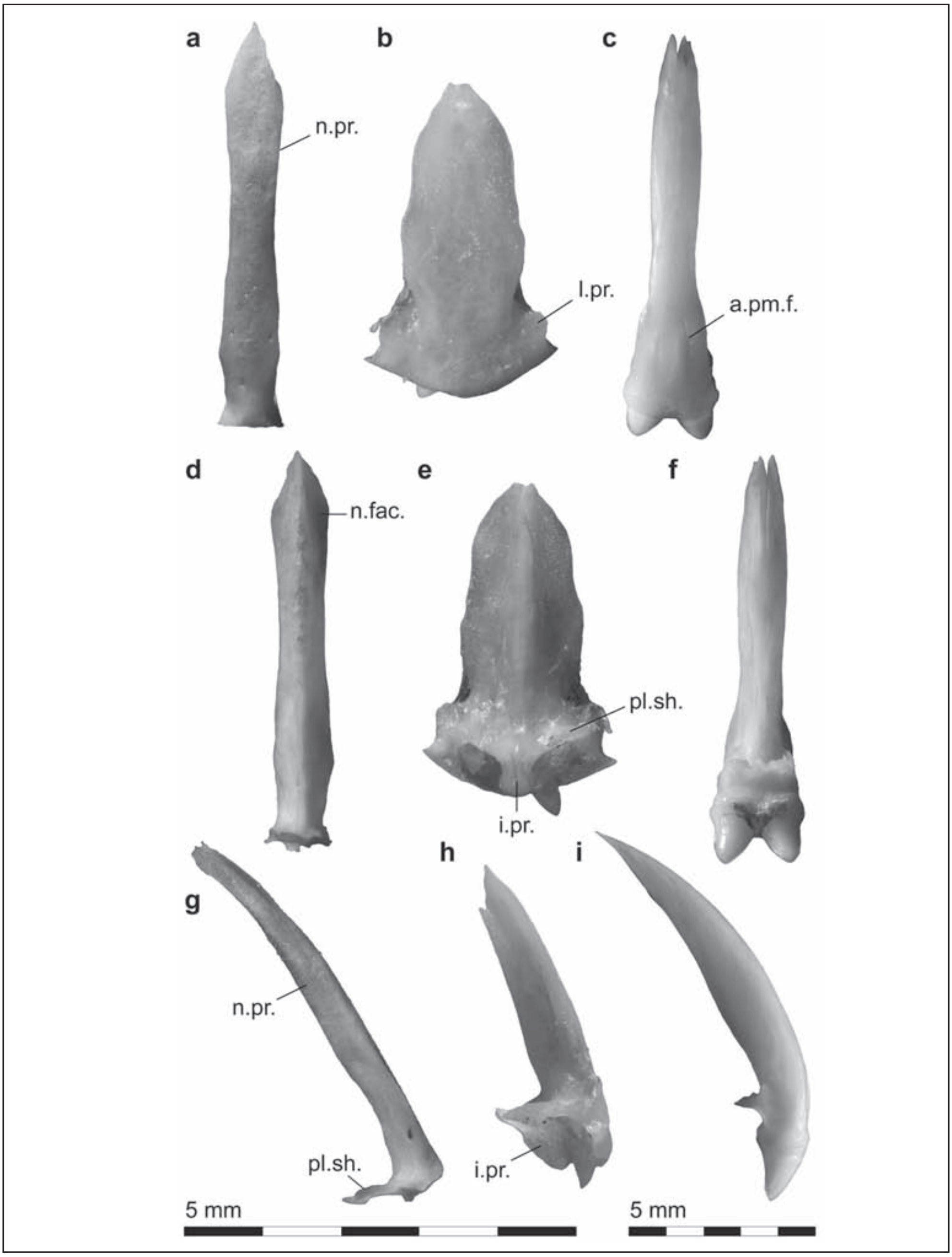

FIG. 2. Premaxillae of select agamids in anterodorsal (upper row), posteroventral (middle row), and right lateral (bottom row) views. (a, d, g) *Agama mossambica*, UF 55339; (b, e, h) *Leiolepis belliana*, UF 62048; and (c, f, i) *Uromastyx princeps*, CM 145044. Abbreviations: a.pm.f., anterior premaxillary foramen; i.pr., incisive process; l.pr., lateral process; n.fac., nasal facet; n.pr., nasal process; pl.sh., palatal shelf; p.pm.f., posterior premaxillary foramen.

The occurrence of a distinct incisive process is quite variable in agamids. One is present in many Agaminae (e.g., *Laudakia stellio, Pseudotrapelus sinaitus*) but highly reduced to absent in others (e.g., *Agama mossambica*: Fig. 2d); present in most (all?) Draconinae; present in *Leiolepis* (Fig. 2e) but absent in *Uromastyx* (Fig. 2f); present in *Hydrosaurus amboinensis*; and present but rather small in *Physignathus cocincinus* and *Pogona vitticeps* (Amphibolurinae). An incisive process is absent in Chamaeleonidae. The presence of an incisive process and its flattened shape in *Tinosaurus* sp. MPH offer little guidance at this point.

The medial apposition of the maxillae behind the premaxilla, recognized early by Siebenrock (1895) as a characteristic of Agamidae*, is also found in Chamaeleonidae (Frost & Etheridge 1989; Siebenrock 1893). (Contact appears to have been lost in a few taxa: see Bell *et al.* 2009.) In these taxa the anteromedial processes of the maxilla are expanded; they partly rest dorsally on the palatal shelf of the premaxilla but also extend posteriorly beyond it. In *Uromastyx* and *Leiolepis*, additionally, the palatal shelf is cloven between the facets for the maxilla, a characteristic that does not occur in examined draconines, amphibolurines (*Pogona vitticeps* and *Physignathus cocincinus*), *Hydrosaurus amboinensis*, or most agamines (except *Laudakia stellio*). However, the feature cannot be evaluated in Chamaeleonidae because the palatal extent of the premaxilla is so highly reduced. The occurrence of cleavage in *Tinosaurus* sp. MPH suggests possible affinity with *Leiolepis* and *Uromastyx*, but additional outgroup comparison is desirable. The exact form of the rounded facets for the maxilla distinguishes *Tinosaurus* sp. MPH from both *Leiolepis* and *Uromastyx*, where the facets are deep, longitudinal indentations immediately adjacent to the median cleft, close to the condition seen in other agamids. No other acrodontan available as a disarticulated skeleton showed facets of a similar form, and they may be an autapomorphy of *Tinosaurus* or some part of it.

The position of the posterior premaxillary foramina in *Tinosaurus* sp. MPH appears somewhat unusual for Iguania, where, as in most other lizards, they are generally located more medially, hidden behind the nasal process. It is possible that a laterally displaced position of these foramina is related to the transformation of the anterior end of the maxilla. It is observed, for instance, that the dorsal process at this end of the maxilla is frequently bifurcated (Smith 2009b), presumably for the subnarial artery. The foramina appear to be laterally displaced in *Leiolepis* (Fig. 2e). Yet, at least some agamids (e.g., *Bronchocela cristatella*) have more normally disposed foramina, and insufficient disarticulated specimens were available to determine if the *Tinosaurus* condition is the rule in Acrodonta.

The posterior and distal decurvature of the tooth tips that causes an appearance of divergence is not uncommon among agamids and was found in *Physignathus cocincinus* and *Leiolepis belliana* (Fig. 2e), among taxa with at least three premaxillary teeth.

Maxilla. Two specimens can be identified as maxillae (Fig. 3). (Other dentigerous specimens are too fragmentary.) The more complete of them, PTRM 19340, is a posterior fragment of a left element that, based on adhering sediment, was probably broken prior to burial. The anterior break passes through the posterior end of the palatine process. The description, unless otherwise noted, is based on this specimen.

Description: The dorsal margin of the posterior remnant of the facial process trends straight posteroventrally (Fig. 3a, b, f.pr.). Just above the level of the palatal shelf (Fig. 3b, c, pl.sh.) there is a sudden inflection (infl.) toward the ventral, and where the dorsal margin drops below the level of the palatal shelf, it begins to curve posteriorly. The inflection point probably marks the boundary between the lacrimal and jugal, although such an inflection is also seen in agamids that appear to lack an ossified lacrimal (e.g., *Pogona vitticeps*). The facial process thus lacks a reentrant on the jugal (see Smith 2009b). The jugal groove (Fig. 3b, j.gr.) is deep posteriorly, extending well below the horizontal level of the anterior portion of the palatal shelf; it is also exposed laterally (Fig. 3a), because the facial process is completely decayed posteriorly. The jugal groove shallows anteriorly and rises along with the palatal shelf, which is more dorsally located anteriorly than posteriorly. The medial edge of the shelf is broadly rounded anteriorly but becomes dorsoventrally compressed posteriorly (Fig. 3c). The shelf curves sharply medially at the anterior-most preserved end of the bone, forming part of the palatine process (Fig. 3b, pl.pr.), but there is no evidence of a facet for the palatine articulation. PTRM 19533, which preserves a slightly more anterior portion of the bone than PTRM 19340, evinces a small superior alveolar foramen (SAF), presumably the posterior-most of many, near the anterior end of the palatine process, which is

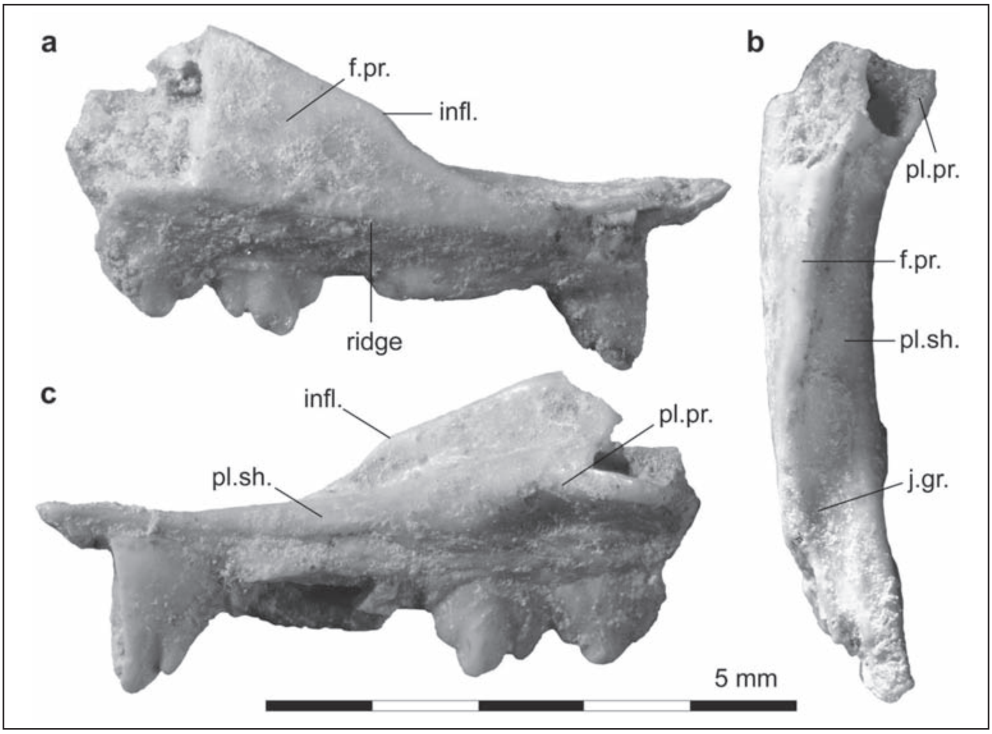

FIG. 3. Left maxilla fragment of *Tinosaurus* sp. MPH, PTRM 19340, in (a) lateral, (b) dorsal, and (c) medial views. Abbreviations: f.pr., facial process (posterior remnant); infl., inflection point; j.gr., jugal groove; pl.sh., palatal shelf; pl.pr., palatine process.

roughly twice as long as a tooth in the same portion of the bone; the same specimen also preserves what is probably the last labial (alveolar) foramen at the same transverse level as the ultimate SAF. The lateral face of the bone is divided into two surfaces by a longitudinal ridge (Fig. 3a); dorsal to the ridge is the laterally directed facial process, ventral to it is a ventrolaterally directed surface. In PTRM 19533 the distance between the jaw parapet and this ridge decreases anteriorly.

Tooth morphology is similar to that previously described for this taxon (Pearson 1998). Tooth implantation is pleuracrodont. The teeth increase in mesiodistal length as well as apicobasal height posteriorly. The lingual tooth surfaces are not well preserved, which probably reflects both wear in life as well as postmortem damage.

Comparisons: PTRM 19340 differs from the maxilla of most agamids in that the palatine facet does not appear to extend to the posterior end of the palatine process of the maxilla. In examined Agaminae (Fig. 4a), *Hydrosaurus*, Amphibolurinae, Draconinae and *Uromastyx* (Fig. 4c), the maxillary process of the palatine is medially extensive posteriorly, so that the facet it forms is found along the entire posterior margin of the palatine process of the maxilla. In contrast, the facet does not extend to the posterior margin of the process in *Leiolepis* (Fig. 4b). This is additionally the case in Chamaeleonidae. Unfortunately, the palatine process is incomplete in both fossil specimens, so this observation must be regarded as tentative.

The posterior remnant of the facial process of the maxilla in Agaminae (Fig. 4d), *Hydrosaurus*, Amphibolurinae, Draconinae and *Uromastyx* (Fig. 4f) bears a reentrant on the jugal, but this is lacking in *Leiolepis* (Fig. 4e; Smith 2009b). The reentrant is lacking in *Tinosaurus* sp. MPH, in Chamaeleonidae, and rarely in other agamids (e.g., *Moloch horridus*;

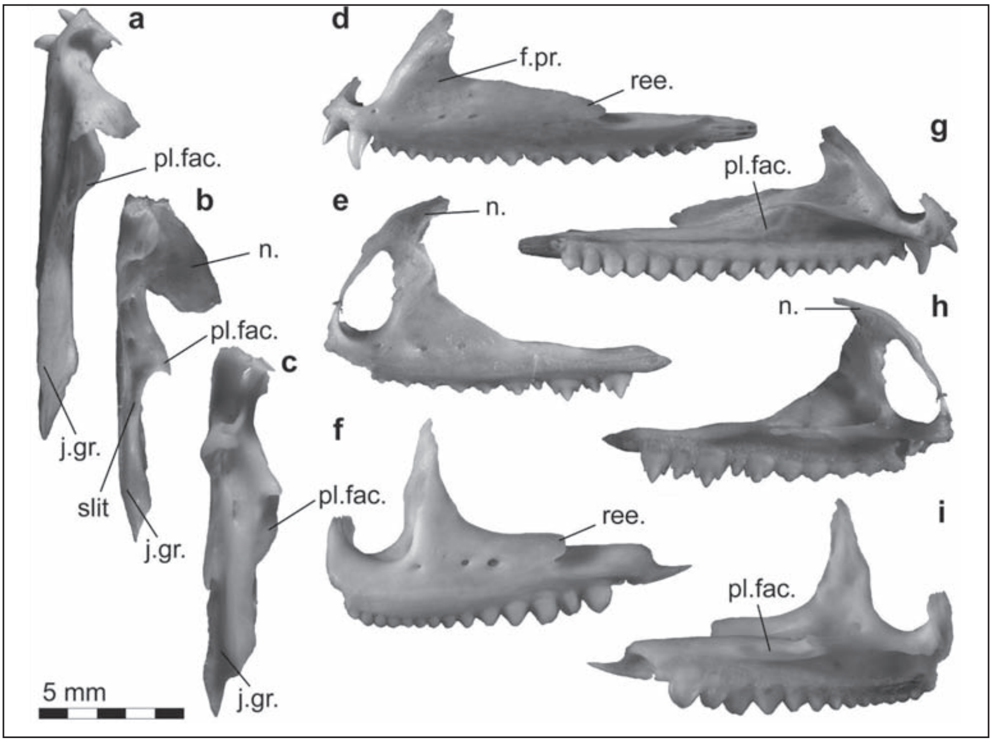

FIG. 4. Maxillae of select agamids in dorsal (left column), lateral (middle column), and medial (right column) views. (a, d, g) *Agama mossambica*, UF 55339; (b, e, h) *Leiolepis belliana*, UF 62048; and (c, f, i) *Uromastyx princeps*, CM 145044. Abbreviations: f.pr., facial process (posterior remnant); j.gr., jugal groove; pl.pr., palatine process; ree, maxillary reentrant on the jugal.

Bell *et al.* 2009). It is unclear whether this feature is autapomorphic of Agamidae* and lost in *Leiolepis*, or whether the state in *Leiolepis* is plesiomorphic. Among living agamids, however, *Tinosaurus* sp. MPH is uniquely similar to *Leiolepis* in this respect.

The posterior remnant of the facial process extends posteriorly well beyond the palatine process in most agamids (although posterior to the reentrant it is completely absent). In *Leiolepis*, however, the posterior extent of the facial process is reduced, extending no farther than the posterior end of the palatine process, fully exposing the jugal in lateral view. The length of the facial process in *Tinosaurus* sp. MPH is intermediate in length, which incidentally shows that there is no simple relationship between facial process length and the presence of a reentrant.

In at least some specimens of *Leiolepis*, there is a longitudinal slit on the dorsal surface of the (narrow) palatal shelf (Fig. 4b). This slit is located midway between the palatine process and the posterior end of the bone. Re-articulation of UF 62048 reveals that the slit receives neither the edge of the jugal nor the ectopterygoid; its presence is presumably related to a yet undetermined feature of the connective tissue. This slit was not found in other agamids available as disarticulated specimens and is absent in *Tinosaurus* sp. MPH. This absence is considered plesiomorphic.

Ectopterygoid. A single, partial right ectopterygoid, PTRM 19134, is associated with this species on the basis of size and its consistency with morphologies commonly encountered in Agamidae* (see below). The bone is lacking parts of the anterolateral and posterolateral processes as well as much of the pterygoid process (Fig. 5).

Description: The maxillary facet (Fig. 5a, mx.fac.) is broad on the ventral surface of the lateral process. Its medial margin is convex, its lateral one straight to weakly concave. The facet is at a high angle to the horizontal (Fig. 5b). A weak lip is developed where the maxillary facet terminates in line with the main body of the bone (Fig. 5a). The lip grows in prominence posteriorly, but the ventral corner of the posterolateral process (Fig. 5a, c, pl.pr.) is then truncated by breakage. The extent of the ventral corner of the process cannot be determined, but it appears to have been more massive than the dorsal corner. The lateral surface of the bone, which articulated with the medial surface of the jugal, is oblique, directed laterally and slightly dorsally (Fig. 5d, j.fac.). Near its posterior end the jugal facet is concave, but moving onto the anterolateral process it is flat, except for a shallow groove just below the dorsal margin. The posterior concave portion is traversed by a small groove that arches from anteroventral to anterior and gives off a few minor branches. The ventrolateral edge of the bone is drawn out into a thin flange, the maxillary and jugal facets meeting one another at an acute angle (Fig. 5b).

The main body of the bone has a slightly convex anterior margin and a concave posterior one (Fig. 5a). The posterior concavity forms the coronoid recess (cn.rec.), which receives the coronoid bone and associated tissues when the jaw is adducted. The surface of the recess is nearly vertical medially but becomes oblique (anteroventral) laterally. At the medial end of the main body are two facets for articulation with the pterygoid, each with a tapering, rounded lateral terminus. The one on the posterior side of the bone is the primitive pterygoid facet (Fig. 5a, c, pt.fac.p.). The one on the anterior side extends just as far laterally as the first (pt.fac.a.). These distinct portions of the pterygoid articulation are separated by a transverse flange of bone whose medial edge is not preserved, and indicate that the pterygoid possessed an additional articular projection in the space between the lateral process of the bone and its anterior part.

The dorsal surface of the bone is flat and smooth (Fig. 5c).

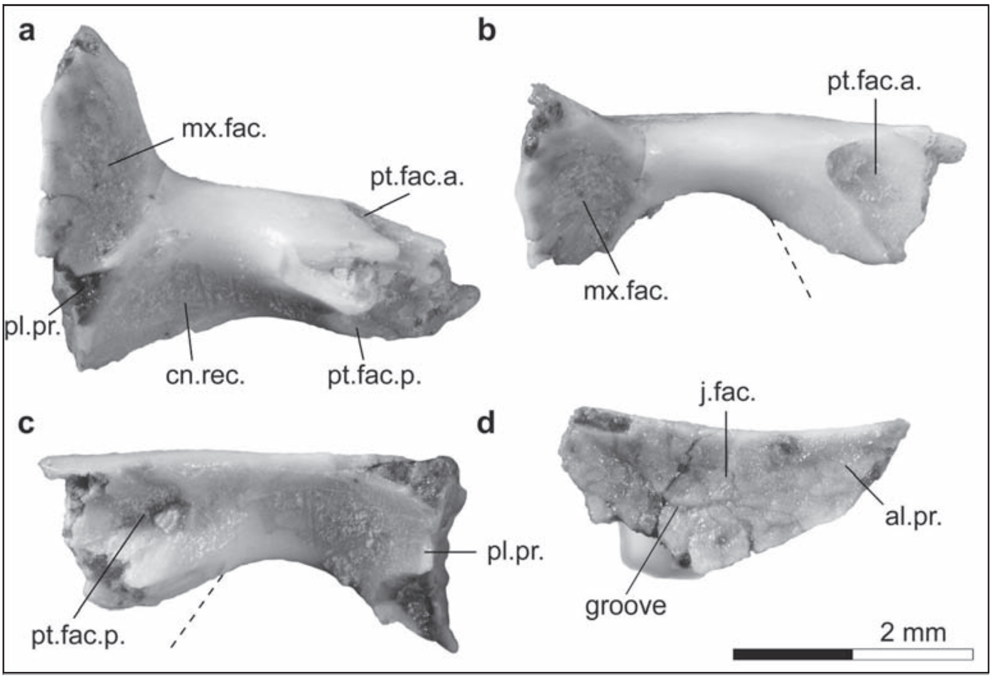

FIG. 5. Partial right ectopterygoid of *Tinosaurus* sp. MPH, PTRM 19134, in (a) ventral, (b) anterior, (c) posterior, and (d) lateral views. Abbreviations: al.pr., anterolateral process; cn.rec., coronoid recess; j.fac., jugal facet; mx.fac., maxillary facet; pl.pr., posterolateral process; pt.fac.a., anterior portion of pterygoid facet; pt.fac.p., posterior portion of pterygoid facet.

Comparisons: By retaining a posterolateral process, this ectopterygoid is plesiomorphic in comparison with Scleroglossa (Smith 2006b), the sister-taxon to Iguania. Although plesiomorphy cannot be used to unite two taxa, I consider it unlikely that PTRM 19134 represents a long-surviving previously unknown lineage of stem-acrodontan or some other lepidosauromorph other than Iguania. Subtle features of this ectopterygoid, in turn, suggest its referral to Acrodonta rather than Iguanidae within Iguania. In iguanids the medial margin of the anterolateral process of the bone usually curves fairly continuously medially to form the anterior margin of the bone, whereas in agamids the change in orientation tends to be more abrupt (Fig. 6a, b). That is to say, the anterior margin of the bone and the medial margin of the anterolateral process can usually be described by a single radius of curvature in iguanids, but in agamids they cannot. This generality holds fairly well, although the agamid condition is not quite so clear

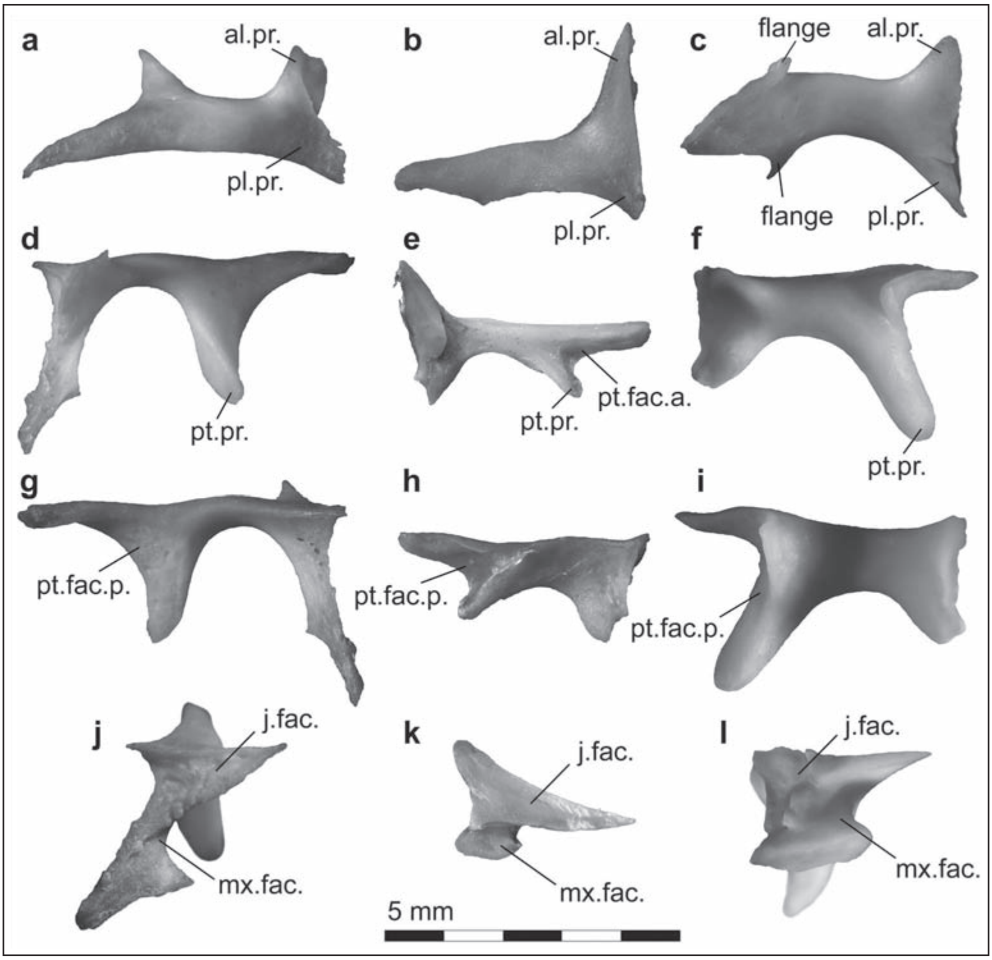

FIG. 6. Ectopterygoids of select agamids in dorsal (first or upper row), anterior (second row), posterior (third row), and lateral (fourth or bottom row) views. (a, d, g, j) *Agama mossambica*, UF 55339; (b, e, h, k) *Leiolepis belliana*, UF 62048; and (c, f, i, l) *Uromastyx princeps*, CM 145044. Abbreviations: al.pr., anterolateral process; cn.rec., coronoid recess; j.fac., jugal facet; mx.fac., maxillary facet; pl.pr., posterolateral process; pt.fac.a., anterior portion of pterygoid facet; pt.fac.p., posterior portion of pterygoid facet; pt.pr., pterygoid process.

in *Uromastyx* (Fig. 6c), and the iguanid condition is not always found in that clade. PTRM 19134 conforms to the agamid condition. Furthermore in Acrodonta, the anterior margin of the neck of the bone and the medial margin of the anterolateral process tend toward a right angle (like in PTRM 19134), where as the angle is usually obtuse in Iguanidae. Another agamid characteristic of PTRM 19134 is the extreme thinness of the ventrolateral edge of the bone (also absent in *Uromastyx*). Finally, the slightly dorsally arched character of PTRM 19134 (Fig. 5b) is fully consistent with Acrodonta but totally inconsistent with Iguanidae. These are the primary reasons for associating PTRM 19134 with Acrodonta, and hence *Tinosaurus* sp. MPH.

The additional articular projection of the pterygoid on the ectopterygoid, as indicated by the dual articulation facet in PTRM 19134, is also found in *Leiolepis belliana* (Fig. 6e). A dual articulation is not directly observable in articulated specimens (UF 62046, 62047, SMF 57471), but even here the semitranslucency of the bone allows determination of where the pterygoid terminates medially and so provides a strong indication of this reinforced relationship between the two elements. In UF 62048 (the only available disarticulated specimen of *L. belliana*), the two portions of the facet have an approximately equal lateral extent and are separated by a sharp, transverse ridge (Fig. 6e, h). An anterior articulation of the pterygoid on the ectopterygoid appeared to be absent in all examined members of Agaminae (Fig. 6d), Draconinae, Amphibolurinae, and *Hydrosaurus*. As far as I am aware, this dual articulation otherwise only occurs in *Dipsosaurus dorsalis* and part of its stem, including the stem taxon *Queironius praelapsus*, also known from the Medicine Pole Hills local fauna (Smith 2011).

Differently derived is the condition in *Uromastyx*, where the pterygoid articulation on the ectopterygoid is also visible anteriorly. In most examined species of the latter taxon, however, the pterygoid articulates entirely on a curious flange found on the anterior margin of the ectopterygoid (Fig. 6c). The primitive posterior articulation of the pterygoid also is braced by a strong, posteriorly directed flange on the ectopterygoid (Fig. 6c). As far as I am aware, these ectopterygoid flanges are unique to *Uromastyx* in Iguania, although a smaller projection in *Moloch horridus* (Bell *et al.* 2009) may be analogous to the anterior flange in *Uromastyx*. In *U. acanthinura, U. princeps*, and most probably *U. geyri*, the anterior and posterior facets for the pterygoid are confluent, i.e., they are not separated by a sharp transverse ridge; in *U. hardwickii*, on the other hand, a broad, rounded ridge is in fact developed between them. In summary, the condition seen in *Tinosaurus* sp. MPH appears to be found only in *Leiolepis* among living acrodontans, but the equally unique condition in *Uromastyx* could have been derived from it, especially considering the basal (Amer & Kumazawa 2005b; Moody 1987) position of *U. hardwickii*.

Usually in Agamidae* (Fig. 6j, l), but not Chamaeleonidae, the ventral corner of the posterolateral process of the ectopterygoid is greatly enlarged (and varies considerably in morphology). In *Leiolepis*, in contrast, the ventral corner (particularly when the flange bearing the maxillary facet is excluded) is relatively smaller. Although both dorsal and ventral corners of this process are broken in PTRM 19134, it appears that the ventral one may have been the stronger (see above), as in most agamids. This is presumably a primitive feature of *Tinosaurus* sp. MPH. The morphology of the ventral corner holds more information, which will become useful when this portion of the bone becomes known in *Tinosaurus*.

Tinosaurus sp. MPH, like *Leiolepis* (Fig. 6h) and *Uromastyx* (Fig. 6i), lacks the extreme dorsoventral thinness and rounded ventral edge of the central portion (neck) of the ectopterygoid which is seen in many Agaminae (Fig. 6g), Draconinae, and Amphibolurinae. In this respect, *Tinosaurus* sp. MPH is also presumably primitive.

The maxillary facet on the ventral surface of the lateral portion of the ectopterygoid faces roughly ventrally in most agamids available as disarticulated skeletons (Fig. 6d). (The condition in chameleons is difficult to evaluate, because the maxillary facet is so highly reduced.) In *Leiolepis*, the medial portion of the maxillary facet also faces ventrally, but laterally the facet curves strongly ventrally and becomes vertical (Fig. 6e). In *Uromastyx*, the maxillary articulation also is transformed, but the homologous surface of the ectopterygoid, still indicated by the ventral surface of the anterolateral process, is rotated such that the surface faces ventrolaterally (i.e., it is rotated in the opposite direction as in *Leiolepis*; Fig. 6f). In *Tinosaurus* sp. MPH, the maxillary facet also curves ventrally, although not as strongly as in *Leiolepis*. This feature is taken to be an apomorphic similarity between the latter two taxa.

Frontal. A frontal morphotype comprising three specimens is referred to this species on the basis of

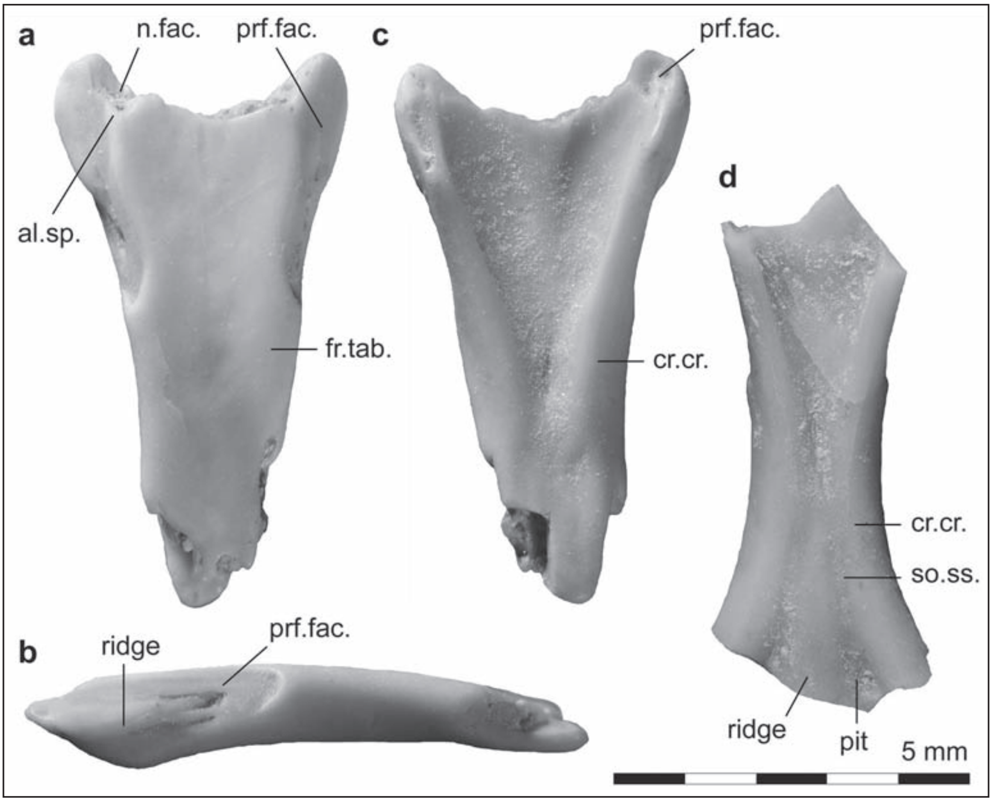

FIG. 7. Frontals of *Tinosaurus* sp. MPH. (a, b, c) PTRM 19113 in dorsal, left lateral, and ventral views, respectively; (d) PTRM 19112 in ventral view. Abbreviations: al.sp., anterolateral spine of frontal table; cr.cr., crista cranii; fr.tab., frontal table; n.fac., nasal facet; prf.fac., prefrontal facet; so.ss., groove marking insertion of solium supraseptale.

size and the presence of apomorphies uniting it with part of Agamidae*.

Description: The bone is distinctly hourglass-shaped, narrowing markedly (by 50%) from its anterior end to the mid-orbital portion (Fig. 7a). The dorsal surface of the frontal is saddle-shaped, weakly (PTRM 19113, 19467) to strongly (PTRM 19112) concave in transverse cross-section (Fig. 7a) and moderately convex in sagittal cross-section (Fig. 7b). The orbital ridges thus become especially pronounced posteriorly. The dorsal surface is nearly smooth, showing only weak irregularities in certain places (Fig. 7a), particularly on the posterior, expanding portion of the bone. The anterior portion of the bone is most completely preserved in PTRM 19113. Here, the anterior end does not show clear breaks, although broken edges (on the right side, for instance) could have been rounded by streamwear. The posterior corner of the nasal facet (n.fac.) is present at the anterolateral-most corner of the frontal table (fr.ta.). The anterolateral spine (al.sp.) of the frontal table (fr. ta.) is thin; it appears that it may also have been short, for it decays rapidly in height, although it is not clear how much its anterior extent would have been exposed dorsally, nor how much may have been removed by streamwear. Medial to the nasal facet is the lateral portion of the mediolaterally broad median spine of the frontal table; the curvature of this portion suggests the spine may have been short, but this is uncertain. As preserved, PTRM 19113 suggests that shelves for overlap of the nasals were greatly reduced, especially toward the mid-line. The prefrontal facets are U-shaped structures (Fig. 7a, b, prf.fac.).

The anterior half is divided by a longitudinal ridge into two surfaces, one facing dorsolaterally, the other ventrolaterally (Fig. 7b). The ridge extends for half the length of the facet, diminishing in prominence from anterior to posterior. Beyond the ridge, the prefrontal facet is directed entirely dorsolaterally (Fig. 7a). Tiny, shallow, well-demarcated, longitudinal grooves are found at the posterior end of the ridge (Fig. 7b).

A strong, triangular excavation for the olfactory tracts is present on the ventral surface of the frontal (Fig. 7c). There is a median swelling of the ventral surface at the anterior-most end of this excavation. The cristae cranii (cr.cr.) are low and rounded in transverse cross-section. Anteriorly, they sweep medially, closely approaching one another but never touching (Fig. 7d). Their lateral surfaces, which form also the lateral surfaces of the bone as a whole, are steep, 10–20° from the vertical. In PTRM 19467 alone there is a pair of tiny foramina on the lateral surface of each crista at mid-orbit. Medial to each crista on the posterior half of the bone is a groove, which corresponds to the attachment site for the dorsal edge of the solium supraseptale (so.ss.; cf. de Beer 1937 and Oelrich 1956). This groove deepens posteriorly, and on the right side of PTRM 19112 it

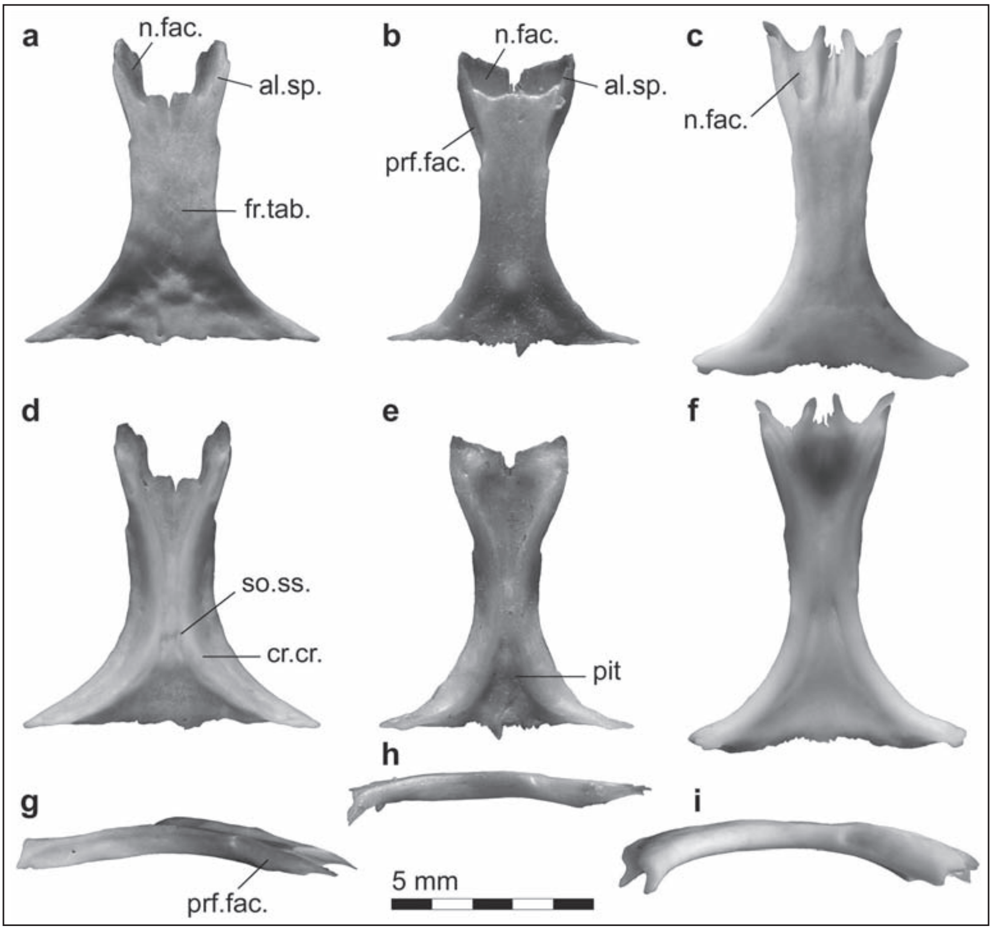

FIG. 8. Frontals of select agamids in dorsal (upper row), ventral (middle row), and right lateral (bottom row) views. (a, d, g) *Agama mossambica*, UF 55339; (b, e, h) *Leiolepis belliana*, UF 62048; and (c, f, i) *Uromastyx princeps*, CM 145044. Abbreviations: cr.cr., crista cranii; fr.tab., frontal table; n.fac., nasal facet; prf.fac., prefrontal facet; so.ss., groove marking insertion of solium supraseptale.

appears to reach its nadir in a small pit, shallowing more posteriorly. A broad, median ridge is developed between the grooves; this ridge narrows anteriorly and attains a depth that nearly equals (PTRM 19112; Fig. 7d) and even exceeds (PTRM 19467) the depth of the cristae cranii. Anteriorly, the grooves terminate at mid-orbit in tiny impressions (Fig. 7c, d). The median ridge then has the appearance of diverging to join the cristae cranii.

Comparisons: The frontal table is concave in transverse cross-section in many acrodontans, including members of Chamaeleonidae, Agaminae (Fig. 8a), Draconinae, some Amphibolurinae (e.g., *Moloch horridus*: Bell *et al.* 2009), and *Hydrosaurus* (Smith 2009a; pers. obs.). It is also concave in many *Leiolepis* (Fig. 8b), particularly larger specimens (e.g., UF 62048, SMF 57471; cf. Smith 2009a). Although the frontal table is flat in *Uromastyx* (Fig. 8c), additional outgroup comparison (Smith 2009b) suggests that a transversely concave frontal could be primitive for Acrodonta; thus, its occurrence in *Tinosaurus* sp. MPH would be plesiomorphic.

Supraorbital flanges (Smith 2009a, b) are lacking in *Leiolepis* (Fig. 8e) and *Uromastyx* (Fig. 8f) but occur in Chamaeleonidae and many other agamid clades, such as Agaminae (Fig. 8d), some Amphibolurinae, *Hydrosaurus*, and Draconinae. This is a derived character in Iguanidae where it occurs (Smith 2009b), but its wide distribution in Acrodonta makes interpretation of this feature difficult. The absence of flanges in *Tinosaurus* sp. MPH could be primitive or derived.

In most agamids, the prefrontal facet of the frontal faces ventrolaterally in its posterior extent, and it is scarcely visible in dorsal view, even anteriorly (Fig. 8a; see also Bell *et al.* 2009, fig. 15). In *Uromastyx*, the prefrontal facet is directed mostly laterally; *U. princeps* showed the most extensive dorsal exposure (Fig. 8c) of all examined species of the genus. Similarly, in examined chameleons, as well as all iguanids except certain members of Tropidurini and Iguaninae, the only portion of the incision exposed dorsally is that found dorsal to the longitudinal ridge on the anterior half of the scar. In *Leiolepis*, in contrast, essentially the entire posterior extent of the prefrontal facet is seen in dorsally (Fig. 8b). In this respect *Tinosaurus* sp. MPH is almost uniquely similar to *Leiolepis*.

The steep orientation of the lateral surface of the cristae cranii in *Tinosaurus* sp. MPH is uniquely similar to what is seen in *Uromastyx*, where they are also nearly vertical (Fig. 8f). In *Leiolepis*, their orientation varies slightly (cf. UF 62046 and UF 62048, Fig. 8e) but generally likens that in many other agamids (Fig. 8d).

The pit developed near the posterior end of the groove for the solium supraseptale in *Tinosaurus* sp. MPH also is well-developed in *Leiolepis* (Fig. 8e), in which it appears to relate to a particularly large projection of the posterodorsal margin of the planum. Except in *Leiolepis* it is very uncommon in examined extant agamids (cf. Fig. 8d, f), found otherwise only in *Calotes versicolor* (but not *C. mystaceus*). Such a pit also occurs in some chameleons (e.g., *Chamaeleo hoehnelii, C. laevigatus, C. roperi*), but apparently not the basal (Rieppel & Crumly 1997; Townsend & Larson 2002) *Brookesia superciliaris* (Siebenrock 1893: fig. 40). This feature is reasonably interpreted as an apomorphy of *Leiolepis* at present, pending more extensive taxon sampling. It is shared by *Tinosaurus* sp. MPH.

The apparent mediolateral thinness of the anterolateral corners of the frontal table of *Tinosaurus* sp. MPH is similar to what is seen in *Leiolepis* and *Uromastyx* (Fig. 8b, c), but those structures are quite variable in agamids, so the significance of this observation is uncertain.

DISCUSSION

Acrodontan phylogeny is currently in flux (e.g., Amer & Kumazawa 2005a, b; Honda *et al.* 2000; Hugall & Lee 2004; Hugall *et al.* 2008; Macey *et al.* 1997, 1998, 2000; Schulte & Cartwright 2009; Schulte *et al.* 2003), and conclusions drawn from new characters discussed here must be consistent with several plausible topologies if they are to be robust to future developments. I consider here the following four hypotheses: (h1) Agamidae* is monophyletic, and *Uromastyx* and *Leiolepis* form a clade that is the sister-taxon to the rest of Agamidae* (Fig. 9a), based on Moody (1980) (see also maximum parsimony results of Honda *et al.* 2000); (h2) Agamidae* is monophyletic, and *Uromastyx* and *Leiolepis* form successively closer outgroups to the rest of the clade (Fig. 9b), based on Macey *et al.* (2000); (h3) *Uromastyx* is basal in Acrodonta, with Chamaeleonidae and *Leiolepis* as successively closer sister-taxa to the rest of Agamidae* (Fig. 9c), based on Schulte and Cartwright (2009); and (h4) *Uromastyx* and *Leiolepis* are sister-taxa, forming a clade that is basal in Acrodonta.

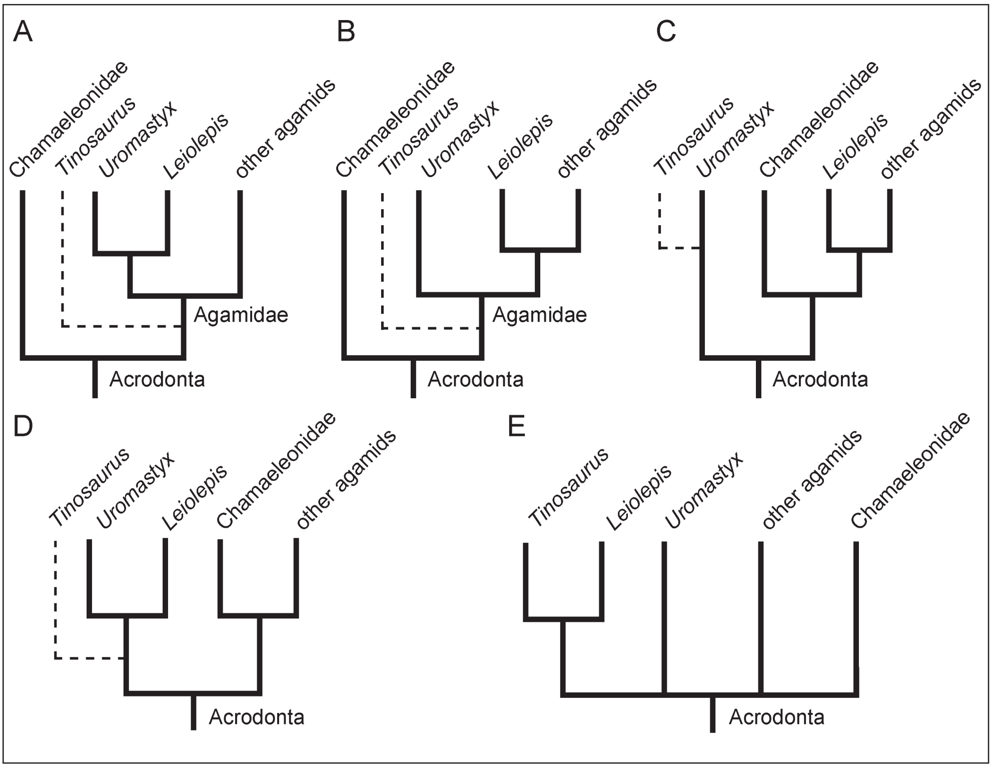

FIG. 9. Various hypotheses of the relationships of *Tinosaurus* sp. MPH within Acrodonta based on data in Table 1. Outgroup constructed using polarity decisions. In parts A–D, the described phylogenetic scaffold was enforced; part E shows unconstrained results. A. *Uromastyx* and *Leiolepis* form a clade that is the sister to the remainder of a monophyletic Agamidae (after Moody 1980; also Honda *et al.* 2000 under maximum parsimony). B. *Leiolepis* and *Uromastyx* form successive outgroups to the remainder of a monophyletic Agamidae (after Macey *et al.* 2000). C. *Uromastyx* is basal in Acrodonta, followed by Chamaeleonidae, *Leiolepis*, and the rest of Agamidae (Schulte & Cartwright 2009); D. *Uromastyx* and *Leiolepis* are sister-taxa, forming a clade that is the sister-group of other acrodontans. These topologies are not intended to cover all possibilities, nor is it implied that they are equally well supported or that the authors espouse their credited hypotheses to the exclusion of others. E. Strict consensus of 3 most-parsimonious trees (length = 13) that result from analysis of data in Table 1.

The characters noted above support a general relationship between North American *Tinosaurus* and the living clades *Uromastyx* and/or *Leiolepis*, but are partly contradictory in detail. *Tinosaurus* sp. MPH shows derived similarity to *Leiolepis* and *Uromastyx* within Acrodonta in the following two respects: strong median cleft on palatal shelf of premaxilla present; and prefrontal facet on frontal rotated to face laterally or dorsolaterally. *Tinosaurus* sp. MPH shows derived similarity to *Uromastyx* within Acrodonta in the following two respects: anterior premaxillary foramina present (at least variably); and nearly vertical orientation of lateral surface of crista cranii on frontal. *Tinosaurus* sp. MPH shows derived similarity to *Leiolepis* within Acrodonta in as many as six respects: relatively high premaxillary tooth count and well-developed lateral processes of premaxilla (depends on tree topology); palatine facet does not extend to posterior end of palatine process of maxilla; dual pterygoid articulations on ectopterygoid, separated by strong, sharp transverse ridge (relationship to condition in *Uromastyx* uncertain); high obliquity

TABLE 1. Character-taxon matrix for examining relationships of *Tinosaurus* sp. MPH. (1) Median cleft on palatal shelf of maxilla absent, 0, or present, 1. (2) Anterior premaxillary foramina absent, 0, or present, 1. (3) Premaxillary tooth count >3, 0, or ≤3, 1. (4) Palatine articulation on maxilla reaches base of palatine process on its posterior border, 0, or does not, 1. (5) Maxillary reentrant on jugal absent, 0, or present, 1. (6) Pterygoid articulates only posteriorly on ectopterygoid, 0, or possess an accessory anterior articulation, 1. (7) Maxillary facet on ectopterygoid trending dosolaterally to roughly horizontal, 0, or trending ventrolaterally, 1. (8) Lateral surface of cristae cranii on frontal strongly oblique, 0, or nearly vertical, 1. (9) Prefrontal facet on frontal hidden beneath frontal table, 0, or visible in dorsal view, 1. (10) Distinct pit for posterior attachment of solium supraseptale on frontal absent, 0, or present, 1.

	1	2	3	4	5	6	7	8	9	10
Ancestor	0	0	0	?	?	0	0	0	0	0
Uromastyx	1	1	0/1	0	1	0	0	1	1	0
Leiolepis	1	0	0	1	0	1	1	0	1	1
Tinosaurus sp. MPH	1	0/1	0	1	0	1	1	1	1	1
Chamaeleonidae	?	?	1	1	0	0	?	0	0	?
Other agamids	0	0	1	0	1	0	0	0	0	0

of maxillary facet of ectopterygoid; posterior portion of prefrontal facet completely exposed in dorsal view of frontal; and pit developed on frontal near posterior end of grooves for insertion of the solium supraseptale.

To test the relationships of *Tinosaurus* sp. MPH, I generated a topological scaffold (constraint) in PAUP* v. 4b10 (Swofford 2002) for each phylogenetic hypothesis mentioned above. Then, with the matrix in Table 1 (based on descriptions and results above), I conducted exhaustive searches for the most parsimonious position of *Tinosaurus* sp. MPH within that scaffold (as done by Bhullar & Smith 2008). The resulting position of *Tinosaurus* sp. MPH with respect to the major acrodontan clades is shown with a dashed line in Figure 9a–d; in none of them is *Tinosaurus* sp. MPH the sister-taxon of *Leiolepis*. On the other hand, when no phylogenetic scaffold is enforced, *Tinosaurus* sp. MPH is always the sister-taxon of *Leiolepis*, regardless of where this clade falls (Fig. 9e). At the least, these results do not provide consistent support for any particular position of *Tinosaurus* sp. MPH. Nevertheless, I find the dual articulation of the pterygoid on the ectopterygoid particularly compelling, and the ectopterygoid is perhaps the most securely referred element. Thus, in the brief discussion below I will treat *Tinosaurus* sp. MPH as if it were securely related to *Leiolepis*.

The earliest record of North American *Tinosaurus* is from the early Eocene (middle Wasatchian, approximately zone Wa4) of Wyoming (Smith 2006b). Assuming that Acrodonta invaded North America only one time, then these remains must also be attributed to the stem of *Leiolepis*, and one may thus conclude that *Leiolepis* had diverged from other acrodontans by the early Eocene. Stem representatives of *Uromastyx*, which under each of the phylogenetic hypotheses summarized in Figure 9a–d should have diverged from other agamids at the same time as or prior to *Leiolepis*, are well represented in the Paleogene of Asia beginning in the early Eocene (Alifanov 2009; Averianov & Danilov 1996).

Direct dispersal of stem-*Leiolepis* from Asia to North America in the early Eocene (cf. Moody 1980) would be one possible interpretation of these data. Yet, the phylogenetic position of European species of *Tinosaurus* from the early Eocene (Augé 1990, 2005; Augé & Smith 1997; Augé *et al.* 1997; Hecht & Hoffstetter 1962; Rage & Augé 2003) must be constrained before a route passing first across the Turgai Strait into Europe and thence North America could comfortably be excluded. To be sure, extant *Leiolepis* are ground-dwellers that prefer open formations (Losos *et al.* 1989) and dig deep burrows (Pianka & Vitt 2003), which may decrease the probability of dispersal by rafting over large water bodies. On the other hand, they are common inhabitants of beach environments (e.g., Losos *et al.* 1989), and the earliest occurrence of *Tinosaurus* in Europe (earliest Eocene: Augé 2005; Augé & Smith 1997) appears to precede its earliest occurrence in North America (Smith 2006a). Still, *Tinosaurus* is rare in the early

Eocene of North America (Smith 2006a), and thus its (true) first historic appearance is not well constrained.

The Eocene record of fossil lizards of North America clearly shows that many taxa presently found in the tropics once had extratropical distributions (Gauthier 1982; Smith 2006a, 2009a, 2011), which presumably relates to the warm, wet, and equable climates of the Eocene. North American *Tinosaurus* suggests the possibility that the agamid lizard *Leiolepis* could show a similar pattern. However, determining whether the historical distribution of this or other tropical agamids also conform to this pattern will require a much more intensive sampling of and attention to the fossil record of the group.

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APPENDIX

Modern comparative osteological specimens examined for this study: Agaminae: *Acanthocercus cyanogaster* (UF 50556), *Agama mossambica* (UF 55339, 55352), *Laudakia stellio* (CM 39115, 39116, UF 68087), *Phrynocephalus maculatus* (UF 71573, 71574), *P. interscapularis* (UF 80248), *Pseudotrapelus sinaitus* (UF 13934), *Trapelus agilis* (UF 74674, 74675), *T. megalonyx* (UF 67819), *T. pallidus* (CM 41289), *T. ruderatus* (UF 71720, 71721); Amphibolurinae: *Physignathus cocincinus* (SMF 61415, UF 71685, 71686), *Pogona vitticeps* (SMF 71829); Draconinae: *Acanthosaura armata* (UF 69015), *Bronchocela cristatella* (UF 42346, 51820), *Calotes mystaceus* (SMF 69754), *C. versicolor* (UF 68490, 71577), *Draco volans* (UF 53599), *Gonocephalus grandis* (UF 61544, 61548), *Japalura polygonata* (UF 63381, 63382), *Lyriocephalus scutatus* (UF 68088), Hydrosaurinae: *Hydrosaurus amboinensis* (SMF 70930); Leiolepidinae: *Leiolepis belliana* (SMF 57471, UF 62046–62048); Uromastycinae: *Uromastyx acanthinurus* (UF 54136), *U. geyri* (UF 144229), *U. hardwickii* (CM 145030, 145031, 145037), *U. princeps* (CM 145043, 145044); Chamaeleonidae: *Chamaeleo chamaeleon* (SMF 33202), *C. hoehnelii* (CM 144863, 144865), *C. roperi* (SMF 84618).

DESCRIBING EAST MALAYSIAN TADPOLE DIVERSITY: STATUS AND RECOMMENDATIONS FOR STANDARDS AND PROCEDURES ASSOCIATED WITH LARVAL AMPHIBIAN DESCRIPTION AND DOCUMENTATION

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ABSTRACT

Our ad hoc survey of 130 books and monographs showed that almost 70% did not present any descriptive information on larval anurans, and when larval stages were included the quality of documentation often tended to be poor. The larval (or developmental) stages of 51 species of east Malaysian frogs still remain unknown. Modern methods and techniques have changed the way we treat larvae taxonomically, and we recommend their adoption in tadpole research. Notably, DNA barcoding allows for unequivocal matching with adult frogs, and digital color photography provides documentation of tadpole features of unprecedented quality, partly replacing traditional drawings. Both techniques are considered essential for the study of tadpoles. Tadpole measurements have now reached a high level of standardization and can be performed quickly, accurately, and easily with digital microscopes. Nevertheless, line drawings and SEM may still be valuable techniques when certain details need to be demonstrated.

Key words: biodiversity, tadpole, inventory, morphology, barcoding, field techniques herpetology, Amphibia, Anura.

INTRODUCTION

General

Declines in amphibian numbers are a global phenomenon but are most widespread and catastrophic in the tropics (Wake & Vredenburg 2008). There is thus an urgent need for studies on all amphibian life stages in the tropics, where entire assemblages are being lost before any acquisition of knowledge of their ecological roles. However, most ecological community analyses address adults and their ecological needs and interactions, whereas larval stages are rarely included (Inger *et al.* 1986, Inger & Voris 1993, Eterovick 2003, Eterovick & Barros 2003, Kopp & Eterovick 2006). In taxon-based books (e.g., Duellman & Trueb 1986, Wells 2007), larval stages usually receive much less attention than adults. This is rather surprising, considering that the biphasic life cycle of anurans imposes dramatically different selective regimes on the aquatic larval stage, the metamorphic stage, and the terrestrial post-metamorphic stage (Wilbur & Collins 1973, Wassersug 1975, 1997; Harris 1999, Hentschel 1999, Rose 2005). Most herpetologists would agree that the tadpole stage is just as crucial as the adult stage for the persistence of the species at a specific locality and for its success and distribution, and may play a decisive role in speciation processes, particularly in tropical assemblages. However, this is not yet reflected in the quantity and depth of contemporary research efforts to record larval diversity and to analyze the specific ecology of this unique life stage.

The recent accelerating increase in species descriptions (based on adults), and thus in the number of known anuran species (AmphibiaWeb 2010, Frost 2010), makes clear that a huge backlog of work, both taxonomic and ecological, is accumulating for studies on larval forms for future workers. Even basic knowledge, such as information on tadpole diets, is patchy and not well understood (Altig *et al.* 2007). We think that the lack of state-of-the-art tadpole descriptions,

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inventory catalogues, and reliable determination keys is a major impediment to scientific progress in biodiversity and ecology research on the larval amphibian semaphoront.

In this paper, we give a brief overview on the status of tadpole descriptions as part of regional surveys and field guides in the literature. We report on our own project to record the tadpole diversity of East Malaysia. The main purpose of this paper is to 1) give a status report on the knowledge on the tadpole diversity in East Malaysia (Borneo); 2) communicate experiences and recommendation on standards and procedures that we have adopted, and 3) to argue that technological progress during the past ten years should change our standards in tadpole research. We think that some aspects of tadpole research are universal and we hope that our recommendations will facilitate the study of tadpole communities elsewhere, usually within tropical settings.

TADPOLE INVENTORIES

Tadpole

In order to briefly review the current attention that tadpoles receive in the herpetological literature, we surveyed a number of field guides, geographic herpetological surveys, and country faunal accounts (see Appendix 1). We included all sources that, to our knowledge, are designed to aid field and laboratory identification or are regional monographs and faunal revisions, published in the last 50 years. Although we do not claim that the list is comprehensive, the picture that emerges from evaluating these sources with respect to the coverage of tadpoles may well be indicative of the attention generally given to tadpoles in herpetological studies.

Among the 130 books and monographs examined, 90 (69.2%) did not present any descriptive information (morphological descriptions, drawings, or images) on tadpole life stages. Color images tend to be rare in published works: only 27 (20.7%) of the publications included color images of tadpoles, 15 (11.5%) for only a few species, and only 11 (8.5%) of the publications included color images of tadpoles for multiple species or all regional species known at the time. Among our sources, only four were exclusively devoted to larval forms (Inger 1985, Chou & Lin 1997, Anstis 2002, Beringhausen 2003). An additional work (Rödel 1998), while not on taxonomy, provides valuable data on tadpoles, including their identification.

When information on tadpoles was provided, we further categorized the quality and style of the illustrations (simple stylized sketches versus high quality line art). We did not try to be objective when assigning publications to one of these two categories, because drawings always are to some degree subjective interpretations of the object by the artist. Although the matching between the drawing and the original object, as well as the scientific precision, cannot be assessed without the object itself, the effort put into producing a quality drawing of a tadpole can usually be judged, and the value of a drawing for species identification is often evident. Examples of meticulously prepared drawings are in Anstis (2002) and Duellman (2001). However, only nine (6.9%) contained high quality line art and 33 (25.4%) contained only simple/stylized sketches.

The level of detail in tadpole textual description varies as much as in the illustrations. Tadpole descriptions cover a wide range, from brief descriptions of a few lines to highly detailed accounts with a wealth of morphological information. The usefulness of a given description for tadpole identification can be augmented if helpful illustrations and an identification key goes along with it. Short descriptions without supporting materials, as in the majority of the sources examined, will usually not suffice to allow reliable identifications and will be prone to ambiguity. An attempt to evaluate the documentation status for Bornean tadpoles has been published earlier (Das & Haas 2005: Tab. 1). For the tadpoles in Peninsular Malaysia, a summary was compiled by Leong (2002), who devised a preliminary scoring system to gauge the relative detail of documentation for each species.

The lack of our knowledge on the tadpole stages of frogs also becomes evident when considering tadpole identification keys. Among the sources examined, 34 (26.2%) provided some sort of identification key or other help for identification. However, some of the keys are to families or genera. Keys to the species level were rarely complete, as tadpoles of many species in the tropics remain unknown.

CURRENT KNOWLEDGE OF EAST MALAYSIAN TADPOLES

All amphibian species from Borneo (and indeed from the rest of the world) have been described largely, if not entirely, on the basis of adult specimens. Knowledge of tadpole descriptions has thus seriously lagged behind. At the last stock-taking, 89 of 160 species (less than 56%) then known from Borneo had known larval stages (Das & Haas 2005). Since this report appeared, larval descriptions of additional species occurring on the island have been published (Inger *et al.* 2006, Haas & Das 2008, Haas *et al.*

2009, Inger & Stuebing 2009, Leong & Teo 2009). New Bornean amphibian species have been described both with (e.g., Matsui *et al.* 2010) and without larval information (e.g., Dehling 2008, Dehling & Grafe 2008, Inger & Stuebing 2009). Data quality is yet another problem, as a significant proportion of larval descriptions lack voucher specimen information, are abbreviated, lack details expected in contemporary descriptions, or are not matched using DNA barcoding techniques. Furthermore, larval descriptions currently listed as available in Das & Haas (2005) are frequently derived from non-Bornean populations that under taxonomic revision may eventually prove to be non-conspecifics. Several familiar groups have been shown in recent years to represent taxonomically cryptic species (see for instance Inger *et al.* 2009).

At the time of this writing we identify the status of larvae of the following 51 species (taxonomically recognized for Borneo) as unknown (32% of all Bornean frogs):

Barbourula kalimantanensis, Ansonia echinata, A. fuliginea, A. latidisca, A. torrentis, Pedostibes everetti, Pelophryne api, P. guentheri, P. murudensis, P. linanitensis, P. rhopophilus, P. saravacensis, Pseudobufo subasper, Calluella brooksi, C. flava, C. smithi, Gastrophrynoides borneensis, Kalophrynus borneensis, K. eok, K. heterochirus, K. intermedius, K. nubicola, K. punctatus, K. subterrestris, Leptobrachella baluensis, L. brevicrus, L. parva, L. palmata, L. serasanae, Leptolalax dringi, L. hamidi, L. maurus, L. pictus, Borneophrys edwardinae, Ingerana baluensis, Limnonectes asperata, L. kenepaiensis, L. paramacrodon, L. rhachodus, Meristogeny jerboa, M. macrophthalmamus, Hylarana baramica, H. laterimaculata, H. picturata, H. megalonesa, Staurois latopalmatus, Rhacophorus everetti, R. fasciatus, R. gadingensis, R. rufipes, and *R. penanorum.*

However, our own efforts have yielded larval samples of the following taxa awaiting formal description in the future: *Calluella* sp., *Kalophrynus* sp., *Leptobrachella baluensis, L. brevicrus, Leptolalax dringi, Limnonectes paramacrodon, Meristogeny jerboa, Rhacophorus everetti, R. gadingensis, R. rufipes,* and *R. penanorum.* In Singapore, the discovery of tadpoles of *Hylarana laterimaculata* has been confirmed and their formal description is being prepared (T. M. Leong, pers. comm.).

RECOMMENDATIONS FOR TADPOLE DESCRIPTIONS

The lack of regional keys and field guides for tadpole identification is a hindrance for ecological and community studies on this important life stage of anurans. Considering the current backlog of taxonomic work in describing tadpoles around the world, it is important to make rapid progress in describing hitherto unknown tadpoles and in revising previous work containing abbreviated tadpole descriptions that were insufficient for reliable field and/or lab identification. Methods recruited for the taxonomic description of tadpoles should ideally be fast, simple, reliable, and should lead to a high quality of description. Although very similar tadpoles of cryptic species may exclude unequivocal identification by morphological methods in some cases, the paramount objective in tadpole descriptions should be to optimize reliable diagnostics as much as possible. Following the experience gained during our project on East Malaysian tadpoles, we would like to communicate some recommendations in this respect.

Line drawings

The current compilation (Appendix 1), and a previously published survey (Das & Haas 2005), show that many tadpole descriptions were in fact published without any illustrative figure of the tadpole concerned. Among published tadpole descriptions with figures, line drawings have been a frequently chosen option for more than a hundred years up to the present (Inger *et al.* 2006). We believe that the historic predominance of line drawings in illustrating tadpoles was mainly due to the ease of production and lack of alternative technologies. Line drawings had clear advantages: 1) easy to make; 2) low cost in producing the drawing and producing the print; 3) clarity with which certain structures can be shown (e.g, mouthparts); 4) relatively simple to reproduce and scale at good quality (via paper photocopy); 5) ease of grouping drawings on plates for interspecific comparisons.

However, these advantages of line drawings are perhaps outweighed by several disadvantages: 1) loss of color information; 2) loss of pigmentation information; 3) researchers may decide to hand the drawing process to an artist who is not familiar with the taxonomically relevant character states (a potential source of additional errors of detail); 4) accuracy of drawings depends on the skill of the artist and the process employed; 5) one and the same individual tadpole drawn by two different artists can look quite different (i.e., non-repeatable); 6) drawings made from preserved specimens may have altered body shapes (bending of axial skeleton, shrinkage of artifact caused by preservatives).

The lack of illustrations and, if present, the predominance of line drawings in the literature with their specific disadvantages, limit the immediate use of published information. In other words, an ecologist planning a community-level study on tadpoles in the tropics will hardly be able to compile enough information from the literature to be able to reliably identify living specimens in a given field situation (not to mention unknown species). The use of line drawings for the illustration of tadpoles was justified in the early days because it was for long the best technique and alternatives were not available. At the end of the 20th century, color analog photography became feasible (see Anstis 2002), but it was expensive and needed training in creating and manipulating images. Furthermore, most journals were unable or reluctant to print color images. The predominance of line drawings is thus mostly a phenomenon of community inertia. Novices in the field tend to do things the way their predecessors did. Although line drawings are still useful for some purposes (clear depiction of the tadpole mouthparts, interspecific comparisons), all other purposes of illustration are, in our opinion, fulfilled better by contemporary photographic techniques.

Tadpole photography

There are excellent examples of tadpole inventories and taxonomic descriptions that demonstrated the usefulness of tadpole color photography (Chou & Lin 1997, Leong & Chou 1999, Anstis 2002, Leong 2004). During the past 10 years, the advent and rapid progress of digital photography has profoundly changed our approach to image acquisition and processing. For the first time catalogues of vast numbers of high quality images can be collected for biodiversity projects at relatively low cost (no film material or complicated post-production work needed). Various software packages (Adobe® Lightroom, Apple® Aperture) allow the handling and meta-data annotation of image catalogues containing several tens of thousands of images, allowing for rapid comparisons of tadpoles among various regions or study sites.

The resolution and quality of images has steadily increased and any camera with a 10 megapixel (MP) sensor chip will satisfy a biologist's needs for image quality in most situations. Image quality can be assessed and adjusted immediately. Along with digital cameras, flash control systems have evolved substantially. All major camera manufacturers offer wireless-controlled flash systems, making multiple flash setups easy to handle in field situations. As most measurements and data exchanges between flash and camera are automatic in today's camera systems, images can be evaluated immediately after exposure on the camera screen. In general, little intervention by the photographer is necessary and the technique is simple and reliable in most field situations.

For tadpole photography we use customized mini-aquaria of 20 x 10 x 4 cm (width x height x depth) with a glass thickness of 4 mm. The aquarium usually contains 2 cm of sand and some rocks to position the tadpole. We anesthetize tadpoles in a separate plastic container with a weak solution of chloretone (approx. 0,1% 1,1,1-trichloro-2-methyl-2-propanol) and transfer specimens to the photo aquarium once anesthetized. However, others (Julian Glos, pers. comm.) prefer adding MS 222 (tricaine methanesulfonate) directly into the aquarium. Mid-column feeders, such as microhylid tadpoles, may assume unnatural postures when anesthetized. Microhylid tadpoles and similar feeding specialists need to be photographed without anaesthesia, which offers challenges in terms of obtaining images from all required perspectives. The eggs of directly developing species are difficult to find in the field. Some eggs of *Philautus* species have been discovered in pitcher plant pitchers (see Malkmus *et al.* 2002). Such clutches are best photographed *in situ.* However, if developmental stages are to be recorded, they must be transported in a plastic box to the lab while maintaining appropriate light, moisture, and temperature conditions.

The preferred lens for tadpole photography is a 100 or 105 mm macro lens. It allows sufficient distance between the front end of the lens and the aquarium to position light modifiers. Furthermore, its telephoto angle of view approaches a parallel projection of view better than a lens with shorter focal length. This is advantageous with respect to the refraction effects (distortion) in the aquarium (air-glass-water transition), particularly towards the periphery of the image. Excellent lighting can be achieved by placing the main flash unit (wirelessly controlled) on top of the aquarium and positioning a second flash with reduced power output to the left of the camera to fill in shadows from an angle. Tadpoles are photographed facing to the left in order to show the position of the spiraculum on the left side of the body in most species. By choosing different background colors (Anstis 2002), it can be ensured that the outline of the tadpole tail fin is clearly visible on the images (Fig. 1). Additional extension tubes allow for magnifications well beyond 1:1 and allow the documentation of finer patterns in pigmentation or details of mouthparts. Such images were much more difficult to achieve with analog film cameras.

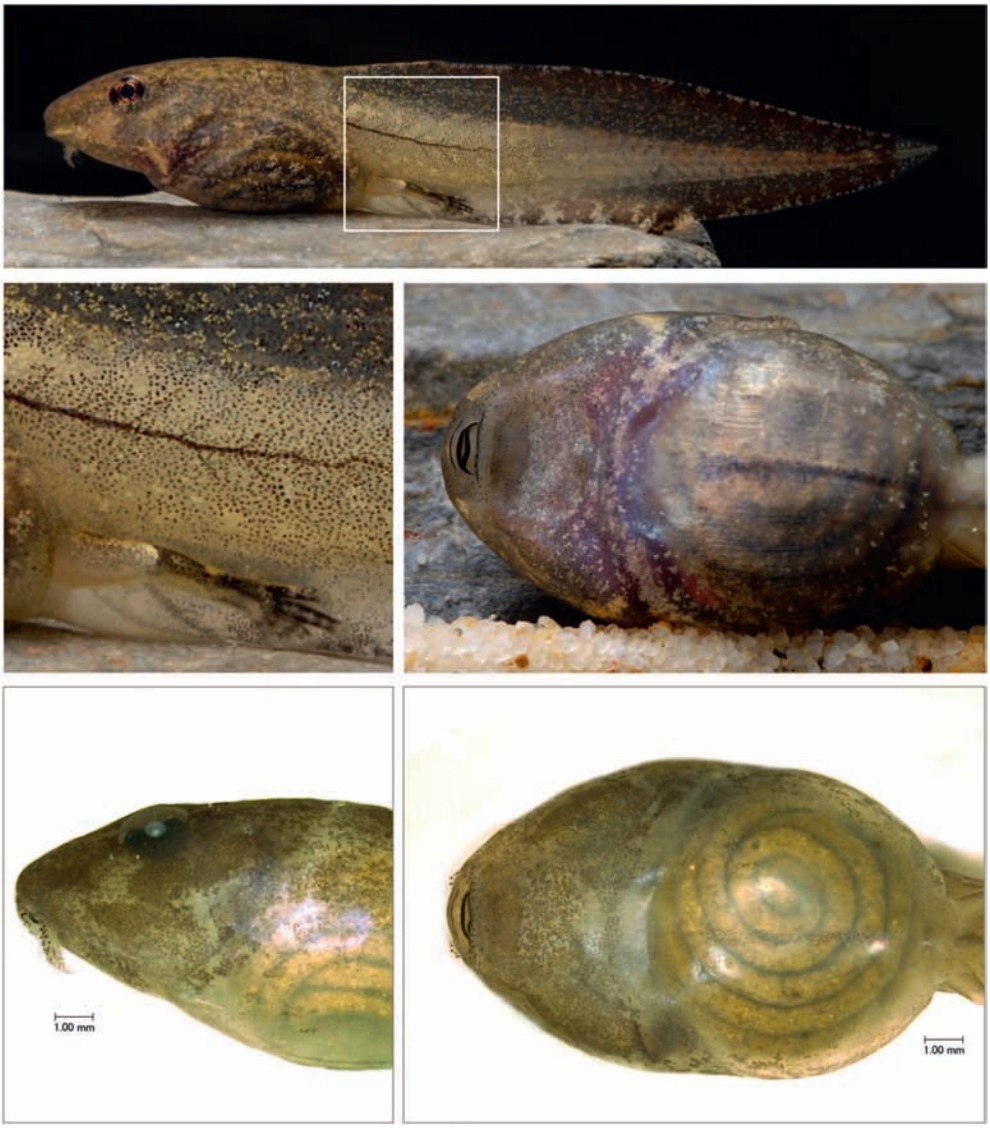

FIG. 1. Lateral view of *Hylarana nicobariensis* (top) from Sabah, digital photograph of an anaesthetised specimen set up in a mini-aquarium (20 x 10 x 4 cm, WHD) (Nikon D80 [10 megapixel sensor], Sigma Macro 105 mm; ISO 250, f/16, wirelessly controlled SB 600 flash from top). In most species a black background is suitable to show the tail fin contour. A magnification (middle left) of the cropped part of the top image (white square) shows the level of detail and limits of resolution with the camera/lens combination used. The ventral perspective of the living tadpole (middle right, same specimen) gives valuable color and pigmentation details. The lower left and right images show the same individual as above after formalin preservation. Backgrounds have been cropped. The color information that can be gained from preserved specimens is largely reduced; compare ventral views and iris in life and in preservation. For scale see bottom images; generated with a Keyence VHX-500 digital microscope..

Further advances in tadpole research can be achieved by applying high speed videography. High speed video recording is an essential tool to record the rapid raking movements of tadpole jaws and keratodonts during feeding (Venesky *et al.* 2010) or the details of various swimming behaviours (Roberts *et al.* 2000). Rapid progress in technology will likely facilitate field work with high speed technology, as the technology gets more affordable and the sensors more sensitive. We sucessfully used a consumer-grade Casio Exilim EX-FH20 digital camera for filming the grazing behavior of *Meristogenys jerboa* in the above-mentioned tank at 400 frames per second, under field conditions.

In summary, properly lit, standardized lateral and ventral digital photographs of tadpoles capture the body shape, proportions, and pigmentation details in far superior quality than any line drawing could accomplish (Fig 1). During our inventory of East Malaysian tadpoles, systematically collected digital color images of tadpoles have proven to be an indispensable tool for their identification. Tadpole photography with modern digital camera equipment can be considered a technological paradigm shift, that 1) makes taking high quality images much simpler than in analog photography; 2) allows the taking of large numbers of images for documentation of variation; 3) provides good color rendition; 4) is superior to drawings in maintaining correct body proportions and showing details; 5) captures valuable details in living specimens that vanish in preservation (silver and golden iridocytes). At present, a number of journals print color images in high quality from digital files.

Measurements

A variety of external characters are accessible to measurement in tadpoles. Although various authors may use slightly different measurements, lists of measurable variables have been proposed (e.g., Altig & McDiarmid 1999; Fig. 2). The intraspecific ontoge-

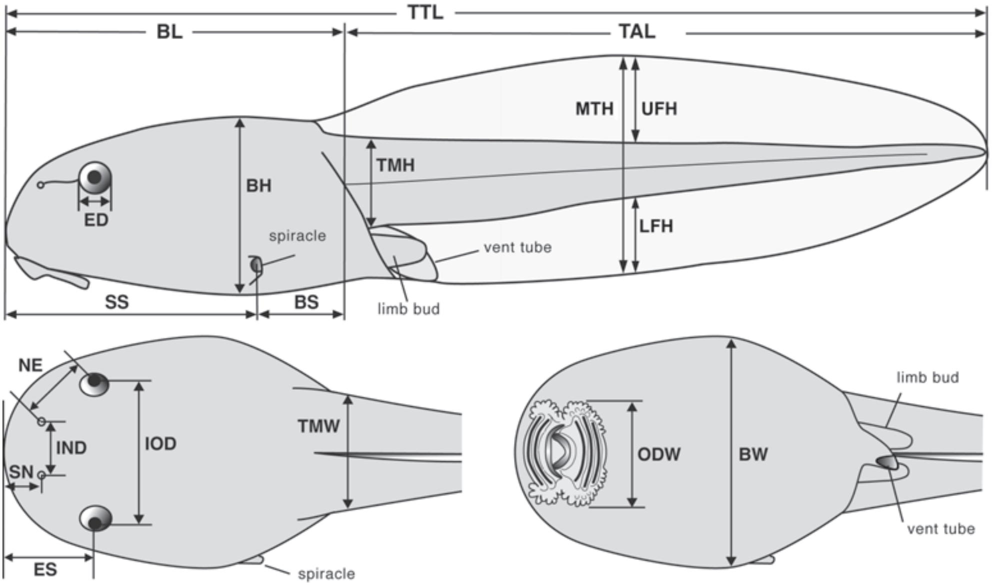

FIG. 2. Proposed standard tadpole body measurements developed from definitions by Altig & McDiarmid (1999). BH, body height; BL, body length from snout to the point where the axis of the tail myotomes meets the body wall; BS, body end to center of spiracle; BW, maximum body width; ED, eye diameter; ES, eye-snout distance; IND, internarial distance (center to center); IOD, interorbital distance; LFH, lower fin height (at MTH); MTH, maximum tail height; NE, distance from center of naris to center of eye; ODW, oral disk width; SN, distance of naris (center) from snout; SS, distance of snout to center of spiracle; TAL, tail length (=TL-BL); TMH, tail muscle height at body-tail junction, where ventral line of musculature meets trunk contour; TMW, tail muscle width at the same level as TMW; TTL, total length; UFH, upper fin height.

netic stability of commonly used measurements has recently been assessed and pertinent literature discussed (Grosjean 2005). Grosjean (2005) showed that a number of external and internal features remain stable during ontogeny, whereas others (such as tail fin height) may vary as a response to external factors. He recommended taking tadpoles of stages 32–40 (Gosner 1960) for tadpole descriptions, because in this phase many taxonomically relevant character states are stable.

Taking measurements has become much more efficient with the advent of digital microscopy. Using camera lucida devices, or measuring eyepieces, has been replaced by calibrated digital imaging. Modern digital microscopes (e.g., Keyence VHX Series) not only allow rapid measurements from calibrated digital images but also offer greater depth of field than standard stereomicroscopes. Digital images thus taken can further be used as backdrops for drawings of any kind.

SEM

After the scanning electron microscope had been devised (von Ardenne 1938) it rapidly became a popular tool in biological sciences in the second half of the 20th century. SEM has been used widely in tadpole research (e.g., Wassersug 1976,1980; Wassersug & Rosenberg 1979, Viertel 1982, Inger 1985, Wassersug & Heyer 1988, Das 1994, Hall & Larsen 1998). SEM was used in tadpole descriptions primarily to show the mouthparts and the internal oral and buccal soft tissues (e.g., Grosjean 2005, Haas & Das 2008). However, if no SEM is available, major qualitative tadpole characters (mouthpart papillation, buccal floor/roof papillation) can be recorded by alternative methods, such as methylene blue (e.g., Anstis 2002, Aguayo *et al.* 2009) or crystal violet (Altig 2007) staining and subsequent capture of images with a digitally equipped microscope. These stains give more contrast to otherwise translucent papilla. SEM will render keratodonts in a 3-dimensional fashion, though keratodonts can be put on microscopic slides and studied by light microscopy as well (Aguayo *et al.* 2009). Thus the unavailability of SEM technology is no hindrance in describing tadpoles at high levels of detail.

DNA barcoding

DNA barcoding uses mitochondrial gene sequences that can be amplified with universal primers in order to facilitate species identification and description, reveal cryptic species, or link highly dimorphic males and females. Furthermore, in biphasic organisms, such as arthropods and amphibians, barcoding techniques are an efficient tool to link tadpoles to their adult semaphoronts. Although it is still debated whether CO1 or 16S is the more efficient gene in amphibian barcoding (Vences *et al.* 2005a, Vences *et al.* 2005b, Smith *et al.* 2008), it is unquestioned that barcoding techniques are a major advance in tadpole research (Inger *et al.* 2006, Haas & Das 2008, Hendrix *et al.* 2008, Haas *et al.* 2009, Randrianiaina *et al.* 2009; see application in Gawor *et al.* 2009). Some researchers have tried to identify tadpoles by raising them through metamorphosis. This approach has been successful with species that develop unique color patterns on their thighs or dorsum at pre- or mid-metamorphic stages, such as *Polypedates otilophus* or *Hylarana luctuosa* among Bornean species. In less conspicuous species, metamorphs may be indistinct from unrelated species that occur in syntopy (e.g., *Polypedates colletti*; pers. obs.) or even highly divergent in their color pattern from adults (*Rhacophorus nigropalmatus*; Ready 2009) making assignments ambiguous or erroneous. Barcoding techniques could clarify previously ambiguous tadpole assignments (Haas & Das 2008, Haas *et al.* 2009). DNA barcoding is 1) easy to perform; 2) relatively affordable; 3) can be done completely by a contractor if a molecular lab is not available; 4) is far more reliable in linking tadpoles to adults than traditional techniques; and 5) allows us to identify any developmental stage from egg to adult.

Data richness and dissemination

The highly variable depth and quality of available tadpole descriptions (Das & Haas 2005) impose limitations on tadpole research. However, some published works point the way towards a standard in depth of treatment (e.g., Inger 1985, Chou & Lin 1997, Leong & Chou 1999, Duellman 2001, Anstis 2002, Leong 2004) for the tadpole faunas of southeast Australia, Taiwan, Middle America, and the Malay Peninsula, respectively. Peer-reviewed journal articles are the preferred method of publishing taxonomic information. This ensures quality, but taxonomic information becomes only slowly available. Dissemination of taxonomic information via internet portals cannot be an alternative, but a supplementary way to provide taxonomic resources. Data from our own project are integrated in Haas & Das (2010). Web publication of supplementary information such as imagery and short descriptions is 1) fast; 2) easily accessible from all parts of the world; and 3) can summarize regional faunal information otherwise too scattered or cryptic to access. Several web portals have been devised for amphibians (e.g., AmphibiaWeb 2010, Frost 2010, Norhayati *et al.* 2010), but to the best of our knowledge only two (Altig *et al.* 1998, Haas & Das 2010) cover larval forms with images for quick reference.

CONCLUSIONS

Recent technological developments provide tools that facilitate the description of tadpoles. Contemporary procedures, such as digital photography and digital microscopy, are not only more efficient and easier to apply than older technologies, but offer a high level of precision and data quality, contributing to the goal of reliable tadpole diagnostics. Efforts to catalogue tadpole communities, particularly in the species-rich tropics, should adopt the new techniques rather than uncritically following outdated schemes of tadpole descriptions. We conclude: 1) Digital photography of living specimens and subsequent color prints in publications are indispensable for tadpole descriptions. Good photographs give a great amount of information and can replace traditional drawings to a large extent. 2) Drawings should be used when they can deliver clarity better than other methods (mouthparts, contour line, interspecific comparisons). 3) DNA barcoding has become affordable and easy to handle. Tadpole identities should initially be confirmed by DNA matching to adults, until reliable morphological diagnostics have been established. 4) Standard morphological features and morphometric traits must be recorded (Grosjean 2005, Altig 2007). Digital microscopes facilitate the taking of measurements. 5) Soft tissue tadpole characters can be examined with staining techniques if an SEM is not accessible. 6) Tadpole descriptions should be published in peer-reviewed journal articles. However, internet portals are a fast and universally accessible, supplementary source to disseminate descriptions, keys, image catalogues, and regional inventories.

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APPENDIX 1. Compilation of field guides, geographic herpetological surveys, and country faunal accounts that have been in used for the past 50 years in the identification of amphibians. Assessment of contents with respect to anuran amphibian larval stages: 0, absent; 1, present; S, short description; L, long detailed description (including measurements).

References	Country/Geographical Region	Morphology data	Color photos/ paintings	High quality line art	Simple/ stylized sketches	Identification keys	Description detail: Absent (0)/ Short (S)/ Long (L)
Ahmed *et al.* (2004)	Endau Rompin, Peninsular Malaysia	0	0	0	0	0	0
Ahmed *et al.* (2005)	Ulu Muda, Peninsular Malaysia	0	0	0	0	0	0
Ahmed *et al.* (2009)	North-east India	0	0	0	0	0	0
Alcala (1986)	Philippines	0	0	0	0	0	S
Alcala & Brown (1998)	Philippines	0	0	0	0	0	0
Almonacid *et al.* (2005)	South America	0	0	0	few spp. of *Atelopus*	0	0
Anstis (2002)	South-east Australia	1	1	1	0	1	L
Auerbach (1987)	Botswana	0	0	0	0	0	0
Baier *et al.* (2009)	Cyprus	0	1 sp,	0	0	0	0
Baloutchi & Kami (1995)	Iran	0	0	0	0	0	0
Baran (2005)	Turkey	0	0	0	0	0	0
Barker *et al.* (1995)	Australia	1	0	0	0	0	S
Behler & King (1979)	North America	0	0	0	0	0	0
Beringhausen (2003)	Germany	1	1	0	0	1	S
Berry (1975)	Peninsular Malaysia	0	0	0	0	0	0
Beshkov & Nanev (2006)	Bulgaria	0	0	0	0	0	0
Branch (2005)	East Africa	0	0	0	0	0	0

References	Country/Geographical Region	Morphology data	Color photos/ paintings	High quality line art	Simple/ stylized sketches	Identification keys	Description detail: Absent (0)/ Short (S)/ Long (L)
Brennan & Holycross (2006)	Arizona, USA	0	0	0	0	0	0
Carruthers (2001)	Southern Africa	1	few spp.	0	0	0	0
Chan-ard (2003)	Thailand	0	0	0	few spp.	0	0
Chanda (1994)	North-east India	0	0	0	0	0	0
Chanda (2002)	India	0	0	0	0	0	0
Channing (2001)	Central and Southern Africa	1	0	1	0	1	S
Channing & Howell (2005)	East Africa	1	0	1	0	1	S
Chou & Lin (1997)	Taiwan	1	1	1	0	1	L
Christie (1997)	Prince Edward County, Ontario, Canada	0	0	0	0	0	0
Cogalniceanu *et al.* (2000)	Romania	0	0	0	1	0	S
Cogger (1994)	Australia	0	0	0	0	0	0
Conant & Collins (1998)	Eastern/Central USA	0	0	0	1	0	S
Corkran & Thoms (2006)	Oregon and Washington, U.S.A. and British Columbia, Canada	0	1	0	0	1	S
Daniel (2002)	India	0	0	0	0	0	S
Daniels (2005)	Peninsular India	0	0	0	0	0	0
Das (2007)	Brunei Darussalam	0	0	0	0	0	0
de Silva (2009)	Sri Lanka	0	0	0	0	0	0
Desroches & Rodrigues (2004)	Quebec, Canada	0	0	0	0	1	S
Disi (2002)	Jordan	0	0	0	0	1	0
Disi *et al.* (2001)	Jordan	0	0	0	0	1	S
Duellman (2001)	Middle America	1	0	1	0	diagnostic table	L
Duguet & Melki (2003)	France, Belgium and Luxembourg	1	1	0	0	1	S
du Preez & Carruthers (2009)	Southern Africa	0	1	0	few spp.	1	0
Dutta & Manamendra-Arachchi (1996)	Sri Lanka	0	0	0	0	0	0
Engelmann *et al.* (1985)	Europe	0	0	0	1	1	S
Fei & Ye (2001)	Sichuan, China	0	few spp.	0	few spp.	1	S
Fei *et al.* (1999)	China	0	few spp.	0	0	1	S
Fei *et al.* (2005)	China	0	0	0	1	1	0
Fei *et al.* (2009a)	China	0	0	0	1	0	S
Fei *et al.* (2009b)	China	0	0	0	1	0	S
Fisher *et al.* (2007)	Canada	0	0	0	0	0	0
Franzen *et al.* (2008)	South-western Turkey	0	1	0	0	0	S

References	Country/Geographical Region	Morphology data	Color photos/ paintings	High quality line art	Simple/ stylized sketches	Identification keys	Description detail: Absent (0)/ Short (S)/ Long (L)
Gallardo (1987)	Argentina	1	0	0	0	0	S
Geniez *et al.* (2004)	Western Sahara	0	0	0	0	0	0
Gibbs *et al.* (2007)	New York, USA	1	0	0	0	0	S
Gilhen (1984)	Nova Scotia, Canada	0	0	0	0	0	S (measurements)
Glandt (2010)	Europe	0	0	0	0	0	S (measurements)
Glaw & Vences (2007)	Madagascar	0	0	0	0	0	0
Goris & Maeda (2004)	Japan	1	0	0	0	0	S
Grismer (2002)	Baja California, Mexico	1	0	0	0	0	S
Günther (1996)	Germany	1	0	1	0	1	L
Guyer & Donnelly (2005)	La Selva, Costa Rica	0	0	0	0	0	0
Henkel & Schmidt (2000)	Madagascar, Mascarene, Seychelles and the Comoro archipelago	1	0	0	0	0	S
Inger (1966)	Borneo	1	0	0	1	1	L
Inger (1985)	Borneo	1	0	0	0	1	L
Inger & Stuebing (1989)	Sabah, Malaysia	0	0	0	0	0	S
Inger & Stuebing (2005)	Borneo	0	0	0	0	0	S
Iskandar (1998)	Java and Bali, Indonesia	1	0	0	1	1	S
Jaafar *et al.* (2008)	Pulau Pinang, Peninsular Malaysia	0	0	0	0	0	0
Jacob *et al.* (2007)	Wallonie (French-speaking Belgium)	0	1	0	0	0	S
Jewel (2008)	New Zealand	0	few spp.	0	0	0	S
Jongbloed & Brown (2000)	United Arab Emirates	0	0	0	0	0	0
Jovanovic *et al.* (2007)	Madagascar	0	0	0	0	0	0
Kabir *et al.* (2009)	Bangladesh	1	one sp. (Clinotarsus alticola)	0	0	0	S
Karsen *et al.* (1998)	Hong Kong	0	0	0	0	0	S
Khan (2006)	Pakistan	1	0	0	0	1	S
Kubicki (2007)	Costa Rica	1	few spp.	0	0	0	S
Kuzmin & Maslova (2005)	Russian Far East	1	0	0	1	0	L
Le Berre (1989)	North Africa	0	0	0	0	1	S
Lee (2000)	Mexico, Guatemala, Belize	1	0	0	1	0	S
Lehr (2002)	Peru	0	0	0	0	0	0
Leviton *et al.* (1992)	Middle East	0	0	0	1	1	0
Lim & Lim (2002)	Singapore	0	few spp.	0	1	0	S

References	Country/Geographical Region	Morphology data	Color photos/ paintings	High quality line art	Simple/ stylized sketches	Identification keys	Description detail: Absent (0)/ Short (S)/ Long (L)
MacCulloch (2002)	Ontario, Canada	0	1	0	0	0	S
Malkmus (2004)	Portugal, Madeira and the Azores Archipelago	0	1	0	0	0	0
Malkmus *et al.* (2002)	Mount Kinabalu, Malaysia	1	few spp.	few spp.	few spp.	genera	S
Manthey & Grossmann (1997)	South-east Asia	1	few spp.	0	1	family	S
Mathew & Sen (2010)	North-east India	0	0	0	0	0	0
Matsuda *et al.* (2006)	British Columbia, Canada	0	0	0	0	0	S
Matz & Weber (1983)	Europe	0	0	0	0	0	S
McCranie & Wilson (2002)	Honduras	1	0	0	few spp.	1	S/L
McKay (2006)	Bali, Indonesia	1	0	0	0	1	S
Menzies (1976)	New Guinea	0	0	0	0	0	0
Minton (1966)	Pakistan	1	0	0	0	0	S
Murphy (1997)	Trinidad & Tobago	0	0	0	0	0	0
Necas *et al.* (1997)	Czech Republic	0	few spp.	0	0	0	S
Nguyen *et al.* (2009)	Vietnam	0	0	0	0	0	0
Nöllert & Nöllert (1992)	Europe	1	0	1	0	1	detailed (as part of key)
Nutphand (2001)	Thailand	0	0	0	few spp.	0	0
Passmore & Carruthers (1995)	South Africa	0	0	0	0	0	0
Pickersgill (2007)	Southern and eastern Africa	1	0	0	1	0	L
Pikacha *et al.* (2008)	Solomon Islands	0	0	0	0	0	0
Poynton (1964)	Southern Africa	0	0	0	0	0	0
Preston (1982)	Manitoba, Canada	0	0	0	1 sp. (Lithobates sylvatica)	1	S
Razzetti & Msuya (2002)	Tanzania	0	0	0	0	0	0
Renjifo (2000)	Colombia	0	0	0	0	0	0
Renjifo & Lundberg (1999)	Urra, Colombia	0	0	0	0	0	0
Rivero (1972)	Venezuela	0	0	0	0	0	0
Rödel (1998)	Ivory Coast	0	few spp.	0	1	0	0
Rödel (2000)	Ivory Coast	1	0	1	1	0	L
Russell & Bauer (2000)	Alberta, Canada	0	0	0	0	1	S
Saleh (1997)	Egypt	0	0	0	0	0	0
Salvador & Paris (2001)	Spain	0	0	0	1	1	S

References	Country/Geographical Region	Morphology data	Color photos/ paintings	High quality line art	Simple/ stylized sketches	Identification keys	Description detail: Absent (0)/ Short (S)/ Long (L)
Savage (2002)	Costa Rica	1	0	0	1	1	S
Schiøtz (1999)	Africa	1	0	0	few spp.	0	S
Schleich & Kästle (2002)	Nepal	1	0	0	few spp.	genus	0
Schleich *et al.* (1996)	North Africa	1	0	0	1	1	S
Shim (2003)	Korea	0	few spp.	0	few spp.	0	0
Shrestha (2001)	Nepal	0	0	0	0	0	S
Stewart (1967)	Malawi	0	0	0	0	0	S for a few spp.
Taylor (1962)	Thailand	0	0	0	0	0	0
Terbish *et al.* (2006)	Mongolia	0	0	0	0	0	0
Thy & Holden (2008)	Cambodia	0	0	0	0	0	0
Trapp (2007)	Greece (mainland)	0	0	0	0	0	0
Tyler *et al.* (2000)	Western Australia	0	0	0	0	0	0
Valakos *et al.* (2008)	Greece	0	0	0	0	1	0
Wager (1986)	South Africa	1	few spp.	0	1	0	S
Wu *et al.* (1987)	Guizhou, China	0	0	0	some b&w photos	0	S
Yang (1991)	Yunnan, China	1	0	0	0	0	S
Yang (1998)	Taiwan	1	few spp,	0	few spp.	0	0
Yang & Rao (2008)	Yunnan, China	0	0	0	0	0	0
Zhao & Adler (1993)	China	0	0	0	0	0	0
Ziegler (2002)	Vietnam	1	1	0	0	0	0

ANURAN SPECIES RICHNESS IN THE DEPARTAMENTO PANDO, BOLIVIA

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ABSTRACT

An updated list of anuran species of the Bolivian Departamento Pando is provided. The list contains 114 species belonging to 13 families. One species (*Dendropsophus brevifrons*) is recorded for the first time from Bolivia. Three other species (*Dendropsophus* cf. *nanus*, *Pristimantis olivaceus* and *Trachycephalus coriaceus*) are recorded for the first time within the territory of the Departamento Pando.

Key words: Amphibia, Anura, species list, new country record, Departamento Pando, Bolivia.

INTRODUCTION

The Departamento Pando represents the northernmost region of Bolivia. It is situated in the southwestern Amazonian basin, within the zone of tall evergreen lowland rainforest. Results of recent herpetological investigations of this region show that lowland Bolivian Amazonia harbors an unusually rich anuran fauna containing still unrecorded and undescribed species (see e.g. Cadle & Reichle 2000, Köhler & Lötters 2001, Cadle & Guerrero 2003, Cadle *et al.* 2003, Padial *et al.* 2004, Reichle 2007, Padial & De la Riva 2009, Angulo & Icochea 2010). Since the available lists of amphibian species of the Departamento Pando (Köhler & Lötters 1999, De la Riva *et al.* 2000) were compiled ten years ago, an updated overview of the anuran species recorded from Pando is needed.

MATERIAL AND METHODS

Own investigations on anuran species diversity of the Departamento Pando were conducted between 1999 and 2008. We thoroughly surveyed 16 localities, selected to cover all main regions of the Departamento (Fig. 1). Many other localities were sampled occasionally during various short-term collecting trips. This work has already resulted in several publications (Moravec & Aparicio 2004a,b, 2005, 2006; Moravec *et al.* 2006, 2008, 2009; Castroviejo-Fisher *et al.* 2011). For the purpose of this overview we combined all our published and still unpublished faunal records with literature data into an updated list of anuran species of the Departamento Pando. Key references providing basic information about the occurrence of the listed species in Pando were included in the list. Notes on several new or biogeographically interesting records are summarized in a separate account. Voucher specimens as well as photo vouchers are deposited in the Colección Boliviana de Fauna (CBF) and the National Museum

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Prague (NMP6V – voucher specimens, NMP6F – photo vouchers).

RESULTS

The updated list of anuran species known to occur in the Departamento Pando (see Appendix I) contains 114 species belonging to 13 families (Aromobatidae 3, Bufonidae 8, Centrolenidae 3, Ceratophryidae 1, Dendrobatidae 5, Hemiphractidae 1, Hylidae 53, Leiuperidae 2, Leptodactylidae 18, Microhylidae 7, Pipidae 1, Ranidae 1, Strabomantidae 11).
New records are listed and commented below.

Centrolenidae
Vitreorana oyampiensis (Lescure, 1975)
Material: CBF 6408–09, NMP6V 74060/1–3

Six males of *V. oyampiensis* (Fig. 2A) were collected in the surroundings of the settlement of San Antonio (11°18'S, 67°23'W; *ca.* 200 m a.s.l.) on 23 November 2007. Until now the species has been recorded from the Guiana region, Colombia, Ecuador, Peru and Brazil (Frost 2009, Guayasamin *et al.* 2009). Cisneros-Heredia & McDiarmid (2007) mentioned the presence of *V. oyampiensis* (as *Cochranella ametarsia*) also in Bolivia, but they did not provide any exact locality. The finding of Muñoz & Aguayo (2009) can be regarded as the first Bolivian country record (Reserva de Vida Silvestre Bruno Racua, provincia Federico Román, Departamento Pando). Thus we provide the second vouchered record of *V. oyampiensis* for Bolivia, lying *ca.* 250 km SW of the first locality. The collected specimens were calling from dense vegetation covering very damp swampy shores of a small stream running through undisturbed *terra firme* forest.

Hylidae
Dendropsophus brevifrons (Duellman & Crump, 1974)
Photo vouchers: NMP6F 11–13.

This first record of *D. brevifrons* for Bolivia is based on three voucher photographs of an adult specimen

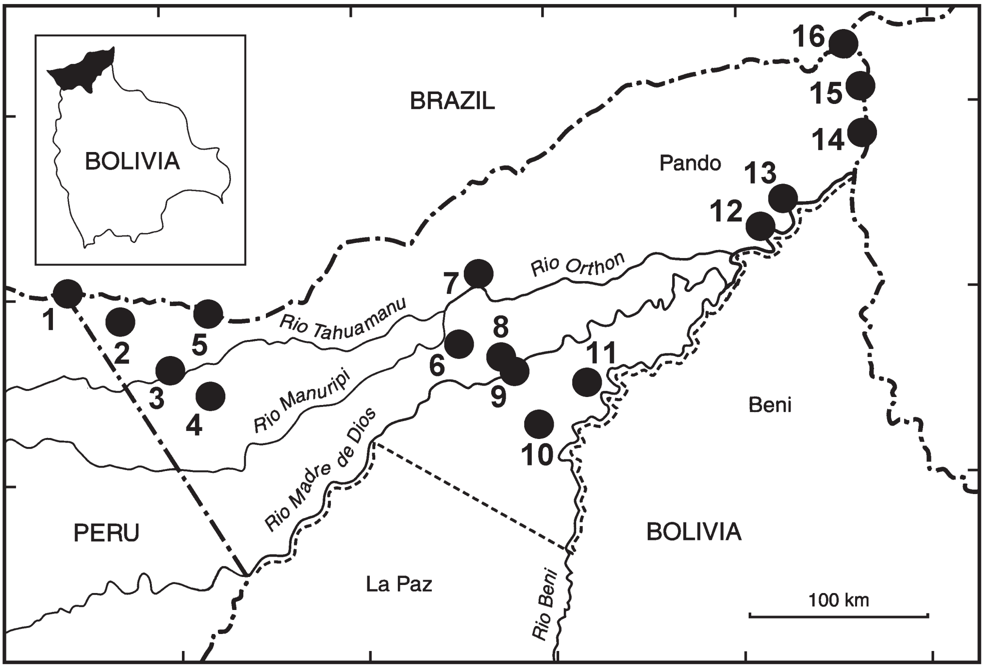

FIG. 1. Schematic map of the Departameto Pando showing the main localities investigated:
(1) Bolpebra, 10°57'S, 69°34'W; (2) Bioceanica, 11°08'S, 69°22'W; (3) Tahuamanu, 11°24'S, 69°01'W; (4) San Antonio, 11°29'S, 68°52'W; (5) Cobija, 11°02'S, 68°45'W; (6) San Antonio, 11°18'S, 67°23'W; (7) Nacebe, 11°00'S, 67°25'W; (8) Sacrificio, 11°23'S, 67°18'W; (9) Sena, 11°29'S, 67°15'W; (10) Canadá, 11°45'S, 67°08'W; (11) Barracón, 11°33'S, 66°56'W; (12) Santa Crucito, 10°44'S, 65°54'W; (13) Palmira, 10°35'S, 65°44'W; (14) Caimán, 10°14'S, 65°23'W; (15) Manoa, 9°41'S, 65°24'W; (16) Piedritas, 9°57'S, 65°20'W.

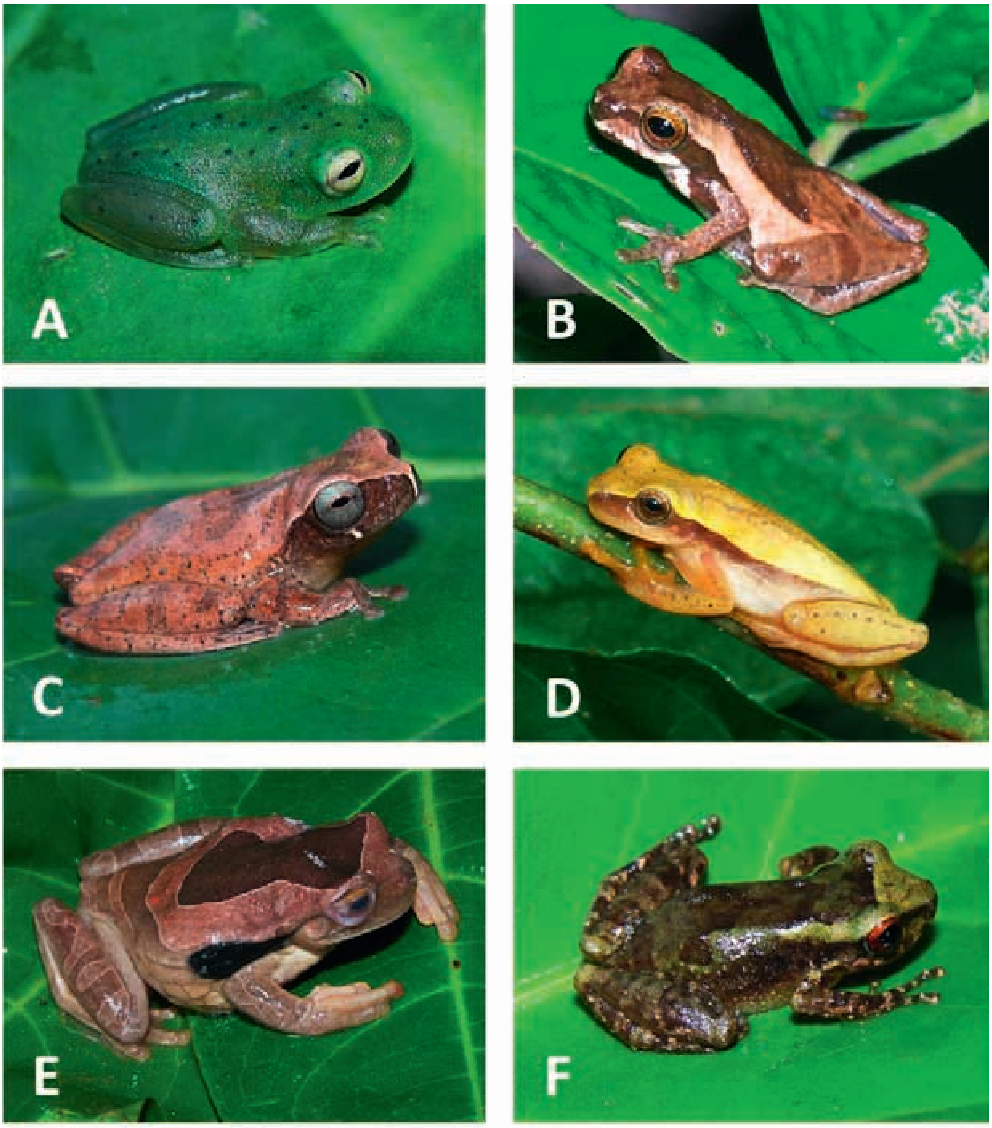

FIG. 2.(A) *Vitreorana oyampiensis*, San Antonio; (B) *Dendropsophus brevifrons*, Tahuamanu; (C) *Dendropsophus koechlini*, Sacrificio; (D) *Dendropsophus* cf. *nanus*, Laguna Murillo; (E) *Trachycephalus coriaceus*, San Antonio; (F) *Pristimantis olivaceus*, San Antonio.

obtained by M. Guerrero-Reinhard and G. Calderón in the area of the Estación Biológica Tahuamanu de la UAP (11°24'S, 69°01'W; *ca.* 280 m a.s.l.) on 1 April 2005 (Fig. 2B). The species is widely distributed in the Guianan region as well as the Central and Upper Amazon basin (Frost 2009), and its occurrence in Bolivia was predicted by De la Riva *et al.* (2000) and Köhler (2000).

Dendropsophus koechlini (Duellman & Trueb, 1989)
Material: CBF 6395, NMP6V 74061

In Bolivia *D. koechlini* was known from the Departamentos Beni, La Paz, and Santa Cruz (De la Riva *et al.* 2000). Recently, Reichle (2007) reported this species also from the south-westernmost corner of the Departamento Pando (settlement of Chivé). Here we record the finding of *D. koechlini* (Fig. 2C) in the vicinity of the settlement of Sacrificio (11°23'S, 67°18'W; *ca.* 180 m a.s.l.), which extends the known range of this species *ca.* 200 km NE to the central Pando. At his locality, several calling males were found in a dense flooded forest on 21 November 2007.

Dendropsophus cf. *nanus* (Boulenger, 1889)

Photo vouchers: NMP6F 14–15.

Our record is based on two voucher photographs (Fig. 2D) taken by M. Guerrero-Reinhard in the area of Laguna Murillo (*ca.* 11°11'S, 66°50'W; *ca.* 150 m a.s.l.) on 15 November 2004. *Dendropsophus nanus* is known from the Bolivian Departamentos Beni and Santa Cruz (De la Riva *et al.* 2000) where it is common in open habitats. In the Departamento Beni dense populations of this species were observed around Riberalta along the border with the Departamento Pando (Moravec & Aparicio 2000). The only record of *D. nanus* for the Departamento Pando (Fugler 1984) was questioned by Köhler & Lötters (1999). Nevertheless, our finding provides further evidence of the occurrence of this (or related morphologically similar) species in this Departament.

Trachycephalus coriaceus (Peters, 1867)

Material: CBF 6420, NMP6V 74062

Two voucher specimens were collected in the surroundings of the settlements San Antonio (11°18'S, 67°23'W; *ca.* 200 m a.s.l.) and San Antonio (11°29'S, 68°52'W; *ca.* 270 m a.s.l.) (Fig. 2E) on 22–26 November 2007. Both individuals were found in disturbed primary forest. In Bolivia, this species was previously known only from Puerto Almacén, in the Department of Santa Cruz (De la Riva 1990, De la Riva *et al.* 2000).

Strabomantidae

Pristimantis olivaceus (Köhler, Morales, Lötters, Reichle & Aparicio, 1998)

Material: CBF 6415–16, NMP6V 74067–68

This species (Fig. 2F) was known from the Bolivian Departamentos Cochabamba and Santa Cruz and from the Peruvian region of Madre de Dios (Köhler *et al.* 1998, Frost 2009). Thus, our records from the surroundings of the settlements of Palmira (10°35'S, 65°44'W; *ca.* 150 m a.s.l.) and San Antonio (11°29'S, 68°52'W; 270 m a.s.l.) made on 18–27 November 2007 fill the gap between the known localities. All collected specimens were males calling from trees *ca.* 10 m above the ground in disturbed primary forest.

DISCUSSION

The updated list of anuran species of the Departamento Pando comprises 114 species (some still awaiting definitive identification). This number more than doubles most recent species lists for the region (Köhler & Lötters 1999, De la Riva *et al.* 2000). Nevertheless, if we take into account the high anuran diversity of the more thoroughly surveyed area of Cuzco Amazónico in neighboring Peru (see Duellman 2005), and the high number of species predicted to occur within the territory of Pando (see De la Riva *et al.* 2000, Köhler 2000, Lötters *et al.* 2007, Reichle 2007), we can expect that our knowledge of anuran richness of the Departamento Pando remains still incomplete (see also Dahl *et al.* 2009). This is in agreement with our current finds of other anuran forms representing candidates for new species – (e.g.) a member of the *Leptodactylus marmoratus* group, which might be associated with one of three cryptic species (so called "Forest Call II") recognized by Angulo *et al.* (2003) in Tambopata Reserved Zone in Peru, or 2-3 different *Scinax* forms identified in Pando by M. Guerrero-Reinhard and M. Jansen (unpublished data).

Considering the number of the known species and those expected to occur in Pando we estimate its anuran richness at ca. 150 species. Moreover, recent DNA barcoding work shows that the number of anuran species in the Guianan and Amazonian regions is highly underestimated and up to 115% additional species may be expected among Neotropical amphibians in lowland rainforest (Fouquet *et al.* 2007). Thus, the real anuran diversity in the Departamento Pando is probably much higher than our current estimation.

The high anuran richness in the Departamento Pando can be seen in light of its geographic position in south-western Amazonia. In this territory, different faunal elements (species widespread in the Amazon basin, upper Amazonian species, south-western Amazonian species, species of peri-Andean forest, lower Amazonian species as well as *cerrado* and *Chaco* species) meet together and form biogeographically heterogeneous anuran communities. Therefore the amphibian fauna of the Departamento Pando deserves long-term thorough research and effective protection.

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APPENDIX 1. List of anuran species known to occur in the Departamento Pando, Bolivia.

Taxon	Key references
Aromobatidae	
Allobates trilineatus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Allobates cf. *femoralis*	Cadle & Reichle (2000), De la Riva *et al.* (2000), Moravec & Aparicio (2005)
Allobates sp.	Köhler & Lötters (1999)[1], Cadle & Guerrero (2003)[1]
Bufonidae	
Rhaebo guttatus	De la Riva *et al.* (2000), Lötters *et al.* (2000)
Rhinella cf. *acutirostris*	Köhler & Lötters (1999), De la Riva *et al.* (2000), Lötters & Köhler (2000)
Rhinella castaneotica	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Rhinella granulosa	De la Riva *et al.* (2000)
Rhinella marina	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Rhinella poeppigii	Moravec & Aparicio (2005)
Rhinella sp. I (*margaritifera* complex)	Cadle *et al.* (2003), Moravec & Aparicio (2005)
Rhinella sp. II (*margaritifera* complex)	Cadle *et al.* (2003), Moravec & Aparicio (2005)
Centrolenidae	
Hyalinobatrachium mondolfii	Castroviejo-Fisher *et al.* 2011
Hyalinobatrachium munozorum	Castroviejo-Fisher *et al.* 2011
Vitreorana oyampiensis	Cisneros-Heredia & McDiarmid (2007)[2], Muñoz & Aguayo (2009)
Ceratophryidae	
Ceratophrys cornuta	Cadle & Reichle (2000)
Dendrobatidae	
Ameerega hahneli	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Ameerega picta	Moravec & Aparicio (2006)
Ameerega trivittata	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Adelphobates quinquevittatus	Cadle *et al.* (2003)
Ranitomeya biolat	Maldonado & Reichle (2007)
Hemiphractidae	
Hemiphractus scutatus	Muñoz (2008)
Hylidae	
Dendropsophus acreanus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Dendropsophus brevifrons	This paper
Dendropsophus joannae	Köhler & Lötters (2001)
Dendropsophus juliani	Moravec *et al.* (2006)
Dendropsophus koechlini	Reichle (2007), this paper

Taxon	Key references
Dendropsophus leali	Moravec & Aparicio (2005)
Dendropsophus leucophyllatus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Dendropsophus marmoratus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Dendropsophus minutus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Dendropsophus cf. *nanus*	This paper
Dendropsophus parviceps	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Dendropsophus rhodopeplus	Moravec & Aparicio (2005)
Dendropsophus riveroi	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Dendropsophus reichlei	Moravec *et al.* (2008)
Dendropsophus salli	Jungfer *et al.* (2010)
Dendropsophus sarayacuensis	De la Riva *et al.* (2000)
Dendropsophus schubarti	De la Riva *et al.* (2000)
Dendropsophus triangulus	Moravec & Aparicio (2004a,b)
Dendropsophus xapuriensis	Moravec & Aparicio (2005)
Dendropsophus sp.	Moravec *et al.* (2008)
Hypsiboas albopunctatus	Jansen *et al.* (2008)
Hypsiboas boans	Cadle & Guerrero (2003)
Hypsiboas calcaratus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Hypsiboas cinerascens	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Hypsiboas fasciatus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Hypsiboas geographicus	Cadle & Reichle (2000)
Hypsiboas lanciformis	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Hypsiboas punctatus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Hypsiboas raniceps	Reichle (2007)
Osteocephalus buckleyi	Cadle *et al.* (2003)
Osteocephalus castaneicola	Moravec *et al.* (2009)
Osteocephalus taurinus	Cadle & Guerrero (2003)
Osteocephalus sp. (A)	Köhler & Lötters (1999)[3], De la Riva *et al.* (2000)[3]
Osteocephalus sp. (B)	Moravec & Aparicio (2004a), Moravec *et al.* (2009)
Phyllomedusa atelopoides	Gonzáles & Reichle (2004)
Phyllomedusa bicolor	Cadle & Reichle (2000), De la Riva *et al.* (2000)
Phyllomedusa camba	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Phyllomedusa palliata	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Phyllomedusa tomopterna	Cadle *et al.* (2003)
Phyllomedusa vaillantii	Cadle & Reichle (2000)
Pseudis paradoxa	Moravec & Aparicio (2004)
Scarthyla goinorum	De la Riva *et al.* (2000)
Scinax chiquitanus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Scinax garbei	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Scinax ictericus	Gonzáles & Reichle (2004)
Scinax nebulosus	Moravec & Aparicio (2004)
Scinax cf. *fuscomarginatus*	Moravec & Aparicio (2006)[4], Jansen (unpubl. data)
Scinax pedromedinae	Moravec & Aparicio (2004)

Taxon	Key references
Scinax ruber	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Sphaenorhynchus lacteus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Trachycephalus coriaceus	This paper
Trachycephalus resinifictrix	Cadle & Reichle (2000), De la Riva *et al.* (2000)
Trachycephalus typhonius	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leiuperidae	
Edalorhina perezi	Gonzáles & Reichle (2004), Moravec & Aparicio (2005)
Engystomops freibergi	Cadle & Reichle (2000)
Leptodactylidae	
Leptodactylus bolivianus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus discodactylus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus didymus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus elenae	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus fuscus	Cadle & Guerrero (2003)
Leptodactylus hylaedactylus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus knudseni	Reichle (2007)
Leptodactylus cf. *labyrinthicus*	Cadle *et al.* (2003)
Leptodactylus leptodactyloides	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus lineatus	Cadle *et al.* (2003)
Leptodact. cf. *macrosternum*	Köhler & Lötters (1999)[5], Cadle *et al.* (2003)[5]
Leptodactylus pentadactylus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus petersi	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus podicipinus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus rhodomystax	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Leptodactylus rhodonotus	Cadle & Reichle (2000)
Leptodactylus simonstuarti	Angulo & Icochea (2010)
Leptodactylus sp. I	Köhler & Lötters (1999)[6], De la Riva *et al.* (2000)[6]
Microhylide	
Altigius alios	Gonzáles & Reichle (2004)
Chiasmocleis bassleri	Cadle *et al.* (2003), Gonzáles & Reichle (2004)
Chiasmocleis ventrimaculata	Cadle *et al.* (2003)
Chiasmocleis sp.	Cadle *et al.* (2003)
Ctenophryne geayi	Gonzáles & Reichle (2004)
Elachistocleis helianneae	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Hamptophryne boliviana	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Pipidae	
Pipa pipa	Moravec & Aparicio (2004), Padial & De la Riva (2005)
Ranidae	
Lithobates palmipes	Reichle (2007)

Taxon	Key references
Strabomantidae	
Oreobates cruralis	Padial *et al.* (2004)
Oreobates quixensis	Cadle & Reichle (2000), De la Riva *et al.* (2000)
Pristimantis altamazonicus	Padial et al. (2004)
Pristimantis fenestratus	Köhler & Lötters (1999), De la Riva *et al.* (2000)
Pristimantis ockendeni	Padial *et al.* (2004)
Pristimantis olivaceus	This paper
Pristimantis reichlei	Cadle & Reichle (2000)[7], Moravec & Aparicio (2005)[7], Padial & De la Riva (2009)
Pristimantis skydmainos	Padial *et al.* (2004)
Pristimantis toftae	Padial *et al.* (2004)
Pristimantis ventrimarmoratus	De la Riva *et al.* (2000)
Pristimantis zimmermanae	Padial *et al.* (2004)

[1] identified as *Colostethus* sp.
[2] identified as *Cochranella ametarsia*
[3] identified as *Osteocephalus leprieurii*
[4] identified as *Scinax parkeri*
[5] identified as *Leptodactylus chaquensis/macrosternum*
[6] identified as *Adenomera andreae*
[7] identified as *Eleutherodactylus danae* or *E.* cf. *danae*

HERPETOLOGY ON THE FRINGES OF THE SUNDA SHELF: A DISCUSSION OF DISCOVERY, TAXONOMY, AND BIOGEOGRAPHY

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ABSTRACT

Updated information on the herpetofaunal composition of the borderlands (upland systems and archipelagos) fringing the Sunda Shelf is presented for Vietnam, Cambodia, and Peninsular Malaysia. It is suggested that the herpetofaunal composition of this region has been shaped by climatic fluctuations throughout Southeast Asia and episodic marine transgressions of the South China Sea, specifically in the region of the Sunda Shelf, resulting in significant degrees of endemism in montane areas and archipelagos. These preliminary findings highlight the understudied nature of these borderlands, especially in Peninsular Thailand and Borneo. Even in the regions discussed, several islands and mountain ranges remain unexplored. As fieldwork progresses into these areas and additional species records are documented, and new lineages discovered and described, it is believed that an awareness of the unappreciated importance of these borderlands to the overall biodiversity and biogeography of Southeast Asia will emerge.

Key words: Southeast Asia, Sunda Shelf, Cambodia, Vietnam, Malaysia, archipelago, herpetology.

INTRODUCTION

The Sunda Shelf is a broad, continental, subaerial extension of Southeast Asia lying beneath the South China Sea that unites the Indochinese Peninsula with the Sundaic regions of Borneo, Java, Sumatra, and the Malay Peninsula (Fig. 1). Its complex tectonic (Hall 1998, 2001, 2002) and climatic history (Woodruff 2003, Bird *et al.* 2005, Outlaw & Voelker 2008, Reddy 2008), coupled with cyclical changes in sea levels over last 5 million years (e.g. Outlaw & Voelker 2008), has contributed to the formation of several archipelagos and mountain systems that now frame the northern, western, and southern fringes of the South China Sea. Since the most recent glacial maximum 18-21 000 years before present (kybp), the Sunda Shelf has gone from being a fully exposed flood plain supporting a mixture of wet evergreen forests, dry deciduous forests, woodland savannahs, and marshlands crisscrossed by a network of rivers and lakes (Sterling *et al.* 2006), to being completely submerged (Sathiamurthy & Voris 2006). This wholesale transformation has happened multiple times over at least the last five million years but has increased in extent and intensity during more recent times (Bird *et al.* 2005, Sterling *et al.* 2006, Grismer & Grismer 2010). This has had a dramatic effect on the biogeography of many species of Southeast Asia in providing numerous opportunities for range expansions and contractions, extinctions, and secondary contact between sister lineages (e.g. Reddy 2008, Matsui *et al.* 2009). For example at 13 kybp, sea levels were approximately 75 m lower than they are today, still leaving large, marshy, partially exposed, land-positive connections between Indochina

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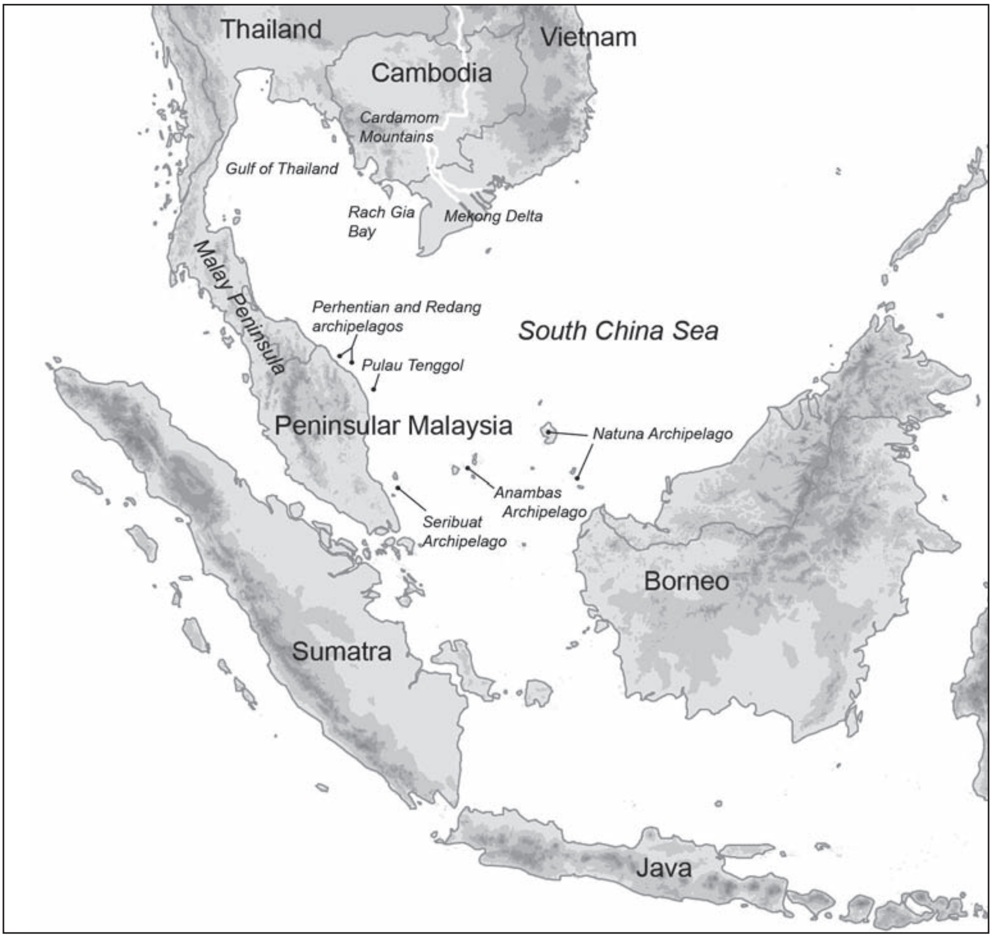

FIG. 1. The Greater Sunda Islands (Borneo, Sumatra, and Java), the borderlands of the Sunda Shelf framing the South China Sea and the Gulf of Thailand, and the archipelagos discussed.

and the Greater Sundas Islands (Sathiamurthy & Voris 2006, Sterling *et al.* 2006). The rapid obliteration of these landbridges due to rising sea levels beginning at 11 kybp, left disjunct populations to evolve in isolation on opposing shores of the newly emerging South China Sea (Grismer & Grismer 2010) as well as isolating several other lineages on the archipelagos currently fringing this area (see below). The warmer and drier climate associated with an expanding sea forced other, more temperate species to retreat upslope with retreating, cool-adapted forests to upland regions (Huges *et al.* 2003, Sterling *et al.* 2006, Outlaw & Voelker 2008, Reddy 2008). The impact on the herpetofauna of such an intricate environmental history manifests itself in high degrees of endemism in upland systems (e.g. Flower 1896, 1899 ; Boulenger 1900a,b, 1903, 1908; Laidlaw 1900, 1901a,b; Smith 1922a, 1935; Smedley 1931c, Grandison 1972, Sly 1976, Dring 1979, Hallerman & McGuire 2001; Lim *et al.* 2002, Das *et al.* 2004, Sanders *et al.* 2004, Vogel *et al.* 2004, Grismer 2011b, Grismer *et al.* 2006b, 2007a,b, 2008a,b,c, 2009a,b,c; Matsui & Ibrahim 2006, Grismer 2007a,b, 2008a,b,c; McLeod & Norhyati 2007, Chan-ard *et al.* 2008, Wood *et al.* 2008a, 2009; Chan *et al.* 2009, Matsui *et al.* 2009) and insular (e.g. Smith 1922b, Ouboter 1986, Darevsky & Sczcerbak 1997, Das & Lim 2000, Das & Grismer 2003, Grismer 2011a, Grismer *et al.* 2003, 2004b, 2006c, 2009c, 2010a,b; J. Grismer *et al.* 2003, Leong *et al.*

2003, Diaz *et al.* 2004, Leong & Grismer 2004, Grismer 2005, 2006a,b, 2011b, Grismer & Das 2006, Youmans & Grismer 2006, Grismer & Ngo 2007, Grismer & Chan 2008, Ngo *et al.* 2008, Chan & Norhayati 2010), fragmented distribution patterns, and sister group relationships across marine and terrestrial biogeographic barriers (Inger & Voris 2001, de Bruyn *et al.* 2005, Outlaw & Voelker 2008, Reddy 2008, Grismer & Grismer 201, Grismer *et al.* 2010c and in press). In general, these biogeographical patterns are more easily observed in the herpetofauna of these regions because they are not usually erased by long-distance dispersal (e.g. Outlaw & Voelker 2008) and remain embedded in the phylogenetic structure and the geographical distribution of this relatively sedentary fauna. Such patterns are just now beginning to emerge as more researchers are beginning to analyze the evolutionary relationships and phylogeographic structure of wide-ranging Indo-Malayan lineages (e.g. Karns *et al.* 2000, Inger & Voris 2001, Evans *et al.* 2003, Matsui *et al.* 2005a, 2010a; Grismer *et al.* in press) as well as publishing the results of explorative field work in some of the more inaccessible continental regions and archipelagos along these borderlands (e.g. Grismer & Ngo 2007, Grismer *et al.* 2007a,b, 2008a,b,d; Ngo 2008, Ngo *et al.* 2008, Stuart & Emmet 2006, Stuart *et al.* 2006) that is foundational to the biogeographical analyses. Reported here are new data from explorations of the coastal and insular regions of southern Vietnam, Cambodia and the Malay Peninsula that will be incorporated into a growing database detailing the biogeographic history of the Indo-Malayan herpetofauna.

SOUTHERN VIETNAM: MEKONG DELTA REGION AND THE ISLANDS OF RACH GIA BAY

The mountainous, continental border framing much of the northern edge of the Gulf of Thailand extends from the Yai and Soi Dao Tai mountains of eastern Thailand through the Cardamom Mountains of southwestern Cambodia, eastward to the Bay Nui Mountains of the Mekong Delta region of southern Vietnam (Figs. 1, 2). Associated with these larger

FIG. 2. The habitat islands of the southern Mekong Delta and the islands of Rach Gia Bay, Vietnam for which herpetofaunal records exist.

ranges are numerous isolated granite and karst uplifts that punctuate the Mekong Delta region, particularly in southern Vietnam (Fig. 2). These borderlands also include numerous offshore islands lying within the 10-m depth contour extending from Ko Chang Island, Thailand to Phu Quoc Island, Vietnam and many of the smaller islands in Rach Gia Bay off the south coast of southern Vietnam (Figs. 1, 2). During the mid-Holocene sea level highstand 4.2 - 7 kybp (Nguyen *et al.* 2000, Sathiamurthy & Voris 2006), the uplifted areas along the coastline and farther inland existed as islands (Sterling *et al.* 2006), effectively limiting gene flow between populations inhabiting them (Grismer & Ngo 2007). During the short time interval following the ocean's regression to its current level, the Mekong River changed course for the last time, turning to the east and no longer draining directly into the Tonle Sap Basin of Cambodia. This diverted massive amounts of deltaic deposits and rapidly formed the current Mekong Delta of southeastern Cambodia and southern Vietnam, fanning eastward from Phnom Penh, Cambodia to the mouth of the Saigon River in the north, and southward to form the entire Ca Mau Peninsula of Vietnam (Attwood & Johnston 2001, Ta *et al.* 2002). What exists today is an extensive alluvial fan (on which little in the way of natural vegetation remains) punctuated by numerous karst and granite habitat islands. The discovery of new species on these small, isolated, rocky habitat islands such as Nui Cam Hill, Tuc Dup Hill, and Hon Dat Hill (Grismer & Ngo 2007, Ngo 2008; Fig. 2), underscores the archipelago-like nature of the southern Mekong Delta region that is mirrored by the growing degree of insular endemism on the small islands off the adjacent coast in Rach Gia Bay (Darevsky & Szczerbak 1997, Grismer & Ngo 2007, Ngo *et al.* 2008, Grismer *et al.* 2008e, 2010a). To date, four endemic species of lizards are known from the habitat islands in the southern delta region (Grismer & Ngo 2007, Ngo 2008) and there still remains many more "islands" in need of exploration. Much the same situation exists with the 90+ islands of Rach Gia Bay (Fig. 2) from which herpetological records are known from only seven (Darevsky & Szczerbak 1997, Darevsky 1999, Grismer & Ngo 2007; Grismer *et al.* 2008e, 2010a; Ngo *et al.* 2008), and from which six endemic species have been reported and several more are in the process of being described (Grismer *et al.* in press, Ngo *et al.* in press). Therefore it is essential to present up-to-date baseline data on the herpetofauna of these islands in order to provide a foundation from which other work may continue.

There are approximately 92 islands within Rach Gia Bay. Many of these occur in close proximity forming archipelagos such as those associated with Phu Quoc Island, Tien Hai Island, Son Hai Island, and Nam Du Island (Fig. 2) whereas others such as Tho Chau, Hon Khoai, Hon Son (=Rai), Hon Tre, and Hon Nghe are generally larger and more isolated (Fig. 2). The islands located near the coast of southern Vietnam, such as the Tien Hai islands and Son Hai islands, tend to have a basement of karst (Fig. 3) whereas the more outlying islands such as Hon Khoai, Hon Tre, Hon Rai, and Phu Quoc have a granite basement (Fig. 4). None of the larger islands except Hon Khoai are covered with primary forest and on most, secondary growth is extensive. Only a few, such as Hon Son, are dominated by viney secondary growth.

Published herepetological records exist for the islands of Phu Quoc (Moler *et al.* 2008), Hon Thom (Darevsky & Szczerbak 1997, Darevsky 1999), Hon Tho Chau (Darevsky 1999), Hon Tre (Grismer & Ngo 2007, Ngo 2008), Hon Son (Grismer *et al.* 2008e), and Hon Khoai (Grismer *et al.* 2010a). To this we add 54 new records for five more islands and 27 new records for islands whose herpetoaunas have already been reported. All new, confirmed records were observed firsthand, collected, and/or photographed by NVT, LLG and/or JLG.

PHU QUOC ISLAND

Phu Quoc Island is by far the largest (*ca.* 675 km^2) and most environmentally diverse island in Rach Gia Bay. It, and the numerous small islands extending from its narrow, southern terminus, form the western edge of Rach Gia Bay and represent emergent offshore fragments of the Bokor Plateau of the Cardamom Mountains of Cambodia (Fig. 2). Moler *et al.* (2008) reported 54 species of amphibians and reptiles from Phu Quoc Island (Table 1) to which we add one frog *Microhyla pulchra* (LSUDPC 2900), one skink *Sphenomorphus maculatus* (LSUDPC 1255), and four colubrid snakes *Dryocalamus davidsoni* (LSUDPC 3083–85), *Lycodon laoensis* (LSUDPC 2995), *Oligodon barroni* (LSUDPC 3192–94), and *Xenochrophis trianguligerus* (LSUDPC 5303). All were observed during the evening along a rocky stream at Phu Quoc National Park (10°17.452'N, 104°02.380'E) during 24–26 July 2007. To this we also tentatively add the turtle *Cycle-*

FIG. 3. A small karst island in the Son Hai Archipelago, Vietnam.

FIG. 4. The granite-based island of Hon Khoai, Vietnam.

TABLE 1. Hereptological records from islands of the Phu Quoc Archipelago.

	Phu Quoc	Hon Thom
Amphihia		
Anura		
Bufonidae		
Duttaphrynus melanostictus	x	
Ranidae		
Limnonectes kuhlii	x	
Occidozygus laevis	x	
Hylarana macrodactyla	x	
Hylarana taipehensis	x	
Hylarana nigrovittata	x	
Microhylidae		
Kalophrynus interlineatus	x	
Kaloula pulchra	x	
Microhyla heymonsi	x	
Microhyla pulchra	x	
Micryletta inornata	x	
Chirixalus nongkhorensis	x	
Polypedates leucomystax	x	
Theloderma stellatum	x	
Cacaelia		
Ichthyophis bananicus	x	
Reptilia		
Chelonia		
Bataguridae		
Cyclemys pulchristriata	x	
Trionychidae		
Amayda cartilaginea	x	
Squamata—Lizards		
Agamidae		
Acanthosaura cardamomensis	x	
Calotes versicolor	x	
Draco indochinensis	x	
Draco maculatus	x	
Physignathus cocincinus	x	
Leiolepedidae		
Leiolepis reevesii	x	
Gekkonidae		
Cyrtodactylus paradoxus		x
Cyrtodactylus phuquocensis	x	
Dixonius siamensis	x	
Hemidactylus frenatus	x	x
Hemidactylus bowringii		x
Hemidactylus platyurus		x
Gehyra mutilata	x	x
Gekko gecko	x	x
Ptychozoon lionotum	x	
Lacertidae		
Takydromus sexlineatus	x	
Sicncidae		
Dasia olivacea	x	
Lipinia vittigera	x	
Lygosoma bowringii	x	
Eutropis macularia	x	x
Eutropis multifasciata	x	x
Sphenomorphus maculatus	x	x
Varanidae		
Varanus salvator	x	x
Squamata—Snakes		
Cylindropidae		
Cylindrophus rufus	x	
Pythonidae		
Broghammerus reticulatus	x	
Colubridae		
Ahaetulla prasina	x	
Boiga cyanea	x	
Chrysopelea ornata		x
Dryocalamus davidsoni	x	
Enhydris bocourti	x	
Enhydris enhydris	x	
Enhydris plumbea	x	
Homolopsis buccata	x	
Lycodon laoensis	x	
Oligodon barroni	x	
Oligodon ocellatus	x	
Pareas carinatus	x	
Psammodynastes pulverulentus	x	
Pyas korros	x	
Xenochrophis piscator	x	
Xenochrophis triangulageris	x	
Elapidae		
Bungaraus candidus	x	
Calliophis maculiceps	x	
Naja siamensis	x	
Viperidae		
Cryptelytrops albolabris	x	
Cryptelytrops cf. *cardamomensis*	x	

mys pulchtistriata. This specimen is based on a partial left posterior plastron. According to Peter Paul van Dijk (*in litt.* 2009), the radiating pattern of each scute restricts it to *Heosemys* or *Cyclemys*. The forward curvature of the anal scute as it goes from the edge of the plastron to the midline is characteristic of *Cyclemys*. *Cyclemys pulchristriata* is the commonest species of *Cyclemys* in this region.

HON THOM ISLAND

Hon Thom is a small island (17 km^2) lying 8 km off the southern tip of Phu Quoc Island, Kien Giang Province (9°57.22'N, 104°01.030'E; Fig. 2). Hon Thom is steep-sided and rocky, reaching 162 m in elevation. Most of the vegetation is secondary deciduous forest scattered among volcanic rock outcroppings, and in the flat coastal areas the forest has been completely cleared and replanted with mangos, jackfruit, and logan. Darevsky (1999) reported nine species of lizards and one species of snake (Table 1). To Darevsky's (1999) list we add *Varanus salvator* which were seen during April 2006 foraging in the estuaries as well as along the forest trails, and *Python reticulatus* which was found raiding a chicken house in the village (Table 1). Identifications were confirmed by the use of Nguyen *et al.* (2009).

HON NGHE ISLAND

Hon Nghe is a small island (25 km^2) lying 14 km off the coast of Chua Hang, Kien Giang Province (10°01.405'N, 104°33.151'E; Fig. 2). Hon Nghe is steep-sided and reaches 338 m in elevation. Much of its forest has been cleared and replanted with mango groves and other fruit trees. Remaining patches of secondary forest occur on the slopes toward the interior of the island and a small outcropping of karst occurs in the island's northeastern section. We report here the first herpetological records for this island, obtained on 19 May 2007 (Table 2). Identifications were confirmed by the use of Nguyen *et al.* (2009). Unfortunately, the voucher photographs were irretrievably lost during a hard-drive crash. Thus these records must remain unconfirmed. Species found were the frogs *Duttaphrynus melanostictus* and *Polypedates* cf. *leucomystax*, the lizards *Calotes versicolor*, *Hemidactylus frenatus*, *H. platyurus*, *Gekko gecko*, and *Varanus salvator*, and the snakes *Broghammerus reticulatus* and *Chrysopelea ornata*. The majority of these species were found in disturbed areas of the plantations and in and amongst human habitations.

HON TRE ISLAND

Hon Tre is a small island (27 km^2) lying 15 km off the coast of Rach Gia City (9°58.342'N, 104°50.955'E; Fig. 2). It is steep-sided, reaching 315 m in elevation and is dominated by secondary and primary semideciduous forest that covers a landscape composed of nearly continuous outcrops of large granite boulders. *Cnemaspis caudanivea* and *Cyrtodactylus eisenmani* are the only species to have been reported from Hon Tre Island (Grismer & Ngo 2007, Ngo 2008) and to those reports we add the frog *Rana taipensis* (LSUDPC 3106) and the lizards *Calotes versicolor* (LSUDCP 2949), *Draco maculatus* (LSUDCP

TABLE 2. Herpetofauna of Hon Nghe, Hon Tre, Hon Son Rai (=Hon Son), Hon Chuoi, Hon Sao, Hon Khoai, Nam Du, and Tho Chau islands.

	Hon Nghe	Hon Tre	Hon Son	Hon Khoai	Hon Sao	Hon Chuoi	Tho Chau	Nam Du
Amphihia								
Anura								
Hyylarana taipensis		x						
Hylarana erythraea			x					
Bufonidae								
Duttaphrynus melanostictus	x	x	x			x	x	x
Rhacophoridae								
Polypedates cf. *leucomystax*	x	x	x	x	x	x	x	x
Ichthyophis sp.			x					

	Hon Nghe	Hon Tre	Hon Son	Hon Khoai	Hon Sao	Hon Chuoi	Tho Chau	Nam Du
Reptilia								
Squamata – Lizards								
Agamidae								
Calotes versicolor	x	x	x		x	x		x
Draco maculatus		x	x	x		x		
Gekkonidae								
Cnemaspis caudanivea		x						
Cnemaspis psychedelica				x				
Cyrtodactylus hontreensis		x						
Cyrtodactylus eisenmani			x					
Cyrtodactylus paradoxus								x
Cyrtodactylus sp.1				x	x	x		
Cyrtodactylus sp.2		x						
Cyrtodactylus sp.3				x				
Cyrtodactylus sp.4							x	
Hemidactylus bowringi							x	
Hemidactylus frenatus	x	x	x	x	x	x	x	x
Hemidactylus platyurus	x	x	x	x	x	x	x	
Gehyra mutilata		x		x			x	
Gekko gecko	x	x	x	x	x	x	x	x
Lepidodactylus lugubris							x	
Ptychozoon trinotaterra		x						
Sicncidae								
Dasia olivacea				x		x	x	
Eutropis longicaudata		x						
Eutropis multifasciata						x	x	
Varanidae								
Varanus nebulosus							x	
Varanus salvator	x	x	x	x	x	x		x
Squamata – Snakes								
Typhlopidae								
Ramphotyphlops braminus		x	x					
Pythonidae								
Broghammerus reticulatus	x	x	x	x	x	x	x	
Colubridae								
Ahaetulla prasina		x		x				
Chrysopelea ornata	x			x				
Coelognathus radiatus							x	
Boiga cyanea		x						
Oligodon sp.			x					
Lycodon capucinus			x	x				x
Viperidae								
Cryptelytrops honsonensis			x					
Cryptelytrops albolabris		x						x

3081), *Gehyra mutilata* (LSUDCP 4086), *Gekko gecko* (LSUDCP 3086), *Hemidactylus fernatus* (LSUDCP 3179), *H. platyurus* (LSUDCP 3089), *Ptychozoon trinotaterra* (unconfirmed), *Eutropis longicaudata* (LSUDCP 3495), and *Varanus salvator* (LSUDPC 5244), and the snakes *Ramphotyphlops braminus* (unconfirmed), *Broghammerus reticulatus* (LSUDPC 0197), *Boiga cyanea* (unconfirmed), *Ahaetulla prasina* (LSUDCP 3033), and *Crypteytrops albolabris* (LSUDPC 3050) (Table 2). All were collected during 27–28 July 2007. *Calotes versicolor* were seen sleeping in vegetation. The *Draco maculatus* was seen 3 m up on the trunk of a large ornamental tree along the coast. The *Hemidactylus*, *Gehyra*, and *Gekko* were common at night on buildings and the *Ramphotyphlops braminus* was found beneath a small rock along the edge of a path in soft soil but escaped from the bag shortly after capture. The *Ahaetulla prasina* was found during the day in disturbed forest crawling through vegetation.

HON SON (=RAI) ISLAND

Hon Rai Island is located 61.2 km southeast of Rach Gia City (9°47.95'N, 104°37.86'E; Fig. 2). This very small island (*ca.* 22 km^2) reaches 405 m in elevation and is composed of large granite boulders that extend from the shoreline to its peaks with little to no primary vegetation remaining. Walking trails across the island have been cut through the highly degraded secondary vegetation that is heavily overrun with large tracts of bamboo and vines. The walking trails cross large expanses of boulder outcrops forming cavities extending as much as 20 m below the surface of the ground. Grismer *et al.* (2008e) reported 10 species of amphibians and reptiles from Hon Rai Island (Table 2) to which we add the frog *Rana erythraea* (heard calling), the caecilian *Ichthyophis* sp. (specimen lost), the lizard *Varanus salvator* (observed along the beach), and the snakes *Oligodon* sp.1 (LSUDPC 5304–11), *Oligodon* sp.2 (LSUDPC 5312–16), and *Lycodon capucinus* (LSUDPC 3242). The report of *Draco sumatranus* (Grismer *et al.* 2008e) is corrected here to *D. maculatus* (LSUDCP 3082), their *Cyrtodactylus* sp.1 has now been described as *C. honsonensis* (Ngo *et al.* 2008), and their *Cyrtodactylus* sp.2 is in the process of being described.

HON CHUOI

Hon Chuoi is a small island (18 km^2) lying 35 km off the east coast of the Ca Mau Peninsula (8°57.031'N, 104°31.315'E; Fig. 2) that reaches 120 m in elevation. Hon Chuoi is covered by secondary evergreen forest on its slopes while the flat, low-lying periphery of the island is composed of coconut, mango, and other planted groves. We report here the first herpetological records for this island, obtained on 24 February 2009 (Table 2). Identifications were confirmed by the use of Nguyen *et al.* (2009). Unfortunately, the voucher photographs were irretrievably lost during a hard-drive crash. Thus these records must remain unconfirmed. Species reported are the frogs *Duttaphrynus melanostictus* and *Polypedates* cf. *leucomystax*, the lizards *Calotes versicolor*, *Draco maculatus*, *Cyrtodactylus* sp.1, *Hemidactylus frenatus*, *H. platyurus*, *Gekko gecko*, *Dasia olivacea*, *Eutropis multifasciata*, and *Varanus salvator*, and the snake *Broghammerus reticulatus*. All species were found in secondary growth along the coast.

HON KHOAI ISLAND

Hon Khoai is a small (8 km^2) island lying 18 km off the southern tip of the Ca Mau Peninsula and is the easternmost island in Rach Gia Bay (Fig. 2). The island reaches 228 m in elevation and is generally steep-sided with a granite basement from which several large boulder crops originate beneath a canopy of primary semi-deciduous forest (Fig. 4). Grismer *et al.* (2010a) made a brief reconnaissance of the northwestern side of the island among an outcrop of granite boulders at approximately 150 m elevation on the island's slope on 24–25 July 2009 and documented the presence of the frog *Polypedates* cf. *leucomystax*, the lizards *Draco maculatus*, *Cnemaspis psychedelica*, *Cyrtodactylus* sp.1, *Hemidactylus frenatus*, *H. platyurus*, *Gehyra mutilata*, *Gekko gecko*, *Dasia olivacea*, and *Varanus salvator*, and the snakes *Broghammerus reticulatus*, *Ahaetulla prasina*, *Lycodon capucinus*, and *Chrysopelea ornata* (Table 2).

HON SAO ISLAND

Hon Sao is a small, satellite island (2 km^2) lying 1 km off the southeast coast of Hon Khoai Island (8°57.032'N, 104°51.064'E; Fig. 2) and reaches 164 m in elevation. Its geology and forest cover is much like that of Hon Khoai. We report here the first herpetological records for this island, obtained on 3 April 2009 (Table 2). Identifications were confirmed by the use of Nguyen *et al.* (2009). Unfortunately, the voucher photographs were irretrievably lost during a hard-drive crash, so these records must remain unconfirmed. Species reported are the frog *Polypedates* cf. *leucomystax*, the lizards *Calotes versicolor*, *Cyrtodactylus* sp.1, *Hemidactylus frenatus*, *Hemidactylus platyurus*, *Gekko gecko*, *Varanus salvator*, and the snake *Broghammerus reticulatus*. Surprisingly, *Cnemaspis psychedelica*, a species endemic and very common on granite boulders on Hon Khoai (Grismer *et al.* 2010a), was not found on Hon Sao.

NAM DU ARCHIPELAGO

The Nam Du Archipelago is a cluster of 17 small islands lying 84 km southwest of Rach Gia City (Fig. 2). The largest island of this group, Nam Du, is elongate in shape, reaches 310 m in elevation, and is dominated by low, secondary, semi-deciduous scrub on a sandstone basement. We surveyed this island on 28–29 June 2009 and present here the results of that survey, representing the first herpetological records for the island (Table 2). *Duttaphrynus melanostictus* (LSUDPC 5048) and *Polypedates* cf. *leucomystax* (LSUDPC 5115) were common at night along the sides of the road near the villages. Several juvenile *Calotes versicolor* (LSUDPC 5051) were seen sleeping in disturbed vegetation along trails and along the sides of roads. *Cyrtodactylus paradoxus* (LSUDPC 5074–76) was found foraging along the rocky areas of coastal bluffs and along rocks within the intertidal zone as well as inland in rocky areas in the forest. *Hemidactylus frenatus* (LSUDPC 5092) and *H. platyurus* (LSUDPC 5094) were common on the walls of buildings in the villages. *Gekko gecko* was heard calling from within houses in the village. A single specimen of *Lycodon capucinus* (LSUDPC 5107) was found foraging among the rocks of the intertidal zone, presumably hunting *C. paradoxus*. *Cryptelytrops albolabris* was reported by locals and remains unconfirmed. *Varanus salvator* was seen foraging in the intertidal area.

HON THO CHAU ISLAND (=CU LAO PANJANG =THO CHU)

Hon Tho Chau Island is the most remote island in Rach Gia bay, located 140 km off the coast from Rach Gia City and is surrounded by seven smaller satellite islands (Fig. 2). Hon Tho Chau Island is 12 km^2 in size, covered in secondary semi-evergreen forest, and reaches 167 m in elevation. Darevsky (1999) reported nine species of lizards and three species of snakes (Table 2). To this we add the frogs *Duttaphrynus melanostictus*, *Kaloula pulchra*, and *Polypedates* cf. *leucomystax*, the lizard *Cyrtodactylus* sp.4 (Ngo *et al.* in press), and the snake *Xenopeltis unicolor*. All records for this island were obtained on 20 July 2008 and 15 July 2009 and their identifications were confirmed by the use of Nguyen *et al.* (2009). Unfortunately, the voucher photographs were irretrievably lost during a hard-drive crash.

Although the islands of Rach Gia Bay form a somewhat environmentally incongruous group, the herpetofauna on them is in generally fairly similar (Tables 1, 2). The majority of the islands surveyed thus far tend to share a similar suite of species that are good overwater dispersers, island colonizers, and human commensals. These include *Duttaphrynus melanostictus*, *Polypedates* cf. *leucomystax*, *Calotes versicolor*, *Draco maculatus*, *Hemidactylus frenatus*, *H. platyurus*, *Gekko gecko*, *Varanus salvator*, and *Broghammerus reticulatus*. Endemics do occur on some islands and where there is one endemic there are usually others (Table 2). For example, *Cnemaspis psychedelica* on Hon Khoai Island exists with *Cyrtodatylus* sp.1. On Hon Rai Island, *Cyrtodactylus* sp.3, *Cyrtodactylus honsonensis*, and *Cryptelytrops honsosensis* are all endemic. Much the same is true for Hon Tre Island, whose endemics include *Cnemaspis caudanivea*, *Cyrtodactylus eisemanae*, and *Cyrtodactylus* sp.2. The exception is the large island of Phu Quoc, whose only endemic thus far is *Cyrtodactylus phuquocensis* (Ngo *et al.* 2010). The large size of this island and its varied habitats are similar to those of the adjacent continent and thus the strong selection pressures attendant on very small islands with restrictive habitats may not be a factor in driving the differentiation of new lineages.

SOUTHWESTERN CAMBODIA: THE CARDAMOM REGION

Cambodia's location in the southern portion of the Indochinese Peninsula places it at the northern end of the Indo-Malayan Forest (Webb 2005), which makes it a critical biogeographical link between Southeast Asian and East Asian herpetofaunas. Several recent studies have demonstrated that many wide-ranging lineages previously considered to be single species are actually composed of multiple species, and the species boundaries within many of these complexes occur within this general region of Indochina (e.g., Wüster *et al.* 1995, Matsui *et al.*1996, 2001, 2005a,b, 2010a; Ota *et al.* 2001, Bain *et al.* 2003, Wood *et al.* in press). Therefore, in

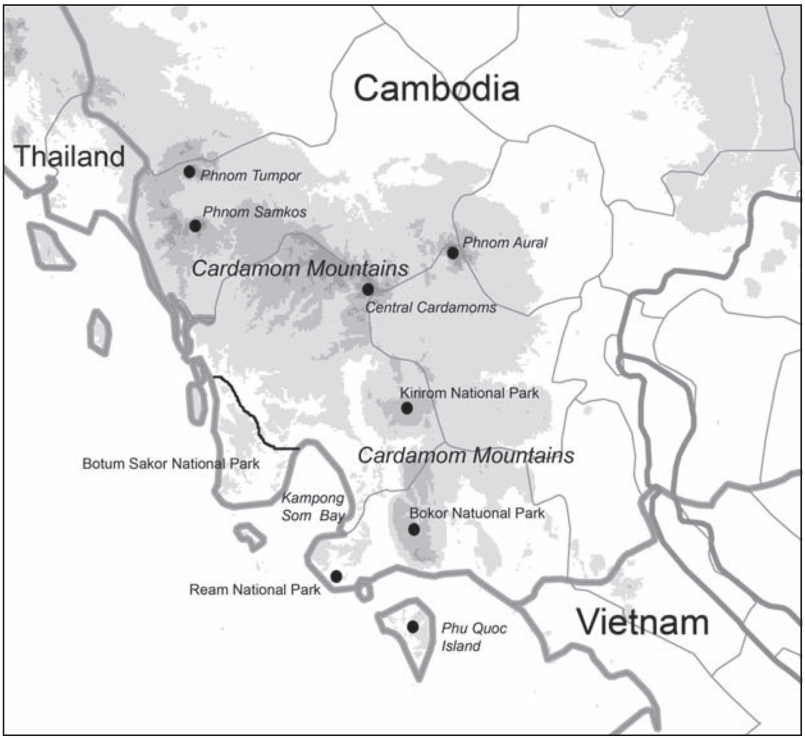

FIG. 5.
The Cardamom region of southwestern Cambodia.

order to more fully understand the historical biogeography of the Indochinese herpetofauna and to implement effective measures of conservation, groundwork from baseline field surveys and alphataxonomic investigations must first be laid. Unfortunately, years of political turmoil and genocide had all but halted any field-based studies in Cambodia, and as such, it lags behind neighboring countries of Indochina, namely Vietnam and Thailand (see Taylor 1962, 1963, 1965; Campden-Main 1969, Deuve 1970, Cox, 1991, Manthey and Grossmann 1997, Inger *et al.* 1999, Ziegler 2002, Chanard 2003, Teynie *et al.* 2004, Stuart 2005, Neang & Holden 2008, and references therein). Only within the last few years has the political situation in Cambodia stabilized enough to enable reasonably safe fieldwork in some areas (e.g. Stuart *et al.* 2006, Stuart & Emmet 2006, Grismer *et al.* 2007a,b, 2008b,d; Bezuijen *et al.* 2009).

Cambodia for the most part is a large floodplain that was formed over the last five million years from shifting drainages of the Mekong River and several of its smaller tributaries (Atwood & Johnston 2001). Currently, the central basin of Cambodia continues to receive drainage from the Khorat Plateau of northeastern Thailand to the north and from the Langiban and Kontum Plateaus of Vietnam in the east. Additionally, seasonal incursions from the Mekong River flowing into the Tonle Sap may increase the size of this lake by as much as 300%, causing it to spread out over much of central Cambodia. Bordering the southwestern edge of this central flood basin is the Cardamom region of southwestern Cambodia. This region is dominated by a rugged, physiographically complex system of mountains that frame much of the northern margin of the Gulf of Thailand (Fig. 5). The Cardamom Mountains begin just beyond the Thai Border in the Khao Soi Dao Mountains and extend 225 km to the southeast through the mountains of Kirirom National Park to the Elephant Mountains of Bokor National Park just east of Kampong Son Bay. From here they emerge offshore as the island of Phu Quoc, Vietnam (Fig. 5). Its conspicuous topography is composed of a series of semi-isolated prominent peaks, plateaus, and associated foothills separated by low-lying regions of varying terrain (Grismer *et al.* 2008b). In Cambodia, the western peaks, Phnom Samkos and Phnom Tumpor, reach 1717 m and 1551 m in elevation, respectively, and maintain regions of disturbed, deciduous dipterocarp forest throughout their intervening areas, and large tracts of lowland and evergreen hill forests along their slopes and upper elevations, respectively (Grismer *et al.* 2008b). The northeastern mountain, Phnom Aural, is the tallest peak in Cambodia, reaching 1813 m, and also maintains significant tracts of deciduous, dipterocarp forests and pristine evergreen forests (Grismer *et al.* 2007a). Between these ranges, the central section of the Cardamom Mountains reaches 1549 m and is dominated by a large plateau of evergreen and pine forests interlaced with a mosaic of grasslands. The Elephant Mountains of Bokor National Park form the continental southeastern portion of the Cardamom Mountains and reach 1087 m in height. The floral composition of this range is greatly affected by continuous, onshore winds arising from the Gulf of Thailand, which promote a mixture of grassland and heath forest (Stuart & Emmet 2006) and shroud the upper elevations of the Bokor Plateau in thick fog for much of the year. The slopes of the Elephant Mountains support tracts of primary evergreen forests and steep, fast-flowing, rocky streams.

A recent uptick in field surveys in the Cardamom region has begun to reveal its extensive herpetofaunal diversity as well as its growing level of endemism (Grismer *et al.* 2007a,b, 2008b,d; Stuart & Emmet 2006). The most recent surveys of the Cardamom Region (Grismer *et al.* 2008b) list 40 species of frogs, one caecilian, 10 turtles, 35 lizards, 51 snakes, and one crocodile, the vast majority of which have been reported from the mountainous areas and the intervening lowlands. Overlooked however, have been the low-lying costal regions between the Cardamom Mountains and the Gulf of Thailand. Two such regions recently surveyed include Botum Sokor National Park and Ream National Park. These national parks are on coastal prominences that form the northwestern and southeastern borders of Kompong Som Bay (Fig. 5). Although they are isolated politically, they are connected around the northern edge of Kompong Son Bay by continuous habitat. As such, their records are combined in Table 3. Surveys of these regions resulted in the discovery of five additional species previously unknown to the Cardamom Region, including the skink genus *Tropidophorus* and the elapid genus *Calliophis*. Additionally, the distributions of 32 species of amphibians and reptiles were extended to include these coastal regions (Table 3).

BOTUM SAKOR NATIONAL PARK

Botum Sakor National Park is located in Kompong Som Province along the southern coast of Cambodia (Fig. 5). It encompasses 1834 km^2 and its coastline is fringed by mangrove swamps and beaches. The interior offers some topographical relief with a small uplift running the length of the park and reaching approximately 335 m in elevation, supporting a semi-deciduous forest. Collections here were made intermittently in various habitats between 5 March and 5 September 2004, 24 April and 23 July 2005, and 18 April and 16 August 2006 by several individuals with Frontier Cambodia.

REAM NATIONAL PARK

Ream National Park is located on the southeastern side of a mountainous prominence due east of Sihanoukville in Kampot Province (Fig. 5). It encompasses 210 km^2 of coastal lands of which nearly one-third are mangrove forests and the rest semi-deciduous forest covering its low mountain ranges. Collections here were made intermittently in various habitats between 10 February and 24 August 2004 and 4 March and 6 July 2005. The species recorded from these areas are listed below.

Kalophrynus interlineatus. – A single specimen collected from Botum Sakor (FMNH 270638) matches the descriptions of this species from Phnom Samkos (Grismer *et al.* 2008b) and the central Cardamom Mountains (Stuart & Emmet 2006).

Micryletta inornata. – Three specimens were collected from Botum Sakor (FMNH 271545–47) which correspond to the description of this species from Bokor National Park (Grismer *et al.* 2008b) and the central Cardamom Mountains (Stuart & Emmet 2006).

Limnonectes cf. *dabanus*. – One adult female collected from Ream (FMNH 270155) is tentatively assigned to *L. dabanus*. As noted by Smith (1922b) and acknowledged by Stuart *et al.* (2006), females and juveniles of the *L. doriae* group are extremely difficult to tell apart. We elect to tentatively assign this species to *L. dabanus* rather than *L. gyldenstolpeii*, which is endemic to the Cardamom region, owing the presence of a dark, inverted V-marking on the upper back (Neang & Holden 2008) which is absent in *L. gyldenstolpeii*. This represents

TABLE 3. Checklist of the herpetofauna of the Cardamom Region. X = data from Grismer *et al.* (2008b) and Grismer *et al.* (2009); 0 = new data reported herein.

	North-west	Central	North-east	South-east	Coastal
CAECILIANS					
Ichthyopidae					
Ichthyophis sp.	x	x			
FROGS					
Megophryidae					
Leptolalax sp.			x		
Megophrys auralensis Ohler, Swan & Daltry 2002		x	x		
Bufonidae					
Duttaphrynus melanostictus Schneider 1799	x	x	x		
Ingerophrynus macrotis Boulenger 1887	x	x	x		
Ingerophrynus parvus Boulenger 1887	x	x			
Microhylidae					
Calluela guttulata (Blyth 1855)	x	x			
Kalophrynus interlineatus (Blyth 1855)	x	x	x		0
Kaloula pulchra Gray 1831	x	x	x		
Microhyla annamensis Smith 1923	x	x			
Microhyla berdmorei (Blyth 1856)	x	x		x	
Microhyla butleri Boulenger 1900	x	x	x		
Microhyla fissipes (Duméril, Bibron & Duméril 1841)	x	x			
Microhyla heymonsi Vogt 1911	x	x	x	x	
Microhyla pulchra (Hallowell 1861)	x	x	x		
Micryletta inornata (Boulenger 1890)	x	x		x	0
Ranidae					
Fejervarya cancrivora (Gravenhorst 1829)			x		
Fejervarya limnocharis (Gravenhorst 1829)	x	x	x		
Hoplobatrachus chinensis (Osbeck, 1756)	x	x	x		
Limnonectes cf. *dabanus* (Smith 1922)					0
Limnonectes gyldenstolpei (Anderson 1916)	x				
Limnonectes kochangae (Smith 1922)	x	x	x	x	
Occidozyga lima (Gravenhorst 1829)	x	x	x		
Occidozyga martensii Peters 1867	x	x	x		0
Paa fasciculispina (Inger 1970)	x	x	x		
Hylarana erythraea (Schlegel 1837)		x	x	x	0
Hylarana faber Ohler, Swan & Daltry 2002	x	x	x	x	
Hylarana macrodactyla (Günther 1859)		x			
Hylarana milleti Smith 1921	x	x	x		
Hylarana mortenseni Boulenger 1903	x	x	x	x	
Hylarana taiphensis van Denburgh 1909	x	x			
Rhacophoridae					
Chiromantis doriae Boulenger 1893		x			
Chiromantis nongkhorensis (Cochran 1927)	x	x	x	x	
Chiromantis samkosensis Grismer, Neang, Chav, & Holden 2007	x				
Chiromantis vittatus (Cochran 1927)	x	x	x		
Philautus cardamonus Ohler, Swan & Daltry 2002	x				
Philautus parvulus (Boulenger, 1893)	x	x	x	x	

	North-west	Central	North-east	South-east	Coastal
Polypedates cf. *leucomystax* (Gravenhorst 1829)	x	x	x		
Rhacophorus bipunctatus Ahl 1927	x	x	x		
Rhacophorus bisacculus Taylor 1962	x	x		x	
Theloderma asperum (Boulenger 1886)			x		
Theloderma stellatum Taylor 1962		x			
TURTLES					
Bataguridae					
Batagur baska (Gray 1831 "1830–35")		x			
Cuora amboinensis (Daudin 1802)	x	x	x		
Cyclemys atripons Iverson and McCord 1997	x	x		x	
Heosemys grandis (Gray 1860)		x			
Malayemys subtrijuga (Schlegel & Miller 1844)		x			
Sibenrockiella crassicollis (Gray 1831)		x			
Testudinidae					
Indotestudo elongata (Blyth 1853)		x	x		
Manouria impressa (Günther 1882)	x	x			
Trionychidae					
Amyda cartilaginea (Boddaert 1770)	x	x	x		
Pelochelys cantori Gray 1864		x			
CROCODYLIA					
Crocodylidae					
Crocodylus siamensis (Müller 1838)	x	x			
SQUAMATA (LIZARDS)					
Agamidae					
Acanthosaura cardamomensis Wooid *et al.* 2009	x	x	x	x	0
Calotes emma Gray 1845	x	x	x		0
Calotes mystaceus Duméril & Bibron 1837	x	x	x	x	
Calotes versicolor (Daudin 1802)	x	x	x	x	0
Draco indochinensis Smith 1928				x	
Draco maculatus (Gray 1845)	x	x	x	x	0
Draco taeniopterus Günther 1861	x	x	x		0
Physignathus cocincinus Cuvier 1829	x	x	x	x	
Pseudocalotes floweri (Boulenger 1912)				x	
Gekkonidae					
Cnemaspis chanthaburiensis Bauer & Das 1996	x				
Cnemaspis neangthyi Grismer, Grismer & Thou 2010	x				
Cyrtodactylus intermedius (Smith 1917)	x	x	x	x	0
Dixonius siamensis (Boulenger 1898)	x	x	x		
Gekko gecko (Linnaeus 1758)	x	x	x		
Gehyra mutilata (Wiegmann 1834)	x		x		
Hemidactylus frenatus Duméril & Bibron 1836	x	x	x	x	
Hemidactylus platyurus (Schneider 1792)	x		x		
Hemiphyllodactylus typus Bleeker 1860					0
Hemiphyllodactylus cf. *yunnanensis* (Boulenger 1903)	x				
Ptychozoon lionotum Annadale 1905		x		x	
Lacertidae					
Takydromus sexlineatus Daudin 1802	x	x			

	North-west	Central	North-east	South-east	Coastal
Scincidae					
Eutropis longicaudata (Hallowell 1857)	x				
Eutropis macularia (Blyth 1853)	x	x	x		
Eutropis multifasciata (Kuhl 1820)	x	x	x		
Lipinia vittigera (Boulenger 1894)	x	x	x	x	
Lygosoma bowringii (Günther 1864)	x	x	x	x	0
Lygosoma quadrupes (Linnaeus 1766)	x				
Scincella melanosticta (Boulenger 1887)	x	x	x	x	0
Scincella rufocaudata (Darevsky & Nguyen 1983)	x	x			
Sphenomorphus indicus (Gray 1853)	x	x	x		
Sphenomorphus maculatus (Blyth 1853)	x	x	x	x	0
Sphenomorphus stellatum (Boulenger 1900)		x			
Tropidoporus microlepis Gunther 1861					0
Leiolepididae					
Leiolepis belliana (Gray 1827)	x		x		
Leiolepis reevesi (Gray 1831)	x		x		
Varanidae					
Varanus nebulosus Gray 1831	x		x		
Varanus salvator Laurenti 1768	x	x	x		
SQUAMATA (SNAKES)					
Typhlopidae					
Ramphotyphlops braminus (Daudin 1803)	x	x			
Typhlops diardii Schlegel 1839	x	x			
Typhlops muelleri Schlegel 1839		x			0
Xenopeltidae					
Xenopeltis concolor Reinwardt in Boie, 1827		x		x	
Pythonidae					
Broghammerus reticulatus Schneider 1801	x				
Colubridae					
Ahaetulla nasuta (Lacépede 1789)	x				
Ahaetulla prasina (Reinwart in Boie 1827)	x	x	x	x	
Amphiesma boulengeri (Gressitt 1937)	x	x	x	x	
Boiga cyanea (Duméril, Bibron & Duméril 1854)	x	x		x	
Boiga dendrophila (Boie 1827)		x		x	
Boiga multomaculata (Boie 1827)		x	x	x	
Boiga siamensis Nootpand 1971	x	x			
Chrysopelea ornata (Shaw 1802)	x	x	x	x	
Coelognathus flavolineatus (Schlegel 1837)	x				
Coelognathus radiatus (Boie 1827)		x	x	x	
Dendrelaphis pictus Gmelin (1789)	x	x	x		
Dendrelaphis subocularis (Boulenger 1888)			x		
Dryocalamus davisonii (Blanford 1878)	x	x		x	
Dryophiops rubescens (Gray in Gray & Hardwicke 1835)			x		
Enhydris bocourti (Jan 1865)		x		x	0
Enhydris plumbea (Boie 1827)	x	x		x	
Gonyosoma oxycephalum (Boie 1827)		x			0
Homalopsis buccata (Linnaeus 1758)	x	x		x	0
Lycodon cardamomensis Daltry & Wüster 2002	x				

	North-west	Central	North-east	South-east	Coastal
Lycodon laoensis Günther 1864	x		x		
Oligodon barroni (Smith 1916)	x				
Oligodon duevei David, Vogel & Van Rooijen 2007	x				
Oligodon fasciolatus (Günther 1864)	x	x			
Oligodon inornatus (Boulenger 1914)	x	x			0
Oreophis porphyraceus (Cantor 1839)	x				
Orthriophis taeniurus (Cope 1861)	x				
Pareas carinatus (Boie, 1828)		x		x	0
Pareas margaritophorous (Jan, 1866)	x	x	x		
Psammodynastes pulverulentus (Boie 1827)	x	x	x	x	
Ptyas korros (Schlegel 1837)	x	x	x		
Ptyas mucosus (Linnaeus 1758)	x				
Rhabdophis chrysargos (Schlegel 1837)	x	x	x		
Rhabdophis nigrocinctus (Blyth 1856)	x	x	x		
Rhabdophis subminiatus (Schlegel 1837)	x	x	x	x	
Sibynophis collaris (Gray 1853)	x				
Sibynophis triangularis Taylor 1965		0			
Xenochrophis flavipunctatus (Hallowell 1860)	x	x	x		0
Xenochrophis trianguligerus (Boie 1827)		x			0
Elapidae					
Bungarus candidus (Linnaeus 1758)	x	x		x	0
Bungarus fasciatus (Schneider 1801)	x	x			
Calliophis maculiceps (Gunther 1858)		0			0
Naja kaouthia Lesson 1831	x				
Naja siamensis Laurenti 1768	x				
Ophiophagus hannah (Cantor 1836)	x				
Viperidae					
Calloselasma rhododstoma (Boie 1827)	x	x	x		0
Cryptelytrops albolabris (Gray 1842)	x	x	x	x	
Cryptelytrops cardamomensis Malhotra, Thorpe & Stuart 2011	x	x	x	x	0
Viridovipera vogeli (David, Vidal & Pauwels 2001)	x	x	x	x	

the first account of this species from the Cardamom region.

Occidozyga martensii. – Three specimens collected at Botum Sakor (FMNH 270625, 270627–28) match the descriptions of this species from the central Cardamom Mountains (Stuart & Emmet 2006) and Phnom Aural (Grismer *et al.* 2007a).

Rana erythraea. – One specimen collected from Botum Sakor (FMNH 270601) corresponds to the description of this species from the central Cardamom Mountains (Stuart & Emmet 2006).

Acanthosaura cardamomensis. – One specimen was collected from Botum Sakor (FMNH 270648) that corresponds to the descriptions of this species (Wood *et al.* 2010) from the central Cardamom Mountains (Stuart & Emmet 2006) and Phnom Aural (Grismer *et al.* 2007a).

Calotes emma. – Two specimens collected from Botum Sakor (FMNH 270567–68) correspond to the descriptions of this species from the central Cardamom Mountains (Stuart & Emmet 2006).

Calotes versicolor. – One specimen of this species found at Botum Sakor (FMNH 270566) corresponds to the description of this species from the central Cardamom Mountains (Stuart & Emmet 2006), the base of Phnom Aural (Grismer *et al.* 2007a), and eastern Cambodia in Mondolkiri Province (Stuart *et al.* 2006).

Draco maculatus. – One specimen of this species found at Botum Sakor (FMNH 270586) and five specimens from Ream (FMNH 270582–85, 270587) correspond to the diagnoses of this species from central Cardamom Mountains and Bokor National Park (Stuart & Emmet 2006) and the base of Phnom Aural (Grismer *et al.* 2007a).

Draco taeniopterus. – One specimen of this species from Botum Sakor (FMNH 270643) and another specimen from Ream (FMNH 270642) correspond to the diagnoses of this species from central Cardamom Mountains (Stuart & Emmet 2006) and Phnom Aural (Grismer *et al.* 2007a).

Cyrtodactylus intermedius. – One specimen of this species found at Botum Sakor (FMNH 270596) and another at Ream (FMNH 270595) correspond to the diagnoses of this species from central Cardamom Mountains (Stuart & Emmet 2006) and Phnom Aural (Grismer *et al.* 2007a).

Hemiphyllodactylus typus. – One specimen of this species found at Botum Sakor (FMNH 270569) corresponds to the diagnosis of this species from Thailand (Taylor 1963). This is the first record of this species from the Cardamom region.

Lygosoma bowringii. – One specimen of this species found at Botum Sakor (FMNH 270599) matches the diagnosis of this species from central Cardamom Mountains (Stuart & Emmet 2006).

Scincella melanosticta. – One specimen of this species found at Botum Sakor (FMNH 270600) and another specimen from Ream (FMNH 270598) correspond to the diagnoses of this species from the central Cardamom Mountains (Stuart & Emmet 2006) and Phnom Aural (Grismer *et al.* 2007a).

Sphenomorphus maculatus. – Two specimens collected from Ream (FMNH 270644–45) correspond to the descriptions of this species from the central Cardamom Mountains (Stuart & Emmet 2006), and eastern Cambodia in Mondolkiri Province (Stuart *et al.* 2006).

Tropidophorus microlepis. – One specimen found at Botum Sakor (FMNH 270606) corresponds to the description of this species from eastern Cambodia in Mondolkiri Province (Stuart *et al.* 2006). This is the first record of this species and genus from the Cardamom region.

Typhlops muelleri. – Two specimens of this species found at Ream (FMNH 271578–79) correspond to the description of this species from the central Cardamom Mountains (Stuart & Emmet 2006).

Enhydris bocourti. – One specimen found at Ream (FMNH 271571) corresponds to the description of this species from the central Cardamom Mountains (Stuart & Emmet 2006).

Gonyosoma oxycephalum. – One specimen collected at Ream (FMNH 271571) corresponds to the description of this species from the central Cardamom Mountains (Stuart & Emmet 2006).

Homalopsis buccata. – One specimen of this species found at Botum Sakor (FMNH 271574) corresponds to the descriptions of this species from the central Cardamom Mountains (Stuart & Emmet 2006) and eastern Cambodia in Mondolkiri Province (Stuart *et al.* 2006).

Oligodon cf. *inornatus*. – One specimen of what may be *O. inornatus* was collected at Ream (FMNH 271565). The specimen is a juvenile (SVL ~ 137 mm) with 15 dorsal scale-rows at midbody and a head that has been partially eaten away. According to Saint Girons (1972), *O. inornatus* is the only species of *Oligodon* in Cambodia with 15 dorsal scale-rows. Saint Girons (1972) did not say where on the body the dorsal scale-row counts were made, but they were presumably made at midbody. David *et al.* (2008a) note that *O. occellatus* and *O. saintgironsi* also have 15 dorsal scale-rows at midbody and David *et al.* (2008b) note that 15 dorsal scale-rows occur just anterior to the vent in *O. taeniatus*, *O. mouhoti*, and *O. duevei*. FMHN 271565 can easily be ruled out as belonging to these latter three species owing to the fact that they have dorsal stripes and no sign of bands at any stage of their lives, and have 17 scale-rows at midbody (David *et al.* 2008b). The color pattern of FMNH 271565, however, is not a close match to that of adult *O. inornatus* either, which is reported to be uniform pale brown above and yellowish below (Taylor 1965, Saint Girons 1972). Instead this specimen (in life) was probably light brown dorsally and has 25 thin, whitish, dorsal bands edged in black and bears square black markings on the lateral edges of most of its ventral scales. The dorsal color pattern superficially resembles that of *O. ocellatus* and *O. saintgironsi* in that it is banded, except that there are 13 bands in *O. ocellatus* and 11–14 in *O. saintgironsi* (David *et al.* 2008a). *Oligodon inornatus* may have a color pattern that changes with adulthood. Similar ontogenetic transformations are known from other species, such as *Oligodon fasciolatus* in northern Malaysia (Grismer *et al.* 2006b).

Pareas carinatus. – One specimen of this species from Botum Sakor (FMNH 271564) and another from Ream (FMNH 271564) correspond to the descriptions of this species from the central Cardamom Mountains (Stuart & Emmet 2006) and eastern Cambodia in Mondolkiri Province (Stuart *et al.* 2006).

Sibynophis triangularis. – A single specimen collected from the central Cardamom Mountains (FMNH 270103) corresponds to the description of material from Mondolkiri Province in eastern Cambodia (Stuart *et al.* 2006). This is the first record of this species from the Cardamom region.

Xenochrophis flavipunctatus. – One specimen collected from Ream (FMNH 271580) corresponds to the description of this species from Thailand (Tayor 1963). It has also been reported from Phnom Tumpor (Daltry & Chheang Dany 2000), the central Cardamom Mountains (Long *et al.* 2002), and Phnom Aural (Swan & Daltry 2002).

Xenochrophis trianguligerus. – One specimen collected from Ream (FMNH 271567) corresponds to the description of this species from the central Cardamom Mountains (Stuart & Emmet 2006).

Bungarus candidus. – One specimen collected from Ream (FMNH 271548) corresponds to the description of this species from Bokor and southern Vietnam (Saint Girons 1972).

Calliophis maculiceps. – One specimen collected from Ream (FMNH 271566) and another from the central Cardamom Mountains at Thma Bang, Koh Kong Province (FMNH 270123) correspond to the description of this species from Cambodia (Saint Girons 1972). These specimens represent the first record of the species and genus from the Cardamom region.

Calloselasma rhodostoma. – One specimen collected from Botum Sakor (FMNH 271577) and another from Ream (271576) correspond to the descriptions of this species from Phnom Aural (Grismer *et al.* 2007a) and the central Cardamom Mountains (Stuart & Emmet 2006).

Cryptelytrops cardamomensis. – One specimen collected from Ream (FMNH 271549) corresponds to the description of this species from the central Cardamoms (Malhotra *et al.* 2011).

These new records indicate that, in general, the herpetofauna of the coastal Cardamom region is a subset of that from various sections of the Cardamom Mountains (Table 3). Nonetheless, the presence of *Hemiphyllodactylus typus* is the first report of this species from Cambodia and *Limnonectes* cf. *dabanus* and *Tropidophorus microlepis*, which do not occur in the adjacent Cardamom Mountains, are found in the more northerly regions in Mondolkiri Province (Stuart *et al.* 2006). These reports would indicate that the herpetofauna of this region is still not completely known.

THE MALAY PENINSULA

The Malay Peninsula is one of the world's longest peninsulas, extending roughly 1660 km from Samut Songkhram, Thailand in the north southward to the southern coast of Singapore. Its topography is sculpted by an imbricating, disjunct series of mountain ranges that begin in the highlands of central Indochina and run nearly its entire length (Fig. 6). In the midregion of the Malay Peninsula in southern Thailand, these ranges are separated for 80 km across a rift valley running between the Tenasserim Mountains in the northwest and the Nakhon Si Thammarat Mountains in the southeast (Fig. 6). Another prominent break in this upland system occurs at the southern end of the Sankalakhiri system and runs from Kangar, Perlis in northwestern Peninsular Malaysia, northeastward to Songkhla, Songkhla Province in southern Thailand (Fig. 6). Both these discontinuities have served as historical barriers to dispersal for many groups and as the impetus for vicariant speciation in others (e.g. Huges *et al.* 2003, Woodruff 2003, de Bruyn *et al.* 2005, Outlaw & Voelker 2008, Reddy 2008, Grismer *et al.* in press). South of the Sankalakhiri Mountains, these upland systems trifurcate just north of the Thai-Malaysian border, fan out, and extend southward through Peninsular Malaysia as the expansive and fragmented Banajaran Timur in the east, the Banjaran Bintang in the west, and the longest and centrally positioned Banjaran Titi Wangsa (Fig. 6).

The Malay Peninsula has long been the focal point of herpetological investigations (e.g. Cantor 1847, Flower 1896, 1899; Butler 1902, 1904; Boulenger 1912, Kloss 1915, 1921; Smith 1930, Berry 1975, Tweedie 1983, Denzer & Manthey 1991, Manthey & Grossmann 1997, Chan-ard *et al.* 1999, Lim & Das 1999, Das & Norsham 2003, Grismer 2011b, Grismer & Pan 2008, Wood *et al.* 2008a,b; Grismer *et al.* 2010b,c) and the complex biogeographical nature of its fauna is only beginning to emerge (Inger & Voris 2001, Pauwels *et al.* 2003, Matsui *et al.* 2009, Grismer 2011a,b; Grismer & Grismer 2010; Grismer *et al.* 2010b,c and in press). These biogeographical patterns have been shaped and reshaped numerous times over the last five million years owing to the intermittent, archipelago-like

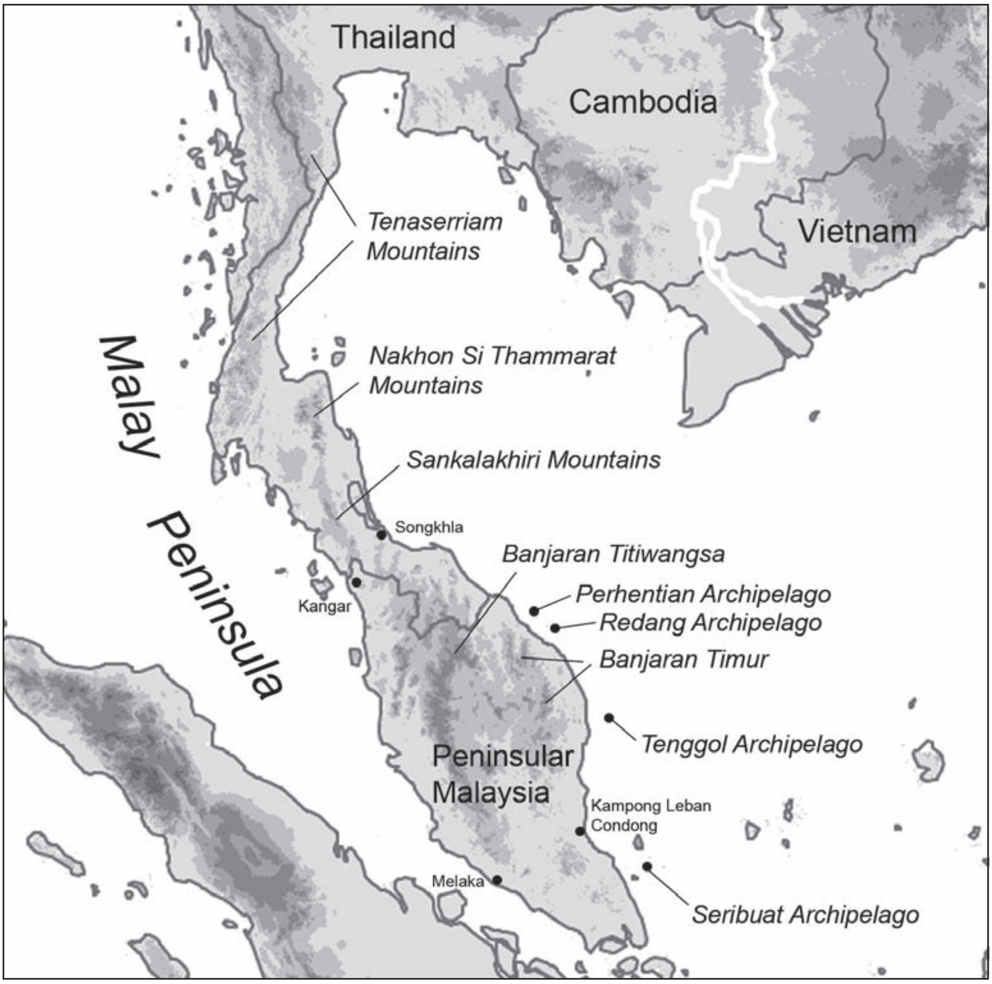

FIG. 6. The Malay Peninsula of southern Thailand and Peninsular Malaysia showing its major mountain ranges and its associated archipelagos for which herpetofaunal records exist.

nature of the Malay Peninsula (Woodruff 2003). Ephemeral seaways cut across the peninsula at the Isthmus of Kra between the Tenasserim and Nakhon Si Thammarat mountains in Thailand and further south between Kangar in northwestern Peninsular Malaysia and Songkhla in southern Thailand, initially multifurcating wide-ranging lineages, while the regression of these same seaways allowed multiple instances of secondary contact and overlap (e.g. Woodruff 2003, Reddy 2008, Grismer *et al.* in press). Such a dynamic geological history manifests itself in tree topology as sister lineages occurring on opposite sides of these vicariant zones in both deep and shallow regions of the same phylogeny (Woodruff 2003, L. Grismer *et al.* in press).

Paralleling the mountain systems of the Malay Peninsula, and Peninsular Malaysia in particular, are a series of shallow-water, landbridge archipelagos and islands (Fig. 6) whose geological origins are tied to those of the adjacent peninsular mountains and the emergence and subsidence of the Sunda Shelf. In the South China Sea, the archipelagos of Redang, Perhentian, and Tenggol, as well as several smaller islands and scattered islands in their general vicinity, are relict mountain tops of the Banjaran Timur of Peninsular Malaysia that became isolated during the most recent glacial minimum. Off the southeast coast of Peninsular Malaysia lies the extensive Seribuat Archipelago, which contains 62 islands extending along the northern and southern shores of the states of Johor and Pahang, respectively (Fig. 6). Over a century of research has indicated that the mountain ranges of Peninsular Malaysia are regions of high herpetological diversity and endemism (e.g. Boulenger 1900a,b; Smith 1922a, 1935; Smedley 1931c, Grandison 1972, Dring 1979, Hallerman & McGuire 2001, Lim *et al.* 2002, Norsham & Lim 2002, Das & Norsham 2003, Leong & Lim 2003, Das *et al.* 2004, Sanders *et al.* 2004, Vogel *et al.* 2004, Grismer *et al.* 2006b, 2008a, 2009a,b,c; Grismer 2007a, 2008a; Matsui & Ibrahim 2006, Norhyati 2007, McLeod & Wood *et al.* 2008a, Chan *et al.*, 2009). Recent studies are now beginning to reveal that an equally, if not more impressive degree of diversity and endemism occurs in the associated offshore archipelagos. This becomes germane as the results from ongoing expeditions on Pulau Langkawi (Grismer & Norhayati 2008, Grismer *et al.* 2006d, 2008c; Grismer & Chan 2010), the Perhentian Archipelago (Grismer & Chan 2008, Grismer *et al.* 2009b, and those records reported herein), the Redang Archipelago (reported herein), the Tenggol Archipelago (reported herein), and especially in the Seribuat Archipelago (see Grismer 2006a, 2011a, Grismer *et al.* 2006a and references therein, and Grismer & Pan 2008) continue to emerge and consistently report new island records and new species previously unknown to science. Reported and reviewed here are the results from various expeditions to some of the archipelagos off the eastern coast of West Malaysia, and new records from the Perhentian, Redang, and Tenggol Archipelagos.

THE EASTERN ARCHIPELAGOS OF PENINSULAR MALAYSIA

The archipelagos of Peninsular Malaysia are proving to be major centers of herpetological endemism and diversity (Grismer & Chan 2008, Grismer *et al.* 2009a, Chan & Norhayati 2010). Off the northeast coasts of Peninsular Malaysia, flanking the state of Terengganu, lie the Redang and Perhentian Archipelagos (Fig. 6). Accounts of its herpetofauna have been published for only one island in the Perhentian Archipelago, Pulau Perhentian Besar, and these are only descriptions of two species (Grismer & Chan 2008, Grismer *et al.* 2009a). However, what fieldwork has been done on these archipelagos is promising. In an unpublished report on the herpetofauna of the Pulau Perhentian Kecil, Pulau Perhentian Besar, and Pulau Redang, Tamblyn *et al.* (2005) reported three species of frogs, 21 species of lizards, and eight species of snakes. Their study, however, was capture and release so the records were not accompanied by voucher specimens or photographs and thus remain unconfirmed. Farther south off the coast of southern Terengganu lies Pulau Tenggol. To date only two species of lizards have been reported from that island (Chan & Norhayati 2010). We report here on a collection of amphibians and reptiles acquired during recent fieldwork on all the islands in the Perhentian Archipelago from 18–20 October 2007, 11–12 March and 22–24 June 2008, and 13–15 September 2009 that confirms 22 of the species records reported by Tamblyn *et al.* (2005) and adds seven unreported species. We also report the first published records from Pulau Redang and new records from Pulau Tenggol based on fieldwork conducted on 10–13 September 2009 and 7–9 September 2009, respectively.

PERHENTIAN ARCHIPELAGO

The Perhentian Archipelago contains 11 islands ranging from 0.01 to 8.7 km^2 in size. The smallest islands are covered with various components of coastal forest, whereas Perhentian Besar and Perhentian Kecil maintain large tracts of lowland dipterocarp forest (Grismer & Chan 2008, Grismer *et al.* 2009c). The islands of this archipelago have a granite basement and large boulder outcroppings (Fig. 7) which add a significant component to their environmental diversity. Reported below are the new species records. Table 4 lists the known herpetofauna.

Duttaphrynus melanostictus. – Several individuals of *D. melanostictus* (LSUDPC 4810–11) were seen during the evenings during all visits on the grounds of various guest facilities on Pulau Perhentian Besar. These specimens match the description of this species from Peninsular Malaysia (Berry 1975).

Ingerophrynus parvus. – Four males were heard calling from a congregation at the edge of a small rocky stream on Pulau Perhentian Kecil. A single spcecimen (LSUHC 8822) was collected. This specimen matches the diagnostic characteristics of this species reported by Grismer (2007b).

Kaloula pulchra. – Several individuals (LSUDPC 3497–98) were seen mating in man-made fountains during the evenings on all visits on the grounds of various guest facilities on Pulau Perhentian Besar.

FIG. 7. Interior lowland forest on Pulau Perhentian Besar, Perhentian Archipelago, Peninsular Malaysia.

These specimens match the description of this species from Peninsular Malaysia (Berry 1975).

Polypedates leucomystax. – This species was commonly observed on Perhentian Besar and Perhentian Kecil (LSUHC 8821) throughout the forest along trails and on the water tanks behind the guest facilities on both islands. These specimens match the description of this species from Peninsular Malaysia (Berry 1975).

TABLE 4. Herpetofauna of the Perhentian and Redang Archipelagos and Pulau Tenggol.

	Perhentian Besar	Perhentian Kecil	Susu Dara Besar	Susu Dara Kecil	Rawa	Seringgeh	Tokong Burong Besar	Redang	Tenggol
FROGS									
Bufonidae									
Duttaphrynus melanostictus	x							x	
Ingerophrynus parvus		x						x	
Microhylidae									
Kaloula pulchra	x							x	x
Rhacophoridae									
Polypedates leucomystax	x	x						x	x
Theloderma licin	x	x							
Ranidae									
Limnonectes blythii								x	
Limnonectes laticeps								x	
Hylarana erythraea	x								
CAECILIANS									
Ichthyophiidae									
Ichthyopis sp.	x								

	Perhentian Besar	Perhentian Kecil	Susu Dara Besar	Susu Dara Kecil	Rawa	Seringgeh	Tokong Burong Besar	Redang	Tenggol
LIZARDS									
Agamidae									
Acanthosaura armata	x	x						x	
Bronchocela cristatella	x	x						x	
Draco formosus									x
Draco sumatranus	x							x	
Gekkonidae									
Cnemaspis kendallii									x
Cnemaspis perhentianensis	x	x							
Cyrtodactylus consobrinus	x								
Cyrtodactylus leegrismeri									x
Cyrtodactylus quadrivirgatus	x								
Gehyra mutilata	x	x	x		x			x	x
Gekko gecko	x?	x						x	
Gekko monarchus	x							x	x
Gekko smithii	x								
Hemidactylus frenatus	x	x	x		x	x	x	x	x
Hemidactylus platyurus	x								
Lepidodactylus lugubris				x					
Ptychozoon kuhli	x								x
Ptychozoon lionotum	x							x	
Scincidae									
Dasia olivacea	x							x	x
Eutropis longicaudata	x							x	
Eutropis multifasciata	x							x	x
Lygosoma quadrupes					x				
Lygosoma bowringii	x								
Sphenomorphus perhentianensis	x								
Varanidae									
Varanus nebulosus	x								
Varanus salvator	x	x	x		x			x	x
SNAKES									
Typhlopidae									
Ramphotyphlops braminus	x								
Pythonidae									
Broghammerus reticulatus	x		x					x	x
Colunridae									
Ahaetulla prasina	x							x	x
Boiga dendrophila	x							x	
Chrysopelea ornata	x								
Dendrelaphis pictus	x							x	
Dryocalamus subannulatus	x								
Gonyosoma oxycephalum	x								
Lycodon capucinus	x								
Lycodon subcinctus	x								
Viperidae									
Tropidolaemus wagleri	x								

Theloderma licin. – One specimen (LUSHC 8820) was collected from within a small, water-filled treehole 1.5 m above the ground in lowland dipterocarp forest on Pulau Perhentian Kecil. Two additional individuals (LSUHC 9410–11) were found in a similar situation on Pulau Perhentian Besar. All three specimens match the description of this species by McLeod & Norhayati (2007). These are the first insular records for this species.

Hylarana erythraea. – Two specimens (LSUHC 8702–03) were collected from a small natural drainage along a trail through disturbed forest on Pulau Perhentian Besar. These specimens match the description of this species from Peninsular Malaysia (Berry 1975).

Ichthyophis sp. – A juvenile (LSUDPC 4155) was collected during the day following a rain shower from a shallow pool on a trail through disturbed forest on Pulau Perhentian Besar. Adults were observed beneath rocks in a shallow stream coursing through lowland dipterocarp forest.

Acanthosaura armata. – Several individuals were observed on all sizes of trees during the day and night throughout the forest on Pulau Perhentian Besar (LSUHC 8726–33). Only a single individual (LSUHC 8823) was seen on Pulau Perhentian Kecil. This population is unique with respect to other *A. armata* in that they have a unicolor, light brown dorsal pattern (Grismer 2011b). These specimens have the diagnostic characters listed for this species in Wood *et al.* (2009).

Bronchocela cristatella. – Several specimens were observed on Perhentian Besar (LSUHC 8737) and Perhentian Kecil islands (LSUDPC 4696) in disturbed vegetation along the trails. These specimens match the diagnosis for this species in Diong & Lim (1998).

Draco sumatranus. – Three individuals were seen on trees in open areas along the forest trails through costal vegetation on Pulau Perhentian Besar. The specimen collected (LSUHC 8692) matches Muster's (1983) diagnosis of this species.

Cyrtodactylus quadrivirgatus. – This species was observed at night on low vegetation in lowland dipterocarp forest on Pulau Perhentian Besar. These specimens (LSUHC 9057–58) have the diagnostic character states for this species listed in Grismer *et al.* (2008c).

Gehyra mutilata. – This species was observed on walls and other man-made structures on both Perhentian Besar and Perhentian Kecil islands (LSUHC 8693, 8706–07). Another individual was collected from within a rock crack on Pulau Susu Dara Besar (LSUHC 9067) and another was observed on rocks beneath coastal vegetation on Pulau Rawa (LSUDPC 5209). These specimens match Manthey & Grossmann's (1997) description of this species.

Gekko gecko (LSUHC 8825). – This species exists in surprising densities in the resorts on Pulau Perhentian Kecil. Tamblyn *et al.* (2005) report its occurrence on Pulau Perhentian Besar but we have only observed *G. smithii* on that island. These specimens match Manthey & Grossmann's (1997) description of this species.

Gekko monarchus. – This species was relatively common at night on the granite boulders in lowland dipterocarp forest on Perhentian Besar (LSUHC 8691) and Perhentian Kecil islands (LSUDPC 4186). During the day, lizards were found beneath granite exfoliations.These specimens match Manthey & Grossmann's (1997) description of this species.

Gekko smithii. – Several lizards were observed on the granite boulders in the lowland dipterocarp forest on Pulau Perhentian Besar. All specimens (LSUHC 8690, 8696) match the description of this species in Manthey & Grossmann (1997).

Hemidactylus frenatus. – This lizard was found in all habitats on Perhentian Besar (LSUDPC 4672) and Perhentian Kecil Islands (LSUHC 8826), on trees on Pulau Rawa (LSUHC 9065) and Susu Dara Besar (LSUHC 9066), beneath trash on the beach on Pulau Seringgeh (LSUHC 9069), and under rocks on Pulau Tokong Burong Besar (LSUHC 9063–64). These specimens match Mathey & Grossmann's (1997) description of this species.

Hemidactylus platyurus (LSUDPC 5000). – This species was commonly found during the day on Pulau Perhentian Besar beneath exfoliations of granite boulders in lowland dipterocarp forest.

Lepidocatylus lugubris. – A specimen (LSUHC 9068) was found within a rock crack during the day on Pulau Susu Dara Kecil. As on small islands in the Seribuat Archipelago, this species does not co-occurr with *Hemidactylus frenatus* unless it is restricted to the intertidal zone (Grismer *et al.* 2006a). The specimen matches the description of this species in Manthey & Grossmann (1997).

Ptychozoon kuhli. – This species was commonly observed at night along the trails through the lowland dipterocarp forest of Pulau Perhentian Besar. As many as seven individuals were seen in one night. These specimens (LSUHC 8674, 8708) match the description of this species in Manthey & Grossmann (1997).

Pytchozoon lionotum. – This species was observed at night along the trails through the lowland dipterocarp forest of Pulau Perhentian Besar in syntopy with *P. kuhli*. These specimens (LSUHC 8709, 9059) match the description of this species in Manthey & Grossmann (1997).

Dasia olivacea. – A single indiviual (LSUDPC 5154–56) was observed on the trunk of a coconut palm along the beach on Pulau Perhentian Besar. The color pattern of this specimen matches the description of this species in Manthey & Grossmann (1997).

Eutropis longicaudata. – A single specimen (LSUDPC 3495) was collected from beneath trash on the beach on Pulau Perhentian Besar which matches the color pattern description of this species in Lim (1998).

Eutropis multifasciata. – This species was commonly seen during the day foraging along the forest floor in lowland dipterocarp forest on Pulau Perhentian Besar. One individual was even found at night in a small stream. These specimens (LSUHC 8704, 9061) match the description of this species in Lim (1998).

Lygosoma quadrupes. – A single specimen was found beneath a log buried in leaf litter in coastal forest on Pulau Rawa (Fig. 8). This specimen (LSUHC 9062) matches the description of this species in Lim (1998).

Varanus nebulosus. – Individulas were seen foraging at the forest edge behind dwellings on the beach on Pulau Perhentian Besar. The color patern of these individuals (LSUDPC 1136) matches the description of this species in Manthey & Grossmann (1997).

Varanus salvator. – This species was common along the beaches on Perhentian Besar and Perhentian Kecil islands. Tracks were observed on the beach on Pulau Rawa and Susu Dara Besar. The color pattern of these individuals (LSUDPC 2819) matches the description of this species in Manthey & Grossmann (1997).

Ramphotyphlops braminus. – A single specimen (LSUHC 8883) from Pulau Perhentian Besar was collected beneath debris along the beach at the forest edge. This specimen matchs the description of this species in Tweedie (1983)

Broghammerus reticulatus. – One specimen (LSUDPC 0197)was found crawling along the beach near the water's edge at night on Pulau Perhentian Besar. Local inhabitants report that this species is also on Pulau Susu Dara Besar and its presence there is considered here to be unconfirmed. This specimen matches the description of this species in Tweedie (1983).

Ahaetulla prasina (LSUDPC 1444). – This species was commonly seen during the day in the ornamental vegetation planted at the resorts on Pulau Perhentian Besar. This specimen matchs the description of this species in Tweedie (1983).

Boiga dendrophila. – A large specimen (LSUDPC 4820) was found at night crawling in a cement drain shortly after an afternoon rain shower on Pulau Perhentian Besar, which confirms the record for this species by Tambyln *et al.* (2005).

Lycodon capucinus. – One specimen (LSUHC 8827) was found beneath debris on the beach on Pulau Perhentian Besar. This specimen matches the description of this species in Tweedie (1983).

Lycodon subcinctus. – A large specimen was collected during the evening while crawling along the edge of a small stream on Pulau Perhentian Besar. The specimen escaped before being photographed or preserved. It is therefore considered an unconfirmed sighting.

Tropidolaemus wagleri. – Several specimens were observed during the night in low vegetation in the lowland dipterocarp forest of Pulau Perhentian Besar. One individual (LSUDPC 4566) observed during the day was perched 1.5 m above the ground on a branch. It remained in the same spot for at least 48 hours. The color pattern of this specimen matches the description of this species in Manthey & Grossmann (1997).

Much of the herpetofauna of this archipelago is a subset of that of the adjacent peninsula in the state of Terengganu (Dring 1979). However, the presence of the endemic species *Cnemaspis perhentianensis* and *Sphenomorphus perhentianensis* are clear indications of the understudied nature of this archipelago. The presence of *Ichthyophis* is the first record of this genus in northeastern Peninsular Malaysia and it is likely the population in the Perhentian Archipelago will prove to be a new species. A decision will follow a molecular analysis.

REDANG ARCHIPELAGO

The Redang Archipelago contains nine islands dominated by the large, butterfly shaped, granite-based island of Redang (90 km^2). Pulau Redang reaches 359 meters in elevation and some primary forest remains on its upper peaks. Lowland rainforest dominates the interior of the island (Fig. 9) and

FIG. 8. Interior coastal forest on Pulau Rawa, Perhentian Archipelago, Peninsular Malaysia.

FIG. 9. Rocky streambed in the interior of Pulau Redang, Redang Archipelago, Peninsular Malaysia.

mangrove communities (Fig. 10) and open beaches (Fig. 11) are common on the northern coast. Unfortunately, tourism and a growing local population are impacting much of its coastline and forested interiors. The island has been designated as an important conservation site for sea turtles, and unpublished studies on the island's herpetofauna strongly suggest it is in need of exploration. The results of preliminary fieldwork conducted on 10–13 September 2009 augment and confirm earlier reports on this herpetofauna presented in an unpublished report by Tamblyn *et al.* (2005) based on an unpublished Malaysian Nature Society survey of 1990 which reported only four species of lizards being observed. Below we add eight species of lizards, six species of frogs, and four species of snakes collected along the Redang Reef Trail on the eastern side of the island. Table 4 lists the known herpetofauna.

Duttaphrynus melanostictus. – Several individuals of *D. melanostictus* were seen during the night on jungle trails and on the grounds of various guest facilities. One specimen (LSUHC 9394) was collected which matches the description of this species from Peninsular Malaysia (Berry 1975).

Ingerophrynus parvus. – Two specimens (LSUHC 4399–4400) were collected at the edge of a puddle in a disturbed area at the head of a trail. These specimens match the diagnostic characteristics of this species reported by Grismer (2007b).

Kaloula pulchra. – A single individual (LSUHC 9403) was found 4 m above the ground on the side of a tree along the forest trail. It matched the description of this species from Peninsular Malaysia (Berry 1975).

Limnonectes blythii. – Several specimens were seen within and along the edge of a small stream at night. Two specimens (LSUHC 9384, 9404) were collected that match the description of this species in Berry (1975).

Limnonectes laticeps. – This species (LSUHC 9295–9398) was found at night along the edges of a rocky stream paralleling the Redang Reef Trail. These specimens match the description of this species in Berry (1975).

Polypedates leucomystax. – Several frogs uttering the iconic "wet fart" call of this species were heard throughout the forest along a small stream. None were collected and thus this record remains unconfirmed.

Acanthosaura armata. – This species (LSUHC 9385–89) was abundant and observed on the trunks of both large and small trees throughout the forest. Like the individuals from Pulau Perhentian Besar and Pulau Perhentian Kecil, the color pattern on the lizards from this population is generally unicolor. Lizards from this population have the diagnostic character states for *A. armata* listed in Wood *et al.* (2009). This population was listed in Tamblyn *et al.* (2005).

Bronchocela critatella. – This species was common on tree trunks in both disturbed areas and along the forest trail. One specimen collected (LSUHC 9390) has the diagnostic character states of this species listed in Diong & Lim (1998).

Draco sumatranus. – This species was common on tree trunks in both disturbed areas and along the forest trail. Two specimens collected (LSUHC 9393, 9406) have the diagnostic character states of this species listed in Muster (1983). This confirms the record of this species in Tamblyn *et al.* (2005).

Gehyra mutilata (LSUDPC 4086). – This species was observed on walls and other man-made structures as well as on tree trunks and leaves in the forest. The color pattern of this specimen matches the description of this species in Manthey & Grossmann (1997).

Gekko gecko (LSUDPC 3438). – This species was common on the sides of houses and tree trunks in disturbed areas as well as on rock outcrops in the forest. The color pattern of this specimen matches the description of this species in Manthey & Grossmann (1997).

Gekko monarchus (LSUDPC 2657). – This species was relatively common at night on the granite boulders in the forest. The color pattern of this specimen matches the description of this species in Manthey & Grossmann (1997).

Hemidactylus frenatus. – This lizard was common on all man-made structures. One individual collected (LSUHC 9407) matches the description of this species in Manthey & Grossmann (1997).

Pytchozoon lionotum. – A single specimen (LSUHC 9409) was observed at night approximately 1.5 m above the ground on the side of tree in a disturbed area. It matches the description of this species in Manthey & Grossmann (1997).

Dasia olivacea (LSUDPC 9391. – Several skinks were observed during the day on the sides of trees and buildings in the resort areas. The color pattern of this specimen matches the description of this species in Lim (1998).

Eutropis longicaudata. – A juvenile specimen was observed basking on rocks in a fountain in a resort.

FIG. 10. Mangrove-dominated estuary on Pulau Redang, Redang Archipelago, Peninsular Malaysia.

FIG. 11. Beach habitat on Pulau Redang, Redang Archipelago, Peninsular Malaysia.

It escaped capture and was not photographed. Its record thus remains unconfirmed.

Eutropis multifasciata. – Several specimens were seen foraging throughout the leaf litter on the forest floor during the day. The specimen collected (LSUHC 9392) matches the description of this species in Lim (1998). This confirms the record of this species in Tamblyn *et al.* (2005).

Varanus salvator (LSUDPC 5263). – Several specimens were observed along the small, brackish waterways near the coast in both disturbed and undisturbed areas. We also observed several tracks in mangrove areas. This confirms the record of this species in Tamblyn *et al.* (2005).

Ahaetulla prasina. – This specimen was not observed but reported as present by several of the local inhabitants. Its status thus remains unconfirmed.

Boiga dendrophila. – We were shown photographs of individuals of this species from the island by the staff at the sea turtle breeding center.

Dendrelaphis pictus. – One specimen (LSUHC 9413) matching the description of this species in Vogel & Van Rooijen (2007, 2008) was found sleeping approximately 2 m above the ground in a small tree in a disturbed area.

Broghammerus reticulatus. – We were shown photographs of individuals of this species from the island by the staff at the sea turtle breeding center.

TENGGOL ARCHIPELAGO

The Tenggol Archipelago comprises a small group of seven rocky islands lying 26 km off the coast of southern Terengganu and represents the southernmost islands of Terengganu's Marine Parks. The rocky interiors of these islands are pristine and unexplored and most islands are covered in primary forest. The largest island of the archipelago, Pulau Tenggol, is less than 6 km^2 in area. Its steep interior reaches nearly 50 m in elevation, giving rise to three main peaks. There is one large beach on the west side of the island and a smaller beach along the east coast. Its pristine interior is covered by coastal and lowland forest that provides a dense canopy for the extensive rocky outcroppings that dominate the island's landscape (Fig. 12). Although there is no permanent fresh water, at least two species of amphibians are present and the varied interior offers numerous microhabitats that support a relatively diverse reptile fauna. The results of the first herpetofaunal survey of Pulau Tenggol are reported here and augment the findings reported in Chan & Norhayati (2010). This survey was concentrated along the hills (4°48.51'N, 103°40.73'E) behind the beach at Air Tawar Bay along the west side of the island. Table 4 lists the known herpetofauna.

Kaloula pulchra. – Individuals were seen in the vicinity of the chalets and on the forest floor. The specimen collected (LSUHC 9375) matches the description of this species by Berry (1975).

Polypedates leucomystax. – One specimen was heard calling from near the chalets. Its presence remains unconfirmed.

Draco formosus. – This species was very common and seen on the trunks of many trees in all habitats. This is a species usually restricted to forest areas, but here it was quite common on trees along the beach. The specimens collected (LSUHC 9360–61, 9365–66) match the description of this species in Muster (1983).

Cnemaspis kendallii. – This species was found in only one small area in the interior of the forest. Here individuals were seen abroad both during the day and night on the trunks and buttresses of trees and on rocks. The specimens collected (LSUHC 9376–77, 9380, 9382) match the description of this species in Grismer *et al.* (2008a).

Cyrtodactylus leegrismeri. – This endemic species was described by Chan & Norhayati (2010). Lizards were abundant and ubiquitous on the island, occurring in every conceivable terrestrial and arboreal habitat.

Gehyra mutilata. – One specimen was collected (LSUHC 9381) from the leaf of a small tree approximately 1 m above the ground in lowland forest. It matches the description of this species in Manthey & Grossmann (1997).

Gekko monarchus. – Several specimens of this species were seen on the chalets and the rocks surrounding the chalets. This species was first reported from Pulau Tenggol by Chan & Norhayati (2010).

Hemidactylus frenatus. – Several specimens of this species were seen on the chalets and the rocks surrounding the chalets. The specimen collected (LSUHC 9383) matches the description of this species in Manthey & Grossmann (1997).

Ptychozoon kuhli. – One individual (LSUHC 9362) was found during the day on the roof of a chalet and matches the description of this species in Manthey & Grossmann (1997).

Dasia olivacea. – Several individuals were seen on trees along the beach and on the roofs of various

FIG. 12. Interior lowland forest on Pulau Tenggol, Tenggol Archipelago, Peninsular Malaysia.

chalets. The specimens collected (LSUHC 9363, 9367) match the description of this species in Lim (1998).

Eutropis multifasciata. – Several specimens were seen foraging on the leaf litter during the day and crawling among the rocky outcrops. We also found three individuals at night sleeping on the sides of trees 2–3 m above the ground. The specimens collected (LSUHC 9368–69) match the description of this species in Lim (1998).

Varanus salvator. – We observed a juvenile near the water's edge as it was foraging among the rocks. It was not collected or photographed and thus the record remains unconfirmed.

Ahaetulla prasina. – This specimen was not observed but reported as present by several of the local inhabitants. Its status thus remains unconfirmed.

Broghammerus reticulatus. – One specimen (LSUDPC 5262) was captured by the staff of the resort as it continually returned to the area. The color pattern of this specimen matches the description of this species in Tweedie (1983).

SERIBUAT ARCHIPELAGO

The Seribuat Archipelago lies off the southeast coast of Peninsular Malaysia and has an environmental diversity that is unparalleled by any other island group in Peninsular Malaysia (Grismer *et al.* 2001a,b, 2006a; Grismer 2011a; Youmans *et al.* 2002, Escobar *et al.* 2003a,b; Wood *et al.* 2003a,b, 2004a,b; J. Grismer *et al.* 2004, Tamblyn *et al.* 2005, Grismer 2006a, 2008b; Fig. 6). This is paramount to the generation and maintenance of its herpetofaunal diversity and its broad array of adaptive types (Grismer *et al.* 2006a). The large islands (> 4.0 km^2) such as Aur, Babi Besar, Pemanggil, Tinggi, Tioman, and Sibu generally maintain extensive tracts of primary dipterocarp forest (Fig. 13). The largest of these, Tioman and Tinggi, also maintain significant sources of permanent fresh water in the form of streams, which harbor aquatic and riparian species not found on the other islands. Pulau Tioman even has a small river system, Sungai Mentawak (Fig. 14), which serves as the only locality in the archipelago for the frog *Hylarana picturata*. Conversely, many of the very

FIG. 13. Interior lowland forest on Pulau Tioman, Seribuat Archipelago, Peninsular Malaysia.

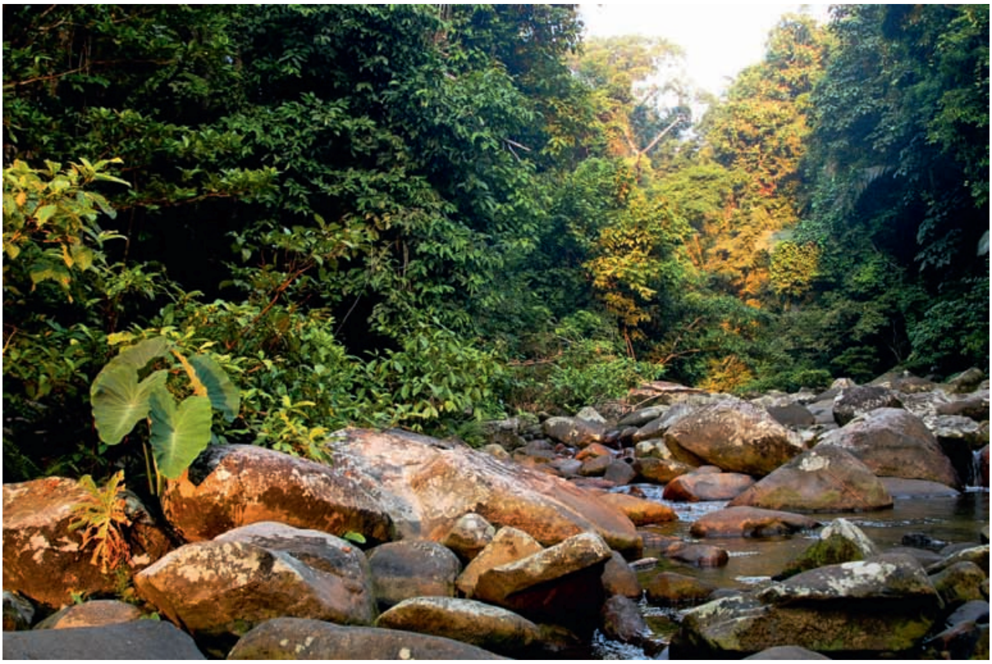

FIG. 14. Sungai Mentawak on Pulau Tioman, Seribuat Archipelago, Peninsular Malaysia.

FIG. 15. Windswept Pulau Tokong Burong, Seribuat Archipelago, Peninsular Malaysia.

small islands (> 0.03 km^2) such as the "Tokongs" are little more than wind-blown, arid, rocky outcrops rising precipitously out of the ocean, supporting only grasses and low-growing shrubs (Fig. 15). But here too, potentially endemic species have been found which occur nowhere else in the archipelago (Grismer 2006a,b). The intermediate-sized islands may be barren (P. Layak), forested (P. Babi Hujong), or combinations of both, such as in the Seribuat group (*sensu* Grismer *et al.* 2006a), and they may or may not support ephemeral bodies of fresh water. Many of the islands in the archipelago, both large and small, are fringed with broad stands of mangroves.

The islands of the Seribuat Archipelago are land-bridge islands that formerly comprised a series of at least three low mountain ranges paralleling the more extensive ranges running the length of the adjacent Malay Peninsula. The summits of these ranges became transformed into a series of three parallel island arcs following the most recent rise in sea level which began to inundate the Sunda Shelf 21 kybp (Voris 2000, Inger & Voris 2001, Sathiamurthy & Voris 2006). It is thus likely that much of the herpetofauna of these islands had a vicariant origin, being effectively isolated on these summits prior to their isolation by rising sea levels. Recent phylogenetic studies (Brown *et al.* in press, Grismer *et al.* in press) are beginning to augment a wider body of evidence (Kottelat 1990, Ng *et al.* 1999, Tan & Mohamed 1999, Yeo & Ng 1999, Yeo *et al.* 1999, Grismer *et al.* 2003, 2004b, 2006c; Leong *et al.* 2003) showing that many of the endemics on the outermost island arc are actually more closely reated to species from Borneo, approximately 540 km to the southeast, than to taxa on the adjacent Malay Peninsula, just 28 km to the west. This isolation, coupled with genetic drift and the selection pressures attendant with living on small islands, was likely the driving force promoting evolutionary change in a number of these newly isolated populations. As a result, a significant portion of the herpetofauna in this archipelago is endemic (see Grismer 2011a, Grismer *et al.* 2006a, Sodhi *et al.* 1999).

Like other regions within tropical megadiversity hotspots (Myers *et al.* 2000), the herpetofauna of Seribuat Archipelago is relatively diverse and undergoing a rapid increase in its content as recent and ongoing fieldwork progresses. This trend has been particularly evident since 2001, with 186 new insular species records being added (Grismer 2006a, Grismer *et al.* 2006a;Table 2 and references therein) and at least 13 new species discovered and described, increasing the total diversity of the archipelago by 60% since the major contributions of Lim & Lim (1999) and Hien *et al.* (2001). Currently there are 24 species of frogs, one species of caecilian, one species of turtle, 41 species of lizards, and 44 species of snakes distributed across the 62 islands of this 100-km-long archipelago (see Grismer 2011a). Such dramatic increases in diversity over such a relatively short period of time clearly indicate that these regions remain significantly understudied and their actual diversity has yet to be realized.

SOUTHERN PENINSULAR MALAYSIA

As delineated by Grismer & Pan (2008), southern Peninsular Malaysia occupies approximately 1620 km^2. It extends from the city of Melaka, Melaka (2°11'57"N, 102°15'16"E) on the west coast to Kampong Leban Condong, Pahang (2°52'19"N, 103°26'03"E) on the east coast, and southward through Singapore (1°15'05"N, 103°49'54"E; Fig. 6). This area occupies roughly the entire state of Johor and the southern section of the state of Pahang and includes all low-lying areas below 150 m as well as the mountainous areas encompassing Gunung Ledang (1276 m) in northeastern Johor, Endau-Rompin in southern Pahang and northern Johor, reaching 1036 m at Gunung Besar, and a system of mountains in central Johor dominated by Gunung Berlumut (1010 m) in the north and extending southward approximately 57 km to Bukit Sisek (430 m) in the south.

Originally, continental southern Peninsular Malaysia was an expansive region of lowland rainforest punctuated by isolated mountains and mountain ranges. Currently, the majority (~65%) of the lowland rainforest has been converted into rubber tree and oil palm plantations. This is especially true of the western half and southern third. Continuous lowland rainforest remains in the northeastern third as well as a few scattered patches in the west. Peat swampforests are found in isolated patches in the east and the west, and freshwater swampforests dominate the southeastern corner. Fringing the coastal areas are isolated stands of mangrove swamps that are particularly noteworthy in the south. Intact montane forest exists in all areas above 300 m, most notably in Endau-Rompin, Johor; the Gunung Berlumut system, and Gunung Ledang. Focused efforts in continental southern Peninsular Malaysia since 2005 have led to the discovery and description of at least five new species, the rediscovery of an extremely rare species (Daicus & Hashim 2004, Grismer & Leong 2005, Grismer 2006c, 2007b; Grismer *et al.* 2007c, 2008a,c; Wood *et al.* 2008b), and an increase in the diversity of the herpetofauna of Endau-Rompin National Park by at least 33% (Wood *et al.* 2008b). To date, five families of frogs representing at least 53 species and one family of caecilian representing an unknown number of species (see below) are confirmed for southern Peninsular Malaysia (Berry 1975, Wood *et al.* 2008b). Not including caecilians, this represents approximately 59% of all the species of amphibians known from Peninsular Malaysia (based on Das & Norsham 2007 and Chan *et al.* 2010) in less than 14% of the total area of the country. The reptilian fauna is even more diverse, with three families of terrestrial and freshwater turtles representing 11 species, eight families of lizards representing 61 species, eight families of non-marine snakes representing 90 species, and one family of crocodilian representing one species (Grismer & Pan 2008; Table 1). Collectively this represents approximately 65% of the reptilian fauna of Peninsular Malaysia (based on Das & Norsham 2007 and Grismer 2008c, Grismer 2011b).

Perhaps of greater importance, however, is role southern Peninsular Malaysia plays in harboring endemic species. Since the description of *Cyrtodactylus sworderi* (Smith 1925), two new species of frogs (*Ansonia endauensis* [Grismer 2006c] and *Ingerophrynus gollum* [Grismer 2007b]) and two new species of lizard (*Cyrtodactylus semenanjungensis* [Grismer & Leong 2005] and *C. pantiensis* [Grismer *et al.* 2008c]) have been described. Additionally, there is another new species of snake (*Macrocalamus* sp.) in the process of being described. Based on the results of over a century of fieldwork in montane regions of central and northern Peninsular Malaysia (Boulenger 1900a,b; Smith 1922a, 1935; Smedley 1931c, Grandison 1972, Dring 1979, Hallerman & McGuire 2001, Lim *et al.* 2002, Norsham & Lim 2002, Das & Norsham 2003, Leong & Lim 2003, Das *et al.* 2004, Sanders *et al.* 2004, Vogel *et al.* 2004, Grismer 2006b, 2007a, 2008a; Matsui & Ibrahim 2006, McLeod & Norhayati 2007, Wood *et al.* 2008a), it is certain that field surveys in the montane regions of southern Peninsular Malaysia will result in the discovery of additional species, many of which are likely to be endemic, and may raise the level of endemism of these habitat-islands to that of the islands in the adjacent Seribuat Archipelago.

The documented herpetofaunal diversity of southern Peninsular Malaysia will undoubtedly increase as a result of the ongoing efforts of field biologists working in this area. These increases will be most dramatic in the severely understudied areas, as suggested by the recent findings from Endau-Rompin, Johor, and Gunung Panti (Grismer & Leong 2005, Grismer 2006c, 2007b; Grismer *et al.* 2008a, Wood *et al.* 2008b). Surveys will also begin in earnest in the upland areas of Endau-Rompin, Gunung Berlumut, and Gunug Ledang, and it is expected that many additional records and potentially new species will be discovered there as well. All these areas should be set aside for purposes of studying and preserving the biodiversity of this region in an effort to protect a significant portion of Malaysia's natural heritage. Additionally, protected areas such as these can be immensely useful for serving as model systems in evaluating the myriad of complex nuances involved in efficient and cost effective ecosystem management which can subsequently be applied to other imperiled regions of Southeast Asia.

DISCUSSION

The data presented here suggest that the herpetofaunal composition of the borderlands fringing the Sunda Shelf from Vietnam to Borneo has been shaped by historical fluctuations in the climate of Southeast Asia and episodic marine transgressions of the South China Sea for at least the last five million years. This has culminated in a diverse herpetofauna and significant degrees of endemism, particularly in montane areas and archipelagos. Unfortunately this herpetofauna still remains woefully understudied. This is most evident in Peninsular Thailand, whose mountainous spine is just now beginning to reveal a large array of endemic species (e.g. Chan-ard *et al.* 2008, Grismer *et al.* 2010c). Although a few species records exist for some of the islands off the east coast of Peninsular Thailand and the southern coast of western Thailand in general works (e.g. Boulenger 1912, Smith 1922b, Bourret 1936, 1937–1941, 1941, 1942; Ouboter 1986, Taylor 1962, 1963, 1965; Chan-ard 2003, and references therein), there are still hundreds of islands fringing this nearly 2000 km of coastline that remain virtually unexplored. Similary, there are no records of amphibians or reptiles from 16 or so islands off the coast of southern Cambodia. We have seen photographs of lizards and frogs (which we cannot identify) from a few of these islands, but nothing has been published. Additional work is also needed in the Anambas and Natunas archipleagos lying between Borneo and the Malay Peninsula (Fig. 1). No focused survey work has been done there since Smedley (1928, 1931a,b) and the most recent comprehensive work is merely a checklist (Leong *et al.* 2003).

Much the same can be said about the island of Borneo. Despite the popular pocket guides (Das 2004, 2006, 2007), books (Inger & Tan 1996, Lim & Das 1999, Stuebing & Inger 1999, Malkmus *et al.* 2002, Inger & Stuebing 2005), and scattered species descriptions (see Das & Norsham 2007 and references therein) on the herpetofauna of northern Borneo, the majority of this island's herpetofauna remains largely unstudied.

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THE TERRESTRIAL REPTILE FAUNA OF THE BIOSPHERE RESERVE CAT BA ARCHIPELAGO, HAI PHONG, VIETNAM

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ABSTRACT

A total of 40 species of reptiles was recorded within two herpetological surveys during May 2007 and April 2008 on Cat Ba Island, Hai Phong, northeastern Vietnam: one species of turtle, 19 species of lizards, and 20 species of snakes. Nineteen species (47.5%) were new records for the island. Compared with previous herpetological surveys on Cat Ba Island, the diversity of terrestrial reptiles recorded during our field work was five times higher than given in Darevsky (1990) and two times higher than indicated by Nguyen & Shim (1997). Taxonomic comparisons revealed that one lizard is endemic, the eublepharid gecko *Goniurosaurus catbaensis* (Ziegler *et al.* 2008), and another new skink species, *Sphenomorphus tonkinensis* (Nguyen *et al.* 2011); the divergent status of other squamate species (e.g., *Pareas* cf. *hamptoni, Viridovipera* cf. *stejnegeri*) is still under examination.

Key words: Vietnam, Cat Ba Archipelago, diversity, new record.

INTRODUCTION

Cat Ba Island is situated in Ha Long Bay, 50 km east of Hai Phong City, northern Vietnam. It is the largest of 366 islands in the Cat Ba Archipelago, has a surface area of approximately 285 km² (FIPI 2006), and is part of an extended region of karst that stretches from southern China to northern Vietnam. The principal terrestrial ecosystem within Cat Ba National Park is tropical moist forest on limestone, which harbors a number of endemic and rare species, foremost of which is the endemic Cat Ba Langur *Trachypithecus poliocephalus poliocephalus* (Trouessart, 1911) (Nadler & Ha 2000; Furey *et al.* 2002; Nadler *et al.* 2002).

In the past two decades, several herpetological surveys have been carried out on Cat Ba Island. In his zoological analysis, Bobrov (1993) recorded 18 lizard species from islands in the Gulf of Tonkin including Cat Ba Island. Darevsky (1990) studied the herpetofauna of some Vietnamese offshore islands and listed seven species of reptiles for Cat Ba. This number was distinctly increased by the eight-day survey conducted by Nguyen & Shim (1997), who reported of 20 species of reptiles including two species of marine turtles. In view of this increasing number of new species records on the one hand, and a still low species number compared with northern mainland Vietnam on the other, we decided to conduct additional herpetological field studies on Cat Ba Island. These led to the discovery of new species of *Goniurosaurus* (Ziegler *et al.* 2008) and *Sphenomorphus* (Nguyen *et al.* 2011). Here, we present the overall result of our reptilian surveys.

MATERIAL AND METHODS

The herpetological surveys on Cat Ba Island took place from 18 to 27 May 2007 and from 20 to 24 April 2008. All survey sites are located inside the core zone of Cat Ba National Park:

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Ang Vat – Me Go (20o48'N, 107o00'E; 80–100 m a.s.l.) (Fig. 4.7): Older secondary tropical moist limestone forest (recovery since 1976) with adjoining open grasslands and former agricultural land. Specimens were collected along forest paths, dry stream beds, and nearby small ponds.

Trung Trang valley near the headquarters of the National Park (20o47'N, 106o59'E; 50–70 m a.s.l.) (Fig. 4.9): Mainly open area consisting of agricultural land surrounded by plantation forest (e.g., *Acacia*). The hill slopes are covered by secondary limestone forest. Specimens were collected at the hill bases, especially in small limestone caves/crevices and nearby small water reservoirs.

Trung Trang cave (20o47'N, 106o59'E; 60–70 m a.s.l.) (Fig. 4.8): Limestone cave, accessible for tourism. A concrete path leads through the cave. The forest in the vicinity of the cave entrance is old secondary forest alternated with patches of primary forest and shrub. Night excursions were conducted both inside and outside of the cave, and also along a waterless stream bed.

Ang Nhoi – Ang Dai (20o50'N, 106o57'E; 40–50 m a.s.l.): Large seasonally inundated swamp surrounded by primary limestone forest.

Tra Bau (20o50'N, 107o02'E; 0–40 m a.s.l.) (Fig. 4.10): Seasonally inundated swamp (Ang Ong Bi) surrounded by secondary limestone forest and steep limestone cliffs with small caves. Here, we also surveyed some patches of mangrove forest and the forest edge along the coast near Tra Bau ranger station (20o49'N, 107o03'E).

Specimens were collected in May 2007 and in April 2008, and were deposited in the following collections: Institute of Ecology and Biological Resources (IEBR), Vietnamese Academy of Science and Technology Hanoi, Vietnam; Department of Herpetology and Ichthyology, Muséum d'histoire naturelle (MHNG), Geneva, Switzerland; Zoological Museum of the Vietnam National University (VNUH), Hanoi, Vietnam; Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany.

To complete our inventory, we included specimens stored in the scientific collection of Cat Ba National Park, specimens collected from previous Cat Ba excursions and subsequently deposited in IEBR, and specimens recorded by us in the local trade or in local shops. Taxonomic identifications were made following Pope (1935), Bourret (1936, 1937), Smith (1935, 1943), Taylor (1963), Stuart *et al.* (2001), Ziegler (2002), Orlov & Ryabov (2004), Spinks & Shaffer (2007), Vogel (2006), Ziegler *et al.* (2007, 2008), Dawson *et al.* (2008), and Nguyen *et al.* (2009). Ventral scales in snakes were counted according to Dowling (1951).

Abbreviations are as follows: a.s.l.: above sea level; SVL: snout-vent length (from snout tip to cloaca); TaL: tail length (from cloaca to tail tip); TL: total length (SVL + TaL).

RESULTS AND DISCUSSION

Testudines

Geoemydidae

Cuora mouhotii (Gray, 1862) (Fig. 2.1)

Specimen examined: One medium-sized specimen confiscated in July 2003 from the illegal trade on Cat Ba Island. The specimen was released inside the forest.

Characteristic features: Carapace high with flat top, three distinct keels and a serrated rear margin; flat top of carapace usually paler than darker sides of carapace; large head with pale markings (see Stuart *et al.* 2001).

Squamata: Sauria
Agamidae

Acanthosaura lepidogaster (Cuvier, 1829) (Fig. 2.2)

Specimens examined: One adult male, IEBR A.0722 (SVL: 94 mm, TaL: 181 mm); one adult female, ZFMK 88103 (SVL: 71 mm, TaL: 134 mm); two juveniles, ZFMK 88104–88105 (SVL: 30.5–31.0 mm, TaL: 45.5–46.0 mm).

Characteristic features: Head large; postorbital spine small, shorter than half the diameter of orbit; two longer spines above tympanum; nuchal crest spines 8 or 9; dorsal crest present, low; no gular pouch; supralabials 10–12; infralabials 11 or 12; mental small, pentagonal; first two or three pairs of chinshields in contact with infralabials, five posterior pairs separated from infralabials by one or two rows of small scales; body compressed; dorsum with some scattered larger keeled scales; ventral scales strongly keeled, 91–107 rows from first gular to precloacal scales; a row of small precloacal scales. Coloration in life varies from green to dark brown, occasionally a bright rhombic pattern present on the neck; dark bars across back and tail (determination after Smith 1935; Taylor 1963).

Natural history notes: Four specimens were collected during daytime on 18 May 2007. Throughout the

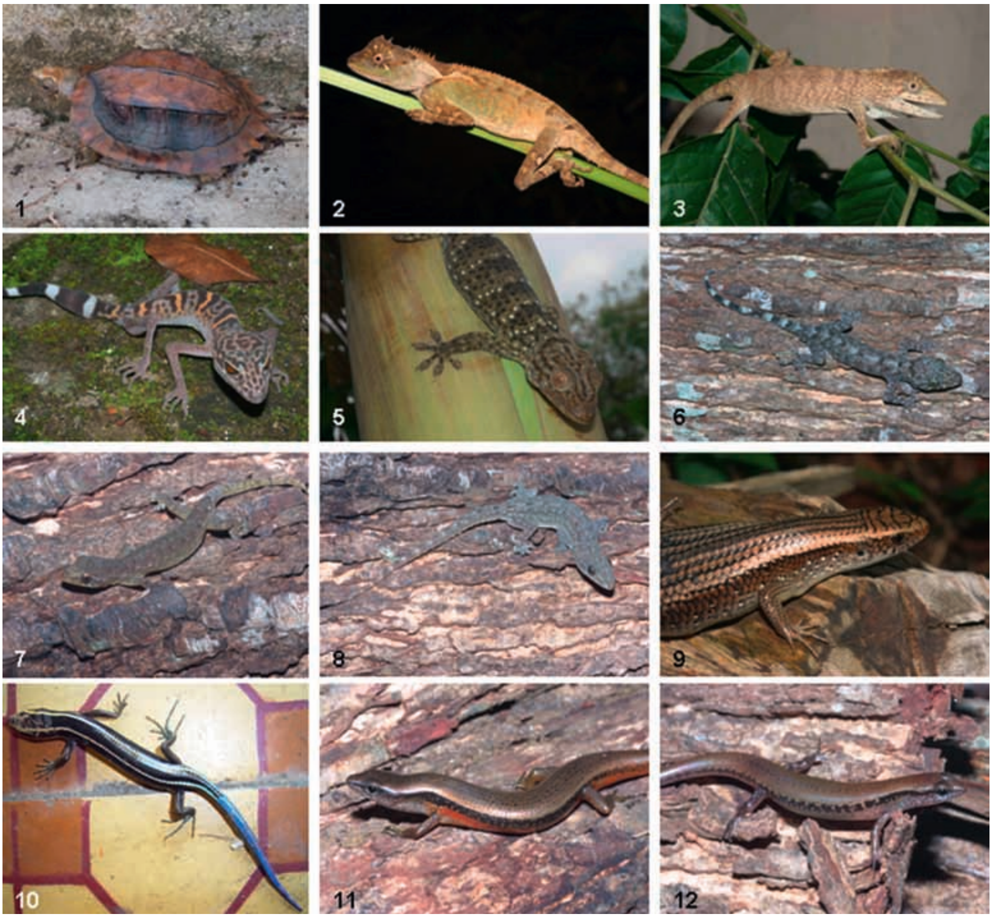

FIG. 2. 1) *Cuora mouhotii*, 2) *Acanthosaura lepidogaster*, 3) *Pseudocalotes brevipes*, 4) *Goniurosaurus catbaensis*, 5) *Gekko gecko*, 6) *Gekko palmatus*, 7) *Hemidactylus frenatus*, 8) *H. garnotii*, 9) *Eutropis multifasciatus*, 10) *Plestiodon quadrilineatus*, 11) *Scincella reevesii*, 12) *Sphenomorphus tonkinensis* (1 & 10 photographs by R. Stenke, remaining photographs by T. Ziegler).

survey period, juveniles and adults were regularly observed on the forest floor, in shrub vegetation and on karst surfaces in Ang Vat – Me Go, Ang Ong Bi, Ang Nhoi, and Ang Dai. The species was one of the most frequently observed lizards on Cat Ba Island.

Draco sp.

Observed by one of the authors (RS) and also reported by rangers from Tra Bau station in Ang Ong Bi.

Remarks: Most probably *Draco maculatus* (Gray, 1845), which was already known from Cat Ba Island by Nguyen & Shim (1997).

Pseudocalotes brevipes (Werner, 1904) (Fig. 2.3)

Specimens examined: One female, IEBR A.0721 (SVL: 64 mm, TaL: 131.5 mm).

Characteristic features: Head large, longer than wide; supralabials 8 or 9; infralabials 7; nuchal crest spines 6, dorsal crest spines absent; subdigital lamellae of fourth toe 18 or 19; fold in front of shoulder absent; midbody scale rows 65–67; middorsal scale row which points straight backwards, lateral scales keeled, ventral scales strongly keeled. Coloration in alcohol: head and dorsal body grayish brown, gular region darker with keeled scales, ventral side gray; light spots present on elbows and indistinct on knees (determination after Hallermann 2000; Hallermann & Böhme 2000).

Natural history notes: A single specimen was found at night, on 23 May, near Tra Bau ranger station sleeping in a tree about 1.5 m above the sea.

Remarks: This is the first record for the island as well as for Hai Phong City.

Physignathus cocincinus Cuvier, 1829

Specimens examined: One subadult, IEBR A.0915 (SVL: 138 mm, TaL: 339 mm).

Characteristic features: Dorsum covered with small scales; distinctly enlarged scale row below infralabials; single enlarged scale at posterior lower jaw region; transversal skin fold in posterior gular region; nuchal, dorsal and tail crests present; laterally depressed tail; toes without distinct lobules; seven femoral pores on each side. Coloration in life green to gray-brown with transversal rows of ocelli/stripes on dorsum and tail (determination after Ziegler 2002).

Natural history notes: The specimen was collected by Nguyen Thien Tao in June 2009 near Trung Trang Cave. Specimen rested at night on a branch above a stream.

Eublepharidae

Goniurosaurus catbaensis Ziegler, Nguyen, Schmitz, Stenke & Rösler, 2008 (Fig. 2.4)

Specimens examined: Holotype: One adult female, IEBR A.0717; paratypes: subadult male, MHNG 2699.49; adult female, VNUH 210507; and adult male, ZFMK 87056 (for measurements see Ziegler *et al.* 2008).

Characteristic features: A new species of the genus *Goniurosaurus* recently described by Ziegler *et al.* (2008). *G. catbaensis* is characterized by the combination of the following characters: body and limbs gracile; nuchal loop thin, protracted posteriorly; three or four thin immaculate dorsal body bands between limb insertions, without dark spotting and with dark, narrow borders surrounding the body bands; dorsal surface and maculate limbs mottled; head pattern consisting of a dark marbling; iris orange-brown; postrostral scales absent; nasal scales surrounding the nare 5 or 6; supranasals meeting in midline behind the rostral suture; supraorbital tubercles enlarged; outer surface of upper eyelid composed of granular scales of about the same size of those on top of head and with a row of 6–9 enlarged tubercles; eyelid fringe scales 52–55; supralabials 8 or 9; infralabials 6–8; body scales granular, with 8–11 granular scales surrounding the dorsal tubercles; axillary pockets deep; digits long and thin with wide subdigital lamellae, claws sheathed by four scales; precloacal pores 16–21.

Natural history notes: Specimens were found at night from 19 to 21 May 2007 in the limestone forest, one specimen was found in a small hole *c.* 2–3 m above the ground on 23 May.

Remarks: Previously, Darevsky (1999) had recorded "*Goniurosaurus lichtenfelderi*" from Cat Ba Island (with a question mark however).

Gekkonidae

Gekko gecko (Linnaeus, 1758) (Fig. 2.5)

Specimens examined: One adult specimen was photographed and released.

Characteristic features: Head very large, snout obtusely pointed; dorsal pale gray with 7 or 8 transverse series of whitish spots.

Natural history notes: The photographed male was found at night on the road near Trung Trang Cave, on 25 May. Vocalizations were heard during late afternoon and at night, between 18–20 May, in Ang Vat – Me Go, Trung Trang Valley, and Ang Nhoi.

Gekko palmatus Boulenger, 1907 (Fig. 2.6)

Specimens examined: IEBR A.0731–A.0732, A.0734–A.0736, A.0738: Six adult males collected from 19 to 25 May 2007; IEBR 3700–3702: one adult male, two adult females, collected on 21 April 2008 on karst outcrops in limestone forest, 80 m a.s.l.; IEBR A.0812: an adult male, collected on 18 June 2007 on karst outcrops in limestone forest; private collection of Herbert Rösler, CPHR 2380, CPHR 2381: two adult males collected from 21 to 25 May 2007.

Characteristic features: SVL up to 68.7 mm (females) and 70.1 mm (males); body and tail slightly dorsoventrally depressed; one pair of dark roundish or somewhat elongated spots in occipital region, smaller but more distinct dark spot in nuchal region, and light broken middorsal stripe evident on body; supralabials 11–15; infralabials 10–12; nostril in contact with rostral, internasals 1 or 2, smaller than nasorostrals; 2–7 spinous ciliary scales; dorsal tubercles in 7–12 rows; extremities lacking tubercles; body scales in 133 rows around midbody (IEBR A.0731); cloacal spur single; precloacal pores 23–29; subdigital lamellae 14–16 under fourth finger, 15–17 under fourth toe; finger and toes broadly webbed; subcaudals enlarged (determination followed Ziegler *et al.* 2006).

Natural history notes: The species was collected in the forest near the headquarters of the National Park, in and around Trung Trang cave, in Ang Nhoi, and in Ang Ong Bi. Specimens were found active at night, and a few also during daytime when hidden inside dark karst caves and rock crevices. One specimen was found at night on a window of Tra Bau ranger station. Numerous specimens were discovered at night on karst outcrops on the sea shore, on stones or on the sandy beach in the immediate vicinity of salt water. One gecko was discovered at night on a small rock surrounded by salt water, from where it tried to escape across the water surface to the beach, which was about 0.5 m distant.

Remarks: This is the first record for the island as well as for Hai Phong City.

Hemidactylus frenatus Duméril & Bibron, 1836 (Fig. 2.7)

Specimens examined: Three females, ZFMK 88108-88110 (SVL: 40.5–46.5, TaL: 39–47 mm) and one male, IEBR A.0742 (SVL: 55 mm, TaL: 63.5 mm).

Characteristic features: Head large; rostral large, much broader than high; nares bordered by rostral, supranasal, two postnasals and first supralabial; supranasals in contact with each other (IEBR A.0742) or separated from each other by 1 or 2 small scales; supralabials 9–11; infralabials 8–10; mental large, triangular; two or three pairs of chinshields, anterior pair in contact and larger than the second, second pair in contact with infralabials laterally; posterior part of back with (IEBR A.0739) or without (IEBR A. 0741–0743) enlarged tubercles; skin fold from axilla to groin and along the hind border of thigh absent; hindlimb does not reach to the axilla; digits free, the first small, not half the length of the second; subdigital lamellae under fourth toe 9 or 10; tail depressed, without denticulated lateral edge; below with a median series of transversely enlarged scales; male (IEBR A.0742) with a continuous series of 36 precloacal-femoral pores. Coloration in alcohol: dorsal head and body grayish, sometimes with indistinct darker markings (determination after Smith 1935; Ziegler 2002).

Natural history notes: Specimens were found at night in buildings at the National Park headquarters, from 19 to 23 May 2007.

Hemidactylus garnotii Duméril & Bibron, 1836 (Fig. 2.8)

Specimens examined: One adult female, IEBR A.0740 (SVL: 42 mm, tail lost).

Characteristic features: Head moderately large and broad; rostral large, nearly as high as broad; nares bordered by rostral, large supranasal, two postnasals and first supralabial; supranasals separated by a small scale; supralabials 12 or 13; infralabials 11; mental triangular; two pairs of chinshields, the anterior pair in contact with each other and larger than the posterior, posterior pair separated from infralabials by small scales; back without enlarged tubercles; ventrolateral skin fold absent but skin fold present along the hind border of thigh; hindlimbs do not reach to the axilla; digits free, subdigital lamellae under the first toe 5 or 6, under fourth toe 13; femoral area with a series of 20 slightly enlarged scales on each side; tail depressed, with denticulated lateral edge at base, posterior part lost. Coloration in alcohol: dorsal head and body grayish with many small white spots; two dark streaks from behind the eye backwards to the shoulder (determination after Smith 1935; Darevsky et al. 1984).

Natural history notes: Specimen was collected in the garden near the headquarters of the National Park.

Remarks: The morphological characters also fit with the description of *H. vietnamensis* Darevsky & Kupriyanova, 1984, except for the following characteristics: supralabials 12 or 13 (9–12 in *vietnamensis*); subdigital lamellae on fourth toe 13 (10 or 11 in *vietnamensis*). This is the first record for the island as well as for Hai Phong City.

Lacertidae

Takydromus sexlineatus ocellatus Cuvier, 1829

Specimens examined: Two adult males from the collection of the National Park: CB R3 (SVL: 52 mm; TaL: 200.5 mm) and CB R4 (SVL: 47.5 mm, TaL: 195 mm).

Characteristic features: Upper head shields rugose; nasals in contact with each other; frontonasal single; supraoculars three, the first largest and in contact with posterior loreal; supraciliaries 3; supralabials 7 or 8; infralabials 5 or 6; temporal scales strongly keeled, 2 or 3 upper rows larger than the others; chinshields in 3 pairs; 19 or 20 scales on a line from behind second chinshield to collar; dorsal scales strongly keeled, 6 rows on the nape, 4 rows across the back; scales on flanks small, in 7–10 rows, bordered above by one and below by two rows of large scales; ventrals strongly keeled, in 10 rows; scales between collar and groin 25; precloacal single, large; one femoral pore on each side. Coloration in alcohol: back brown with two light dorsolateral stripes from behind the eye to tail base; flanks of CB R3 with a series of white black-edged ocelli (determination after Smith 1935; Ziegler & Bischoff 1999; Ziegler *et al.* 1998).

Scincidae

Eutropis longicaudatus (Hallowell, 1856)

Specimens examined: One adult female, ZFMK 88115 (SVL: 111 mm, TaL: 175 mm) and one male, CB R1 (SVL: 82.5 mm, TaL: 210 mm).

Characteristic features: Supranasals in contact with each other; postnasal single; frontonasal broader than long; prefrontals in contact with each other; interparietal separates parietals posteriorly; a pair of nuchals; supraoculars four; supraciliaries 6 or 7; loreals two; preocular single, small; presuboculars two; lower eyelid scaly; supralabials 7; infralabials 5 or 6; midbody scale rows 26–28, dorsal scales in 7 or 8 rows, median rows weakly keeled; subdigital lamellae on fourth toe 24–26. Coloration: black brown; lateral stripe dark brown, from behind the eye to the base of tail, margin with white spots; ventral greenish-yellow (determination after Smith 1935; Taylor 1963; Ziegler 2002).

Natural history notes: This species was commonly seen in all types of open habitat on the island.

Eutropis multifasciatus (Kuhl, 1820) (Fig. 2.9)

Specimens examined: One female, CB R.2 (SVL: 72 mm, TaL: 89 mm) and one juvenile, IEBR A.0729 (SVL: 34 mm, tail: lost).

Characteristic features: Supranasals separated from each other by rostral; postnasal single; frontonasal broader than long; prefrontals in contact with each other posteriorly; interparietal separates parietals posteriorly; a pair of nuchals; supraoculars four; supraciliaries 5 or 6; loreals two; preocular single, presuboculars two; lower eyelid scaly; supralabials 7; infalabials 6 or 7; ear opening oval; midbody scales in 30 rows, dorsal scales in 7 or 8 rows (5 or 6 rows keeled); subdigital lamellae under fourth toe 18–20. Coloration: dorsum brown; lateral stripe black with white spots; ventral whitish (determination after Smith 1935; Taylor 1963; Ziegler 2002).

Natural history notes: This species was observed in all types of open habitat on the island. One gravid female was photographed on 19 May 2007.

Lygosoma quadrupes (Linnaeus, 1766)

Specimens examined: Two adults from the collection of the Cat Ba National Park, CB R5–R6, (SVL 58.5–62.5 mm, tail lost and regenerated).

Characteristic features: Body very elongated; snout rounded; prefrontal widely separated; parietals in contact with each other posteriorly; supraoculars four; supralabials 6; infralabials 6; postnasal single; loreals two; ear opening punctiform; midbody scales in 24–26 rows; dorsal scales smooth; limbs very short (forelimb 5 mm, hind limb 6.5–7.5 mm), widely separated when adpressed; subdigital lamellae under fourth finger 5 or 6. Coloration in alcohol: light brown above; ventral cream (determination after Smith 1935; Taylor 1963).

Plestiodon quadrilineatus Blyth, 1853 (Fig. 2.10)

Specimens examined: One juvenile, IEBR A.0813 (SVL: 27.5 mm, TaL: 40.5 mm).

Characteristic features: Frontoparietals in contact with each other; second supraocular larger than first; nasal small, followed by a postnasal; loreals two, anterior shorter than posterior; supralabilas 8; midbody scales in 20 rows, two median dorsal rows broader than the laterals; paravertebral scales 51. Coloration in alcohol: back bluish-black; two light dorsolateral stripes from the tip of snout to the tail, another pair of light stripes along upper lip to groin; posterior half of tail blue (determination after Smith 1935; Bourret 1937).

Natural history notes: One specimen was collected on 9 June 2007 in Tra Duong, Gia Luan commune, on the ground inside secondary forest.

Scincella reevesii (Gray, 1838) (Fig. 2.11)

Specimens examined: Three males, IEBR A.0727–A.0728, 3699 (SVL: 47.1–52.9 mm, TaL: 65.0–91.4 mm).

Characteristic features: Rostral large, rounded anteriorly, visible from above; nostril in the nasal; supranasals absent; frontonasal wider than long; prefrontals large, in contact anteriorly; frontal shorter than frontoparietal and interparietal together; parietals large, in contact posteriorly; nuchals in two or three pairs; supraoculars four; supaciliaries 7 or 8; postnasals absent; loreals two; supralabials 7; primary temporal single; secondary temporals two; infralabials 6; ear-opening oval; lower eyelid with transparent window; midbody scales in 30 or 32 rows, smooth, ½+6+½ or 8 rows across the dorsum between lateral stripes; paravertebral scales 67; ventral scales 59–69 rows from the first chinshields to precloacals; limbs pentadactyl, overlapping when adpressed; subdigital lamellae 11 under fourth finger, 19 or 20 under fourth toe. Coloration in alcohol: Margins of eyelids with white stripes; dorsum brown with or without dark spots; light dorsolateral stripes present but indistinct; lateral stripes black with white spots; ventral cream (determination after Smith 1935; Taylor 1963; Ouboter 1986).

Natural history notes: Two specimens were collected on 19 May 2007 and another one on 22 April 2008, during the daytime, on the ground inside a plantation forest.

Remarks: Darevsky (1990) also listed *S. melanosticta* (Boulenger, 1887) for Cat Ba Island.

Sphenomorphus indicus (Gray, 1853)

Specimens examined: One female, IEBR 3705 (SVL 73.6 mm, TaL 110.8 mm).

Characteristic features: Rostral rounded, visible from above; nostril in the nasal; supranasals absent; frontonasal wider than long; prefrontals separated from each other; parietals large, in contact posteriorly; one pair of nuchals; supraoculars four; supraciliaries 8; loreals 2; supralabials 7; infralabials 7; secondary temporals 2, lower one overlapping upper one; lower eyelid scaly; midbody scales smooth, in 36 rows; paravertebral scales 70; ventral scales 67; limbs pentadactyl, subdigital lamellae 11 under fourth finger, 17 or 18 under fourth toe. Coloration in alcohol: margins of eyelids with white stripes; dorsum brown without dark spots; lateral stripes black; ventral cream (determination after Smith 1935; Taylor 1963; Ziegler 2002).

Natural history notes: The female was collected during the day on 22 April 2008, on the forest floor. This specimen contained nine yellowish-white eggs.

Remarks: This is the first record for the island as well as for Hai Phong City.

Sphenomorphus tonkinensis Nguyen, Schmitz, Nguyen, Böhmer & Ziegler, 2011 (Fig. 2.12)

Specimens examined: Holotype: Adult male, IEBR A.0730.

Characteristic features: A representative of the genus *Sphenomorphus* based on the combination of the following morphological characters: SVL 45.3 mm; prefrontals present; supranasals absent; lower eyelid scaly; tympanum sunk; dorsal scale smooth; inner precloacals overlapping outer precloacals; tip of longest toe reaching to wrist when adpressed; hind limbs with five digits; digits with a single row of lamellae (after Shea & Greer 2002; Greer *et al.* 2006; Nguyen *et al.* 2011).

Natural history notes: The specimen was collected in open habitat, in a valley bordered by secondary limestone forest on hill slopes. It was found during daytime under leaf litter inside the secondary forest, at an altitude of *c.* 100 m.

Remarks: The specimen represents a new species which was described recently (Nguyen *et al.* 2011).

Varanidae

Varanus salvator (Laurenti, 1768)

Specimens examined: Observed several times by one of the authors (RS).

Characteristic features: Coloration and pattern were species-specific.

Natural history notes: Observations took place inside the forest and in the shore area, e.g. at Tra Bau ranger station. One animal was observed by NQT in Ang Ong Bi, on 23 May 2007.

Remarks: *Varanus salvator* (Laurenti, 1768) has already been documented for Cat Ba Island by Nguyen & Shim (1997).

Squamata: Serpentes

Pythonidae

Python molurus (Linnaeus, 1758) (Fig. 3.1)

Specimens examined: One confiscated subadult specimen that was subsequently released. Another python was observed by RS on the offshore island Dong Cong, on 27 October 2007.

Characteristic features: Coloration and pattern were species-specific.

Colubridae

Ahaetulla prasina (Boie, 1827) (Fig. 3.2)

Specimens examined: One adult female, ZFMK 88112 (SVL: 785 mm, TaL: 425 mm), and another subadult specimen, deposited in the scientific collection of Cat Ba National Park (TL: 415 mm).

Characteristic features: Horizontal pupil; head long and narrow, with a pointed snout, but snout without dermal appendage; mental groove present; loreals two; preocular single, postoculars 2 or 3; one anterior, two posterior temporal scales; supralabials 9 or 10, fourth to sixth in contact with the eye; midbody scales in 15 rows; ventral scales 2 + 184–199; subcaudal scales 152–161, divided; anal plate divided (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: One female was collected at night, on 25 May 2007 inside secondary forest, near the headquarters of the National Park. The snake was found in the branches of a small tree about 1.5 m above the forest floor. In that same night, a second adult specimen was seen but not collected.

Remarks: Our finding represents the first record of *A. prasina* for Cat Ba Island as well as for Hai Phong City.

Amphiesma stolatum (Linnaeus, 1758) (Fig. 3.3)

Specimens examined: One adult male, deposited in the collection of the Cat Ba National Park (TL: 505 mm).

Characteristic features: Numerous large, black dorsal blotches on the nape as well as above and below the light dorsolateral stripes; postocular streak lacking; internasals narrowed anteriorly; loreal single; preocular single; postoculars three; supralabials 8, third to fifth in contact with the eye; midbody scales in 19 rows; ventral scales 3 + 147; subcaudal scales 80, divided; anal plate divided (determination after Bourret 1936; David *et al.* 2007).

Boiga guangxiensis Wen, 1998 (Fig. 3.4)

Specimens examined: One subadult, IEBR A.0904 (SVL: 467 mm, TaL: 143 mm); one adult male, ZFMK 88117 (SVL: 940 mm, TaL: 343 mm).

Characteristic features: Maxillary teeth enlarged, grooved posterior; vertebral scale row distinctly enlarged; loreal single; preocular single; postoculars two; three anterior and 3–6 posterior temporals; supralabials 8 or 9, third to fifth or fourth to sixth in contact with the eye; midbody scales in 21 rows, smooth on dorsum; ventral scales 1 + 261–266; subcaudal scales 142–144 divided; anal plate entire (determination after Tillack *et al.* 2004; Ziegler *et al.* 2007).

Natural history notes: One specimen was collected at night, on 25 May 2007, in the secondary forest near the headquarters of the National Park. The snake was found near the main forest path in the branches of a small tree, about 1.5 m above the forest floor. Most probably we saw another, large specimen of that species approximately 10 m above the forest floor, in a large forest tree near the Trung Trang cave entrance. The adult male specimen (ZFMK 88117) was found in the rice wine collection of a local trader in Cat Ba town and bought on 25 May 2007.

Remarks: We regard the high supralabial count in the subadult specimen (especially well discernible on the right head-side) as an irregularity. The same applies for the high posterior temporal count, deriving from a very large upper anterior temporal. The latter could not be observed in the adult male specimen, which showed the normal condition of three posterior temporals. Our finding represents the first record of *B. guangxiensis* for Cat Ba Island as well as for Hai Phong City.

Chrysopelea ornata (Shaw, 1802) (Fig. 3.5)

Specimens examined: One medium-sized specimen from the rice wine collection of a local trader in Cat Ba town; the specimen was deep inside a bottle that was being offered for sale. Therefore, we were not allowed to further inspect the specimen and could only photograph it on 26 May 2007.

Characteristic features: Coloration and pattern were species-specific.

Remarks: Our finding represents the first record of *C. ornata* for Cat Ba Island as well as for Hai Phong City.

Coelognathus radiatus (Boie, 1827) (Fig. 3.6)

Specimens examined: One specimen deposited in the scientific collection of the Cat Ba National Park (TL: 660 mm).

Characteristic features: Body with four black stripes anteriorly; head with black occipital crossbar and black lines radiating from the eye; loreal single; preocular single; postoculars two; supralabials 8, third to fifth in contact with the eye; midbody scales in 19 rows; ventral scales 2 + 227; subcaudal scales 86, divided; anal plate undivided (determination after Ziegler *et al.* 2007).

Natural history: A second dead specimen was found by RS inside a lychee plantation near the National Park headquarters, on 2 November 2003.

FIG. 3. 1) *Python molurus*, 2) *Ahaetulla prasina*, 3) *Amphiesma stolatum*, 4) *Boiga guangxiensis*, 5) *Chrysopelea ornata*, 6) *Coelognathus radiatus*, 7) *Dinodon meridionale*, 8) *Enhydris chinensis*, 9) *Pareas* cf. *hamptoni*, 10) *Psammodynastes pulverulentus*, 11) *Rhabdophis subminiatus*, 12) *Rhynchophis boulengeri* (1 photograph by D. Schrudde, 7 & 8 by R. Stenke, remaining photographs by T. Ziegler).

Dendrelaphis ngansonensis (Bourret, 1935)

Specimens examined: One adult female, ZFMK 88116 (SVL: 845 mm, TaL: 407 mm).

Characteristic features: Absence of a light lateral stripe along the flanks framed with black; loreal single; preocular single; postoculars two; two anterior, three posterior temporals; supralabials 9, fourth to sixth in contact with eye; midbody scales in 15 rows; vertebral scales enlarged; ventral scales 2 + 181; subcaudal scales 138, divided, anal plate divided (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: The female specimen, a road-kill, was collected by RS about 1 km north of the National Park headquarters, beginning of May 2007. The road is bordered by bamboo plantations and shrub.

Remarks: Nguyen & Shim (1997) list *D. pictus* as occurring on Cat Ba Island. *D. ngansonensis* was considered a synonym of *D. pictus*. However, Ziegler

& Vogel (1999) demonstrated that *D. ngansonensis* warrants distinct taxonomic status. At this stage it remains unclear whether *D. pictus* occurs on Cat Ba Island or was merely confused with *D. ngansonensis* by Nguyen & Shim (1997). Our finding represents the first record of *D. ngansonensis* for Cat Ba Island as well as for Hai Phong City.

Dinodon meridionale Bourret, 1935 (Fig. 3.7)

Specimens examined: One adult photographed by RS in May 2004.

Characteristic feature: Scalation (keeled dorsals, anal consisting of a single plate), coloration and pattern were species-specific.

Natural history notes: One specimen was found killed on 7 May 2004, without a head, inside a part of Ang Dai valley that is used for agriculture. Another specimen was seen and photographed in October 2009 by TZ inside a karst cave crevice at a height of about 3.5 m.

Remarks: Our finding represents the first record of *Dinodon meridionale* for Cat Ba Island as well as for Hai Phong City.

Enhydris chinensis (Gray, 1842) (Fig. 3.8)

Specimens examined: One adult photographed by RS on 28 March 2005.

Characteristic features: Scalation of head, coloration, and pattern were species-specific.

Natural history notes: The snake was caught at a fish/shrimp farm on a small offshore island (Dong Cong) NW of the main island Cat Ba and was subsequently released.

Remarks: This is the first record for Cat Ba Archipelago as well as for Hai Phong City.

Oligodon chinensis (Günther, 1888)

Specimens examined: One adult female, IEBR 1226 (SVL: 452 mm, TaL: 89 mm).

Characteristic features: Rostral distinctly visible from above, dorsal scales smooth; head short; indistinct, body cylindrical; dorsal pattern consisting of transversely placed, narrow dark blotches, separated by dark crossbars; loreal single; preocular single; subocular absent; postoculars two; one anterior and one posterior temporals; supralabials 8, fourth to fifth in contact with eye; midbody scales in 17 rows; ventral scales 1 + 182; subcaudal scales 53, divided; anal plate entire (determination after Bourret 1936; Ziegler *et al.* 2007).

Natural history notes: The specimen was collected on 22 June 2002 by NQT on the ground, near the headquarters of the National Park.

Pareas cf. *hamptoni* (Boulenger, 1905) (Fig. 3.9)

Specimens examined: One adult female, IEBR A.0905 (SVL: 440 mm, TaL: 143 mm).

Characteristic features: Mental groove absent; prefrontals in contact with eye; loreal single; preoculars two; suboculars two; postoculars two; supralabials 8; midbody scales in 15 rows; anterior vertebral scales slightly enlarged, posterior upper dorsal scales slightly keeled; ventral scales 192; subcaudal scales 93, divided; anal plate entire (determination after Bourret 1936; Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: We collected the female specimen at night, on 22 May 2007, in a dry stream bed inside secondary forest near the headquarters of the National Park. The snake was found in the branches of a small tree about 1 m above the forest floor.

Remarks: Ziegler (2002) summarized the complicated taxonomic history of the *Pareas hamptoni* group (including the taxon *tonkinensis*). The high numbers of ocular and temporal scales (2 or 3 anterior temporals, four posterior temporals) and the six maxillary teeth of the single record from Cat Ba Island do not allow a proper identification at this stage. Pope (1935) listed 7–9 maxillary teeth as characteristic for the taxon *tonkinensis* (nowadays *P. hamptoni*), whereas 4–6 maxillary teeth are diagnostic for the taxa *chinensis* and *kuangtungensis* (= *P. chinensis*). However, Pope (1935) stated that his key may not be expected to work in every case because many characters are extremely unstable in this genus. Only further studies, including molecular approaches, on *Pareas* samples from northern Vietnam and southern China, including insular populations, may lead to a better understanding of the often complicated taxonomy. Our finding represents the first record of *Pareas* cf. *hamptoni* for Cat Ba Island as well as for Hai Phong City.

Psammodynastes pulverulentus (Boie, 1827) (Fig. 3.10)

Specimens examined: One adult male, ZFMK 88113 (SVL: 335 mm, TaL: 91 mm), one adult female, IEBR A.0906 (SVL: 420 mm, TaL: 96 mm), and one subadult, ZFMK 88114 (SVL: 266 mm, TaL: 56 mm).

Characteristic features: Viperid-like, triangular-shaped head; maxillary teeth enlarged, grooved posterior; pupil vertically elliptic; mental groove present; loreal single; preoculars 1 or 2, postoculars 2 or 3; 1 or 2 anterior, 2 or 3 posterior temporals; supralabials 8, third to fifth in contact with eye; midbody scales in 17 rows; dorsal scales smooth, vertebral scale row not enlarged; ventral scales 2–3 + 164–168; subcaudal scales 49–61, divided; anal plate entire (determination after Bourret 1936; Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: The subadult specimen was collected during the day in a dry stream bed of the secondary forest near the headquarters of the National Park. The adult male specimen was collected in the same habitat but at night in a small tree approximately 1 m above the forest floor. The female specimen, again a roadkill, was collected by RS about 700 m north of the National Park headquarters, on 7 May 2007. The road in this area is bordered by bamboo plantations and shrub. With three additional records from daytime and five additional records during the night this species was the commonest recorded snake on Cat Ba Island throughout our survey in May 2007, regularly observed by RS prior to and after the survey, in different types of habitats.

Remarks: Our finding represents the first record for Cat Ba Island as well as for Hai Phong City.

Ptyas korros (Schlegel, 1837)

Specimens examined: One adult male, deposited in the scientific collection of the Cat Ba National Park (TL: 1128 mm).

Characteristic features: Dorsum brown, posterior dorsal scales with blackish brown margins; eye large; loreals 2; preoculars 3 (one presubocuolar plus one very large scale); postoculars 2; supralabials 8, fourth and fifth in contact with the eye; midbody scales in 15 rows; dorsals smooth; ventral scales 165; subcaudal scales 128, divided; anal plate divided (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: We discovered one specimen on 21 May 2007 during daytime in an agricultural area near the headquarters of the National Park.

Rhabdophis subminiatus (Schlegel, 1837) (Fig. 3.11)

Specimens examined: One adult female, deposited in the scientific collection of Cat Ba National Park (TL: 730 mm).

Characteristic features: Body uniformly olive green; a black line stretching from the eye to the supralabials; loreal single; preocular single; postoculars three; supralabials 8, third to fifth in contact with the eye; midbody scales in 19 rows; dorsals keeled, except outermost row in anterior body half; ventral scales 3 + 160; subcaudal scales 65, divided; anal plate divided (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: The female contained large eggs (up to 2.5 cm in diameter).

Remarks: This is the first record for Cat Ba Island as well as for Hai Phong City.

Rhynchophis boulengeri Mocquard, 1897 (Fig. 3.12)

Specimens examined: One adult female, IEBR A.0902 (SVL: 706 mm, TaL: 228 mm).

Characteristic features: Presence of a long pointed nasal appendage covered with small scales; interstitial skin on the sides of the body bluish-black and white; loreal single; preocular single; postoculars 2; two anterior and two posterior temporals; supralabials 9, fourth to sixth in contact with eye; midbody scales in 19 rows; ventral scales 3 + 206; subcaudal scales 102, divided; anal plate divided (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: The specimen was collected during the night, on 23 May 2007, at the forest edge along the coast near Tra Bau ranger station. This specimen was discovered on a tree approximately 3 m above the shore. While trying to capture the specimen, it dumped down into the water and tried to escape by swimming towards the open sea.

Remarks: This is the first record for Cat Ba Island as well as for Hai Phong City.

Xenochrophis flavipunctatus (Hallowell, 1860) (Fig. 4.1)

Specimens examined: One female, ZFMK 88111 (SVL: 365 mm TaL: 74+ mm).

Characteristic features: Dorsal pattern consisting of small dark blotches and streaks, larger on the sides; dorsolateral dots small, white to yellow; a well-defined nuchal V-shaped marking; two well-defined subocular streaks, the posterior one extending from the eye to the corner of the mouth then meeting the V-marking; ventral and subcaudal scales all with entire, broad dark markings; midbody scales in 19 rows; ventral scales 2 + 138; subcaudal scales 36+, divided; anal plate divided (determination after Vogel & David 2006; Ziegler *et al.* 2007).

Natural history notes: The specimen was found on 18 May 2007 in the immediate vicinity of the headquarters of the National Park. It was killed by local people near the guesthouse.

Remarks: The species was listed under the name *X. piscator* by Nguyen & Shim (1997).

Elapidae

Bungarus multicinctus Blyth, 1861 (Fig. 4.2)

Specimens examined: One adult male, ZFMK 88118 (SVL: 1225 mm, TaL: 125 mm); in addition, we were able to make some scale counts [marked by *] of an adult female (TL: 780 mm), that was found preserved in the rice wine collection of a local trader in Cat Ba town, on 26 May 2007.

Characteristic features: Back with black and white rings, white body bands not entirely encircling the body, venter white; tail tip not distinctly blunt but somewhat pointed; 26*–38 narrow white crossbars on body and 9* or 10 on tail; loreal absent; preocular single; postoculars two; 1 or 2 anterior, 2 or 3 posterior temporals; supralabials 7, third to fourth in contact with eye; midbody scales in 15 rows; vertebral scale row enlarged, not distinctly keeled; ventral scales 2*–3 + 213*–224; subcaudal scales 40–49*, undivided; anal plate entire (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: The specimen was collected during the night, on 22 May 2007, in the secondary forest near the headquarters of the National Park. The snake was found near the main forest path crawling in the undergrowth of the forest ground, about 3 m from a small pond. A second large specimen, which was not collected, was discovered immediately after the capture of the adult male in the same habitat, at only a few meters distance.

Naja atra Cantor, 1842 (Fig. 4.3)

Specimens examined: One adult female, found in the rice wine collection of a local trader in Cat Ba Town, on 25 May 2007 (TL: 1320 mm).

Characteristic features: Dark dorsum, spectacle-shaped dorsal neck pattern between ventrals 5 and 10, not connected with light gular region; gular region with dark fleck on each side, followed by dark transversal band; loreal absent; preocular single; postoculars three; supralabials 7; two anterior, 2 or 3 posterior temporals; midbody scales in 21 rows; dorsals smooth; ventral scales 2 + 171; subcaudal scales 48, divided; anal plate undivided (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history notes: We discovered an escaping specimen on 19 May 2007. Characteristic were the dark dorsum and the gray venter. The large specimen was seen at night in the undergrowth of secondary forest, near the main entrance of Trung Trang cave.

Remarks: Most probably this species was listed under the name *Naja naja* by Nguyen & Shim (1997). Our finding represents the first record of the species for Cat Ba Island.

Sinomicrurus macclellandi (Reinhardt, 1844) (Fig. 4.4)

Specimens examined: One adult was photographed on the ground in a bathroom at the headquarters of Cat Ba National Park, in the morning of 1 October 2002.

Characteristic features: Coloration and pattern were species-specific (e.g. Vogel 2006).

Remarks: This is the first record for Cat Ba Island as well as for Hai Phong City.

Viperidae

Protobothrops mucrosquamatus (Cantor, 1839) (Fig. 4.5)

Specimens examined: One adult male was discovered preserved in the rice wine collection of a local trader in Cat Ba town, on 25 May 2007 (TL: 995 mm).

Characteristic features: Head long, narrow; dorsum gray to reddish brown; supralabials 10; dorsal scales strongly keeled, midbody scales in 25 rows; ventral scales 216; subcaudal scales 90; anal plate undivided (determination after Ziegler 2002; Ziegler *et al.* 2007).

Natural history: We saw a medium-sized specimen at night, on 19 May 2007, inside the forest in the vicinity of Trung Trang cave. The specimen was hanging in a tree about 1.6 m above the ground, but was able to escape before collecting. Another specimen, a roadkill, was photographed on 3 December 2005. It was discovered at night on the ground next to the entrance of a house. Furthermore, RS observed this species at many different places – at Viet Hai ranger station (in secondary forest and shrub), on Cat Dua Island (on rocks and in a shrub), in the primary forest west of Gia Luan, and close to agricultural land in the vicinity of Hien Hao and around Gia Luan.

FIG. 4. 1) *Xenochrophis flavipunctatus*, 2) *Bungarus multicinctus*, 3) *Naja atra*, 4) *Sinomicrurus macclellandi*, 5) Portrait of *Protobothrops mucrosquamatus* (road kill), 6) *Viridovipera* cf. *stejnegeri*, 7) Secondary limestone forest in Ang Vat – Me Go, 8) Trung Trang Cave, 9) Open habitat and plantation forest, bordered by secondary limestone forest, 10) Coastal habitat near Tra Bau ranger station (1, 4, 5 photographs by R. Stenke, remaining photographs by T. Ziegler).

Viridovipera cf. *stejnegeri* (Schmidt, 1925) (Fig. 4.6)

Specimens examined: One adult male, IEBR A.0903 (SVL: 515 mm, TaL: 130 mm); one adult female, ZFMK 88106 (SVL: 415, TaL: 88 mm); one juvenile, ZFMK 88107 (SVL: 210, TaL: 50 mm).

Characteristic features: Eyes orange in juveniles and females, reddish orange in males; postocular streak lacking in adult males, females, and in juveniles; tail surface mottled with rusty brown or reddish brown; spinose hemipenis; separation of the first supralabial from the nasal; midbody scales in 21 rows; ventrals 4 + 162 (male), 164 (female) and 163 (juvenile); subcaudal scales 71 (male), 65 (female) and 72 (juvenile); anal plate entire (determination after Campden-Main 1970; David *et al.* 2001).

Natural history notes: The male and female were collected at night, on 18 May 2007. Specimens were found in a secondary forest tree near the main forest path close to the headquarters of the National Park. The snakes were *c.* 1 m distant from each other, *c.* 1–1.5 m above a small pond. The male was digesting an adult *Polypedates leucomystax*, that were abundant in the shrubs and trees around the pond. The female contained large eggs. The juvenile was collected at night, on 26 May 2007, on leaves at about a height of 1 m in secondary forest. Another juvenile was found in the same habitat at night, on 25 May 2007, but was not collected.

Remarks: Most probably this species was listed under the name *Trimeresurus albolabris* by Nguyen & Shim (1997). Our findings represent the first record of the species for Cat Ba Island as well as for Hai Phong City. However the taxonomic status, compared with mainland populations, is currently under morphological and molecular research.

FURTHER RECORDS AND SPECIES OF CONSERVATION CONCERN

In comparison with results of previous surveys on Cat Ba Island, the diversity of terrestrial reptiles recorded during our field work was five times higher than that given in Darevsky (1990) and twice as high as indicated by Nguyen & Shim (1997) (Fig. 1). Additionally, Nguyen & Shim (1997)[1], Darevsky (1990, 1999)[2], and Orlov *et al.* (2003)[3] list the following five species as occurring on Cat Ba Island: Dibamidae: *Dibamus bourreti* Angel, 1935[1,2]; Scincidae: *Scincella melanosticta* (Boulenger, 1887)[2]; Typhlopidae: *Ramphotyphlops braminus* (Daudin, 1803)[1,2]; Colubridae: *Dendrelaphis pictus* (Gmelin, 1789)[1] (but see discussion above); *Opisthotrophis andersonii* (Boulenger, 1888)[3]; Elapidae: *Bungarus fasciatus* (Schneider, 1801)[1]; and Viperidae: *Cryptelytrops albolabris* (Gray, 1842)[1,2] (but see discussion above). Adults of *Ophiophagus hannah* (Cantor, 1836) and *Bungarus fasciatus* (Schneider, 1801) were observed by us in the rice wine collection of a local trader in Cat Ba town. However, these animals may also originate from the mainland so we did not list them as part of the reptilian fauna of Cat Ba Island. Further evidence (i.e. photographs or specimens with locality

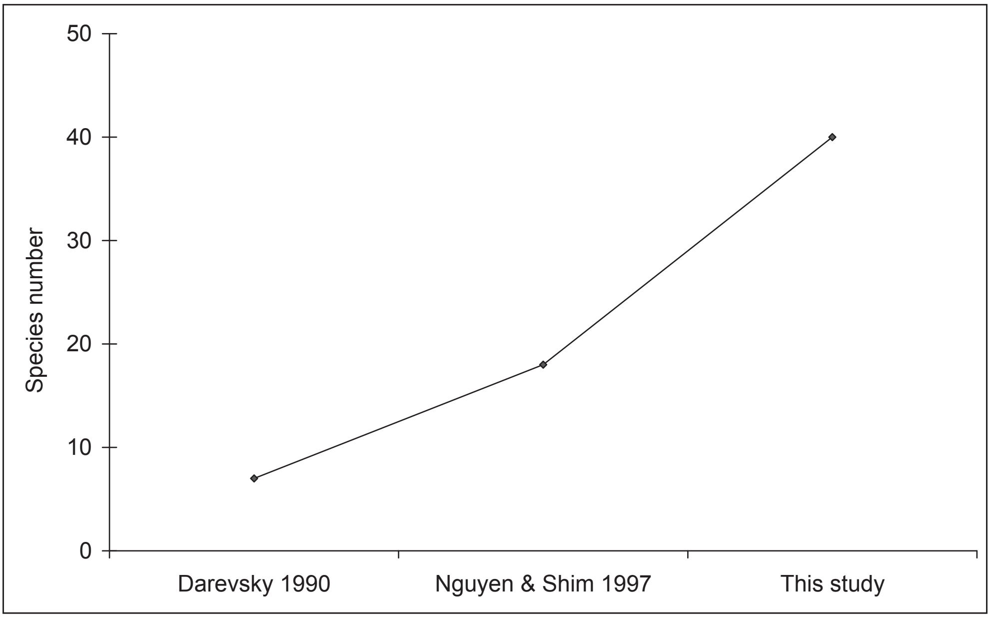

FIG. 1. Terrestrial reptile species accumulation from Cat Ba Island.

TABLE 1. List of threatened reptile species recorded from Cat Ba Island.

Scientific name	IUCN 2008	VNRB 2007	CITES 2008	Dec. 32 2006
Physignathus cocincinus		VU		
Gekko gecko		VU		
[*Varanus salvator*]		EN	II	IIB
[*Python molurus*]	LR/nt	CR	I	IIB
Coelognathus radiatus		EN		IIB
Ptyas korros		EN		
Bungarus multicinctus				IIB
Naja atra		EN	II	IIB
Cuora mouhotii	EN		II	

Notes: IUCN: IUCN Red List, VNRB: Vietnam Red Data Book: CR: critically endangered, EN: endangered, VU: vulnerable, LR/nt: near threatened; CITES: I, II = Appendix I and II; Dec. 32: Governmental Decree No 32/2006/ND-CP: IB = Group IB (prohibited exploitation and use for commercial purpose), IIB = Group IIB (limited exploitation and use for commercial purpose); [ ]: Only photographic record or observation

data) is still needed. In addition, it is likely that a dead juvenile king cobra of about 80 cm total length was seen as a road kill by trained project staff close to Khoan Cao ranger station in August 2003. The snake had yellow rings and bright yellow ventral scales, but there is no specimen or photograph available for confirmation.

Among the 40 reptile species recorded from Cat Ba Island, two species are listed in the IUCN Red List (2008), seven species are listed in the Vietnam Red Data Book (Tran *et al.* 2007), four in the CITES appendices (2008), and five species are protected by governmental law (Decree No 32/2006/ND-CP) (Table 1).

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APPLICABILITY OF DNA BARCODING TO MUSEUM SPECIMENS OF BIRDS FROM THE DEMOCRATIC REPUBLIC OF THE CONGO

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Abstract. The ornithological collections of the Royal Museum for Central Africa in Tervuren and the Royal Belgian Institute of Natural Sciences in Brussels contain approximately 155 000 specimens collected in the Democratic Republic of the Congo (DRC). They include type specimens and other samples from historical populations that represent an exceptional source of information for exploring how habitat fragmentation due to deforestation or global climate changes affect patterns of biodiversity in African birds. By attempting to obtain DNA sequences from these archive collections we intend to make them useful for genetic studies and to contribute to a reference library of DNA sequences, thus allowing the future identification of Central African bird species through DNA barcodes. Our project aims to sequence approximately 950 museum specimens, representing 225 species, collected between 1845 and 2008. Our preliminary results reveal that the degradation of DNA in most museum specimens does not allow the amplification of the standard DNA barcode fragment (694 bp). Nevertheless, we have been able to sequence shorter fragments (298 bp and 100 bp) for the majority of the selected specimens, implying that the collections in the RMCA and the RBINS contain DNA information that remains useful for barcoding purposes. More elaborate experiments might yield longer DNA sequences for phylogenetic and phylogeographic studies.

Key words: Democratic Republic of the Congo, DNA barcoding, COI, Aves, museum sample, archival DNA.

INTRODUCTION

Natural history collections hold unique and irreplaceable samples of historical populations. Museum specimens play a crucial role in the study of biodiversity, biological invasions, habitat loss, global climate change, pathogens and disease vectors as well as environmental contaminants (Suarez & Tsutsui 2004). Early publications demonstrated that genetic information from museum specimens adds an accurate historic reference to the study of extant populations (Thomas *et al.* 1990, Roy *et al.* 1994). More recently, comparisons between extant biomaterial and archival DNA have contributed to the identification of living descendants of presumably extinct species e.g. a Galapagos tortoise (Poulakakis *et al.* 2008) and the giant sable antelope (Pitra *et al.* 2008). The genetic analysis of historical mammal specimens has also clarified the phylogenetic position of the extinct Alpine lynx (Gugolz *et al.* 2008), the quagga (Leonard *et al.* 2005), three tenrec genera (Asher & Hofreiter 2006), and the taxonomic status of the extinct kouprey (Bovinae) (Hassanin & Ropiquet 2004, 2007). At a population level, archival DNA has enabled the direct measurement of the genetic variability in a pre-bottleneck population of the greater prairie chicken (Bouzat *et al.* 1998). The information on historical genetic variability may allow the estimation of past population sizes (Ramakrishnan *et al.* 2005), useful for wildlife conservation (Leonard 2008). More resolved phylogenies have been obtained using complete mitochondrial genomes of the Tasmanian tiger (Miller *et al.* 2009) and Mediterranean tortoises (Parham *et al.* 2006), or using nuclear DNA from old bird collections (Irestedt *et al.* 2006).

In addition to their historical value, museum samples represent an essential link between biological data and taxonomic knowledge and provide a means to verify the taxonomic identity of the sequenced specimens (Pleijel *et al.* 2008). For example, using DNA sequences from type specimens, Stuart *et al.*

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TABLE 1. Detail of the number of samples, number sequenced, and sequences used. Percentages are given between parentheses in comparison with the sampling effort.

	Sampling effort	Sequenced				Not sequenced	Sequences used [b]
		100 bp	298 bp	694 bp	Total	0 bp	
Specimens (total)	951	326 (34%)	313 (33%)	82 (9%)	721 (76%)	230 (24%)	621 (65%)
RMCA	667	187 (28%)	236 (35%)	52 (8%)	475 (71%)	192 (29%)	386 (58%)
RBINS	256	139 (54%)	76 (30%)	5 (2%)	220 (86%)	36 (14%)	215 (84%)
UCZM	19	0	0	17 (90%)	17 (90%)	2 (10%)	14 (74%)
WML	1	0	1 (100%)	0	1 (100%)	0	1 (100%)
MBC[c], Korea	8	0	0	8 (100%)	8 (100%)	0	5 (62%)
Species[3]	225	132 (59%)	121 (54%)	18 (8%)	186 (83%)	39 (17%)	177 (79%)
Genera	84	57 (68%)	48 (57%)	4 (5%)	75 (89%)	9 (11%)	69 (82%)
Families	45	31 (69%)	34 (76%)	2 (4%)	41 (91%)	4 (9%)	38 (84%)
Orders	13	12 (92%)	8 (62%)	2 (15%)	13 (100%)	0	13 (100%)

[1] Only sequences that have a minimum 100 bp overlap with the standard (Folmer *et al.* 1994) and the universal mini-barcode (Meusnier *et al.* 2008) are used.

[2] Migratory Birds Center, National Park Research Institute, Korea National Park Service.

[3] Only specimens identified at the species level are taken into account.

(2008) were able to recognize misidentifications in incongruent studies on the diversity of Asian leaf turtles. Voucher specimens therefore constitute necessary reference material for the Barcode of Life Initiative, which aims to sequence a standard DNA fragment of the cytochrome *c* oxidase subunit I gene (COI) for all animal species (Hebert *et al.* 2003). This approach requires a DNA reference library as comprehensive and accurate as possible in order to be useful for species identification (Meyer & Paulay 2005). Previous studies, in the context of the All Birds Barcoding Initiative (ABBI), have demonstrated the effectiveness of COI barcodes to identify North American (Kerr *et al.* 2007), Korean (Sook *et al.* 2006), and Neotropical bird species (Kerr *et al.* 2009). Although most avian DNA barcodes were obtained from fresh samples, DNA barcoding of birds from museum collections has already been shown to be useful in determining the taxonomic relationship between living and extinct or endangered species, e.g. quails in New Zealand (Seabrook-Davison *et al.* 2009) or the ivory-billed woodpecker (Fleischer *et al.* 2006).

However, obtaining DNA sequences from museum specimens is often a challenge. DNA molecules become increasingly fragmented with time. Fixation treatments and storage conditions severely affect the DNA extraction process and downstream applications. Finally, tissue sampling methods should be adapted in order to safeguard the integrity of the museum specimens (Wandeler *et al.* 2007). In order to address some of these difficulties, a number of protocols has been developed for DNA extraction of archival samples in general (Rohland *et al.* 2004, Rohland & Hofreiter 2007), from feathers (Horvath *et al.* 2005), or from toe-pads of dried bird skin collections (Mundy *et al.* 1997). Furthermore, depending on the collections, the specimens, and even the type of tissues, DNA appears to be very variable in quality and quantity (Wandeler *et al.* 2007).

The bird collections of the Royal Museum for Central Africa in Tervuren (RMCA) and the Royal Belgian Institute of Natural Sciences in Brussels (RBINS) hold *ca.* 155 000 well-documented voucher specimens from the Democratic Republic of the Congo (DRC). Some of these originate from areas that are difficult to access or from historical populations that might have become strongly reduced or even extinct. They also include type specimens, which represent the ultimate reference material for species identification and which testify to the existence of taxa in an area for which the fauna is poorly known (Louette *et al.* 2010). The existence of these two important collections is an important opportunity, especially when compared to regions such as the Indomalayan region, where the past and current ornithological sampling effort has been poor and where only a small proportion of its bird fauna is represented in vouchered tissue collections (Sodhi *et al.* 2007). In view of the arguments above, this study looks at the potential value of the bird collections of the RBINS and the RMCA for DNA barcoding.

MATERIAL AND METHODS

The number of specimens sampled was 951 (RMCA: 667, RBINS: 256, UCZM: 19, WML: 1, Korea National Park Service: 8). They represent 225 morphologically identified species belonging to 84 genera (Table 1). This exploratory study focused on genera where a morphological taxonomic expertise was available within the institutions concerned (e.g. *Accipiter* and *Ploceus*). On average, we selected four specimens per species (Appendix). Thirty-seven species are represented by a single specimen, but some species of the genera *Accipiter* and *Ploceus* were intensively sampled (up to 46 specimens per species). Reliably identified specimens (adult specimens with typical morphology) were selected from different geographic localities. In addition, some unreliably identified specimens (e.g. juveniles or individuals with a peculiar morphology) were used to test the effectiveness of DNA barcoding in detecting possible misidentifications.

Tissue sampling, and pre- and post-PCR manipulations were performed in different rooms in order to prevent contamination. Further, we never processed conspecific samples simultaneously in order to allow the detection of cross-contamination between samples in adjacent tubes. Tissue samples were taken from toe-pad skins (Mundy *et al.* 1997), lysed overnight, and total genomic DNA was extracted using NucleoSpin tissue kits (Macherey-Nagel). Moreover, total DNA yield was visualized by gel electrophoresis for a set of samples of different ages in order to estimate the size-range of DNA fragments in the DNA extracts. In order to be able to amplify DNA fragments from highly degraded samples, we attempted to amplify different fragment sizes using three primer combinations that always involved the same forward primer (Fig. 1). To achieve

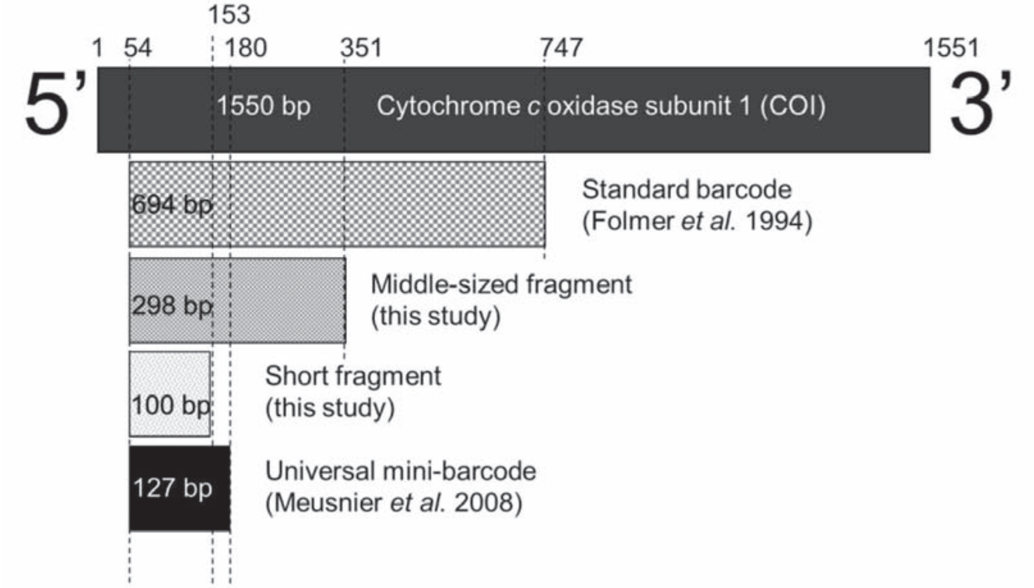

FIG. 1. Relative position of the different DNA fragments amplified and sequenced in this study on the cytochrome *c* oxidase subunit 1 (COI) gene sequence of *Buteo buteo* (GenBank accession number NC_003128) and the universal mini-barcode (in black). Relative nucleotide positions on the COI gene fragment are given at the top of the figure. Lengths (bp) of the fragments are given in the respective rectangles representing the fragments.

this goal we used the degenerated primers BirdF1d (5'-TCAACCAACCACAAAGAYATYGGYAC-3') and BirdR1d, (5'-ACGTGGGAGATGATTCCGAAKCCKGG-3') modified after Hebert *et al.* (2004) and Lohman *et al.* (2008) for the standard DNA barcode region (694 bp); BirdF1d and BirdH351d (5'-CCTGCTCCWGCTTCTAYDGT-3') to amplify a 298 bp DNA fragment corresponding to the first half of the standard DNA barcode, and BirdF1d together with BirdH153d (5'-ACGATTACRTTGTARATYTGRTC-3') to amplify a short DNA fragment (100 bp) representing the first part of the standard DNA barcode. This "mini-barcode" region corresponds to the first 100 bp of the universal DNA mini-barcode (127 bp) proposed by Meusnier *et al.* (2008).

After preliminary tests failed to amplify the standard DNA barcode for most samples, we targeted the middle-sized fragment (298 bp) to obtain the best balance between sequence length and number of successful amplifications. Finally, we also tried to amplify the 100 bp fragment for the samples that failed in the previous PCR assays. We evaluated the DNA quantity and quality of the 248 samples from RBINS with a ND-1000 Spectrophotometer (NanoDrop) to be able to use a constant final concentration of *ca.* 3 ng/µl DNA template in each PCR. The amplified fragments were directly sequenced using an ABI 3130xl Genetic Analyzer (Applied Biosystems). DNA sequences were checked for quality and aligned by hand. Since Sefc *et al.* (2007) demonstrated the occurrence of single base errors (double peaks and artifact substitutions) in PCR products obtained from museum bird specimens, we read all double peaks as ambiguity codes. We calculated K2P distances using MEGA 4 (Tamura *et al.* 2007) and used TaxonDNA v.1.5a12 (Meier *et al.* 2006) to cluster sequences based on pairwise distances and check the accordance between these clusters and the identification of the voucher specimens.

RESULTS

DNA sequencing. The systematic DNA barcoding of 951 museum specimens representing 225 morphologically identified species belonging to 84 genera produced 721 sequences (76% of the sampled specimens). Forty-three percent of them correspond to the middle-sized fragment, 45% to the short fragment, and 11% to the standard DNA barcode fragment (Table 1). The effect of the age of the specimen collection on the results (Fig. 2.) shows that even if

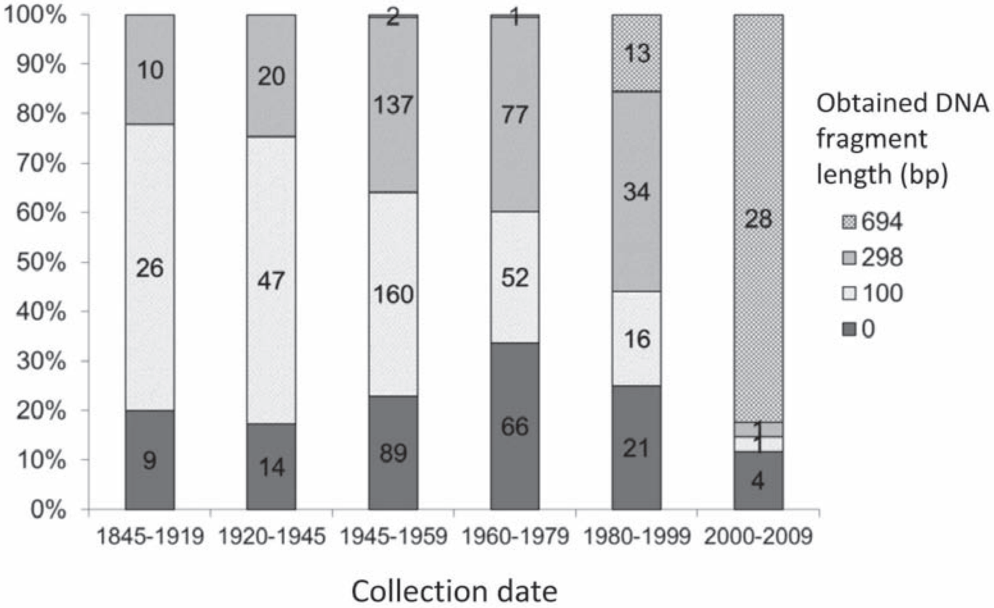

FIG. 2. Histogram showing the effect of the collection date on the success rate of obtaining different sizes of DNA sequences. Absolute numbers are given in the columns.

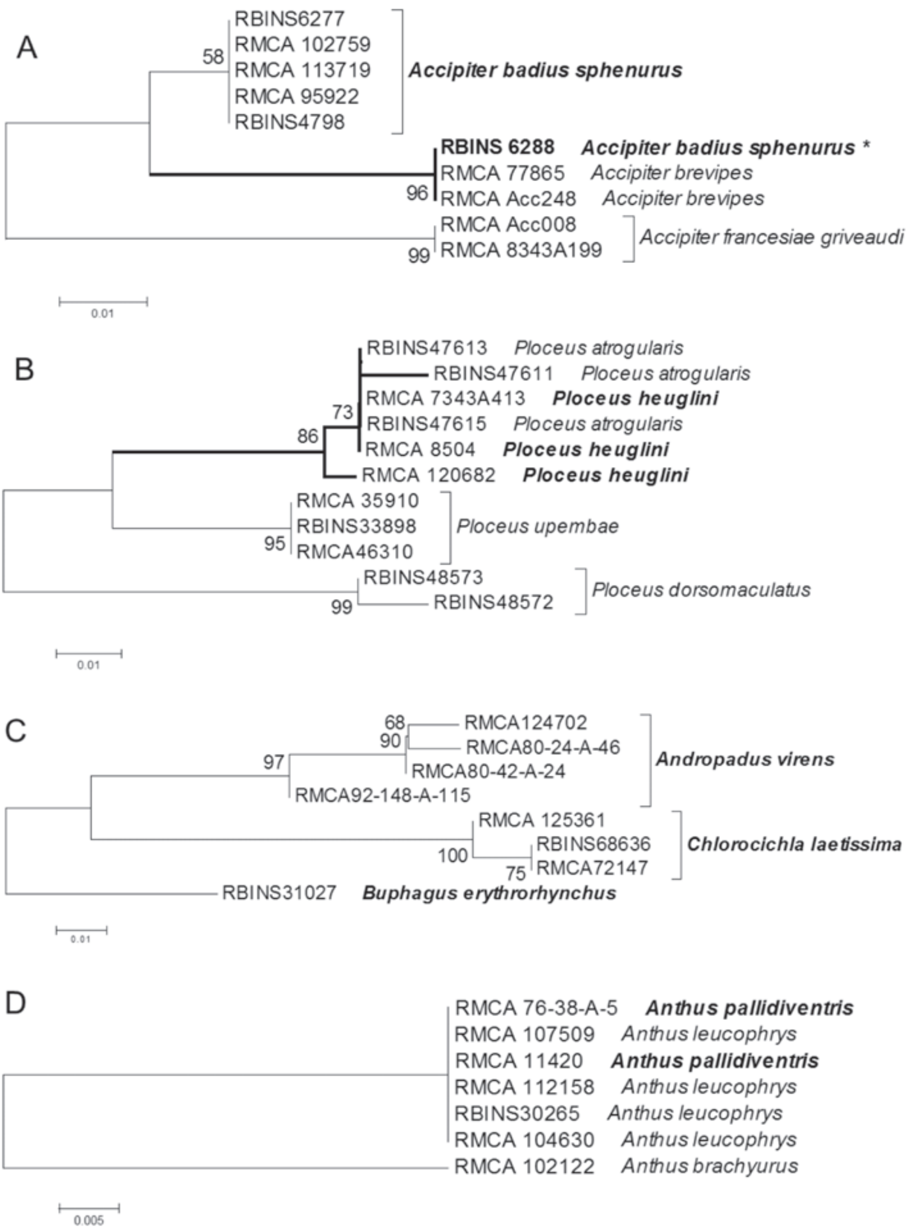

FIG. 3. Neighbor-joining trees constructed with K2P genetic distances of a selection of DNA (mini-) barcodes. A. Mislabeling: specimen No. RBINS 6288 was labeled years ago as *Accipiter badius sphenurus* but its COI fragment is similar to those of specimens identified as *Accipiter brevipes*; identification was corrected after close inspection showed the skin was indeed referable to *Accipiter brevipes*. B. Synonymy: specimens labeled as *Ploceus atrogularis* and *P. heuglini* have COI sequences that cluster together in one clade. It appears that different synonymic species names were applied in the different collections. C. Intraspecific variation in 100 bp sequences from specimens identified as *Andropadus virens* and *Chlorocichla laetissima*. D. Sequences from specimens identified as *Anthus pallidiventris* and *Anthus leucophrys* cluster together in one clade.

the overall success rate of obtaining a sequence varies from 66% to 88%, the proportion of short fragments (100 bp) versus middle-sized fragments (298 bp) increases with the age of the voucher specimens. It is important to point out that we detected no frameshifts or stop codons, which might have indicated the presence of nuclear mitochondrial DNA (numt). Double peaks were found at a rate of 10^{-4} per base pair, i.e. three times less than the $3x10^{-4}$ per bp found by Sefc *et al.* (2007).

We assembled a data set of 621 sequences that had a minimum overlay of 100 bp with the standard (Folmer *et al.* 1994) and the universal mini-barcode (Meusnier *et al.* 2008). Based on initial morphological identifications, they represent 177 species (i.e. 79% of the selection) belonging to 69 genera (i.e. 82% of the selection) (Table 1). On average, we obtained 2.9 sequences per species (range: 0-34). Sixty-four species belonging to the genera *Accipiter* and *Ploceus* were sampled more intensively. In contrast, 62 species (28% of the selection) are represented by a single sequence and cannot therefore be validated by conspecific sequences.

DNA barcoding. Two neighbor-joining trees based on pairwise K2P distances between all 621 sequences were done with complete and pairwise deletion. Both trees distinguish clusters of similar sequences that allowed the correct taxonomic assignment of the unreliably identified specimens. In a few cases, misidentifications (e.g. by mislabeling) were revealed (Fig. 3A.). In contrast, some cases of unexpectedly low genetic divergences between specimens with different species names agree with their taxonomic status as synonyms (Fig. 3B.). On the genus level, our sequences allow the correct allocation of 65 of the 69 genera for which a sequence is available. Nevertheless, we have to consider that the resolution of the resulting tree depends on the taxonomic groups and the fragment length considered. Based on the 100 bp sequences, genera *Phodilus* and Pseudochelidon (represented in our sampling by species *Phodilus prigoginei* and *Pseudochelidon eurystomina*) cannot be distinguished like in the case of *Malimbus* and *Ploceus*. On the species level, sequences of 122 morphologically identified species cluster unambiguously in the neighbor-joining tree. Even intraspecific variability is visible in the 100 bp sequences of some species (e.g. Fig. 3C.). The other 55 species are lumped together with sequences of other species (e.g. Fig. 3D.). Therefore, species identification based on the obtained DNA barcodes of our bird collections appears to be only accurate in 69% of the cases. However, most species with an ambiguous DNA barcode belong to the genera *Ploceus* (Ploceidae), *Anthus* (Motacillidae), and *Indicator* (Indicatoridae), taxonomically the most complex groups in our data set. The proportion of species identified morphologically that can unambiguously be distinguished by the DNA barcodes is very variable among genera, ranging from 50% for the genus *Ploceus* to 100% (e.g. for the genus *Ardeola*). Here we emphasize that identifications of voucher specimens are reliable and this imprecision is thus most probably due to the restricted set of characters present in the sequences obtained.

DISCUSSION

This DNA barcoding approach showed that short DNA sequences can be obtained at a reasonable rate of success. For our collections, the amplification of the middle-sized fragment appears to be an adequate approach for specimens collected in the past 50 years. It is short enough to get a satisfactory success rate (> 45%) and still allows more information to be obtained than from the short fragment. For specimens older than 50 years we recommend targeting the short fragment for a better success rate (> 57%). These results confirm that the minimalist barcode approach increases the overall success rate when sequencing degraded DNA from museum specimens (Hajibabaei *et al.* 2006, Meusnier *et al.* 2008).

The success rates found here are based on two different collections and may depend on the tested species since, for example, the size of the tissue sample used for DNA extraction correlates with the size of the bird specimen. Therefore these rates may serve as an indication for other projects or collections but cannot replace an exploratory experiment on the collection under study. Because preservation methods and conservation conditions may vary considerably in the usage of fixative agent, the temperature and the humidity in the collection room or the different handlings made by researchers, etc., DNA quality can be significantly different even among samples of similar age (Wandeler *et al.* 2007).

In our study, standard protocols (i.e. DNA extraction kits, standardized PCR conditions) were used. The only alteration was the use of three different combinations of degenerated primers. This implies that further improvements of the procedure, such as a more efficient DNA extraction method (e.g.

phenol-chloroform) or manipulations at the PCR stage (e.g. amplifications with primers more specific to the group of interest, testing different polymerases, reamplifications of PCR products), will probably increase the success rate. Unfortunately, testing all possible improvements during this pilot study would have been too expensive and too time-consuming. Alternatively, the overlapping of short fragments allows the assembly of larger fragments. In addition, next-generation sequencing technologies that are able to read billions of short fragments per run (Metzker 2010) also offer excellent opportunities to work with degraded DNA. The results presented here are, from this point of view, promising for the utilization of bird specimens from museum collections as a source of historical genetic information.

The DNA barcodes produced are of great importance for the All Bird Barcoding Initiative since they concern birds from the Afrotropical region, a region where only 587 of an estimated total of 2384 species are considered to be barcoded (ABBI 2011). Nonetheless, we have to consider that the barcodes produced only give a partial indication of the intraspecific genetic variation of the species because the sampling covers only part of their entire geographic range. Ideally, the sampling has to take the evolutionary history of the species into account (Zhang *et al.* 2010). This precaution is all the more relevant since several studies have shown a high level of intraspecific diversity in African birds that are widely distributed in montane regions (Bowie *et al.* 2006, Kahindo *et al.* 2007) as well as in lowland rainforests (Marks 2010). For example, in our set of sequences we observed a single haplotype with the COI marker (298 bp) in three specimens of *Platysteira peltata* collected in two different localities in the Upemba National Park (DRC, Katanga) whereas Njabo *et al.* (2008) discovered a substantial haplotype diversity with marker ND2 (1041 bp) in this species with a broad geographic distribution. Substantial genetic divergences were also observed over a short distance as revealed by Voelker *et al.* (2010) with *Cossypha anomala* in tropical montane areas where a diversification of the Africa's forest avifauna seems to take place (Fjeldså & Bowie 2008). At this stage, it is premature to draw definitive conclusions on the species identification efficiency of the resulting DNA barcodes because the relatively large proportion of ambiguous DNA barcodes observed can be due to both DNA (mini-)barcoding and taxonomical artifacts. First, the limited size of the mini-barcodes may lack the information necessary to distinguish a large number of well-differentiated species (Hajibabaei *et al.* 2006, Wiemers & Fiedler 2007). This probably explains the lower percentage of species correctly delineated by the COI marker compared to studies using the standard barcode fragment (Aliabadian *et al.* 2009). Secondly, in some animal groups with numerous species and where morphology is less variable, taxonomic knowledge can overlook the presence of multiple taxa within a traditional species (overlumping). Alternatively, different morphotypes can inappropriately be recognized as individual species (oversplitting) (Funk & Omland 2003). However, in birds several studies have shown that even recently diverged sister species pairs have fixed nucleotide substitutions that can serve as diagnostic characters (Tavares & Baker 2008, Kerr *et al.* 2009). These hypotheses will have to be tested in every taxon where we observe discrepancies between DNA barcoding and morphology. There is no doubt that this first phase of DNA barcoding, even when done in a systematic manner, raises scientific questions that require a second phase of more detailed investigations in close collaboration with bird taxonomists.

In summary, the application of DNA barcoding to avian collections from the DRC provided (i) information on the DNA quality of the museum collection, as it is feasible to obtain fragments of 100-300 bp, (ii) new DNA barcodes for birds from the Afrotropics, where the estimated proportion of barcoded bird species is currently the lowest of all biogeographical regions (ABBI 2011), and (iii) species identification based on the DNA barcodes which contributed to the correction of the species assignment of some specimens in the collections and raised taxonomic questions that need to be addressed in close collaboration with taxonomists.

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APPENDIX

Species	Ns.	Nsq.	Accession numbers
Accipiter badius	24	12	JF312106 JF312127 JF312113 JF312120 JF312110 JF312111 JF312088 JF312119 JF312136 JF312105 JF312090 JF312159
Accipiter brevipes	4	4	JF312114 JF312152 JF312109 JF312192
Accipiter castanilius	4	1	JF312150
Accipiter erythropus	3	1	JF312092
Accipiter francesiae	46	34	JF312089 JF312196 JF312098 JF312179 JF312176 JF312175 JF312169 JF312099 JF312097 JF312104 JF312086 JF312163 JF312167 JF312168 JF312093 JF312094 JF312171 JF312162 JF312177 JF312164 JF312165 JF312166 JF312178 JF312174 JF312173 JF312172 JF312170 JF312096 JF312189 JF312100 JF312101 JF312102 JF312103 JF747507
Accipiter gentilis	2	2	JF312084 JF312195
Accipiter gularis	2	2	JF312215 JF312115
Accipiter madagascariensis	2	1	JF312117
Accipiter melanoleucus	4	3	JF312091 JF312187 JF312188
Accipiter minullus	11	10	JF312137 JF312147 JF312133 JF312123 JF312116 JF312158 JF312211 JF312212 JF312213 JF312207
Accipiter nisus	12	6	JF312087 JF312085 JF312161 JF312190 JF312191 JF312194
Accipiter ovampensis	2	1	JF312121
Accipiter rufiventris	3	1	JF312144
Accipiter soloensis	7	4	JF312185 JF312184 JF312181 JF312182
Accipiter tachiro	29	15	JF312143 JF312202 JF312214 JF312197 JF312210 JF312209 JF312198 JF312208 JF312205 JF312201 JF312204 JF312199 JF312200 JF312203 JF312142
Accipiter toussenelii	14	2	JF312129 JF312151
Accipiter virgatus	1	1	JF312186
Afropavo congensis	1	0	n.a.
Agapornis swindernianus	1	1	HQ997940
Alethe poliocephala	3	2	HQ997979 HQ998071
Anaplectes rubriceps	3	1	HQ998336
Andropadus virens	4	4	HQ998164 HQ998272 HQ998275 HQ998298
Anomalospiza imberbis	6	6	HQ998036 HQ998057 HQ998344 HQ998404 HQ998415 HQ998432
Anthus bocagei	3	0	n.a.
Anthus brachyurus	5	1	HQ998117
Anthus cinnamomeus	9	5	HQ998185 HQ998196 HQ998197 HQ998246 HQ998252
Anthus itombwensis	3	1	HQ998304
Anthus katangae	2	2	HQ998176 HQ998224
Anthus lacuum	3	2	HQ998203 HQ998206
Anthus latistriatus	3	2	HQ998287 HQ998303
Anthus leucophrys	17	4	HQ998004 HQ998122 HQ998135 HQ998143
Anthus lineiventris	4	1	HQ998008
Anthus pallidiventris	5	2	HQ998148 HQ998259
Anthus similis	14	2	HQ998145 HQ998175

Species	Ns.	Nsq.	Accession numbers
Anthus vaalensis	9	5	HQ998005 HQ998006 HQ998007 HQ998190 HQ998225
Apalis alticola	3	3	HQ997986 HQ997987 HQ997988
Apalis goslingi	2	2	HQ998120 HQ998124
Apalis kaboboensis	2	2	HQ998253 HQ998293
Apalis porphyriolaema	3	3	HQ998180 HQ998288 HQ998316
Apalis schoutedeni	1	0	n.a.
Apus caffer	1	1	HQ997974
Ardeola idae	6	5	HQ998184 HQ998202 HQ998219 HQ998226 HQ998227
Ardeola ralloides	12	9	HQ998156 HQ998186 HQ998192 HQ998194 HQ998204 HQ998215 HQ998234 HQ998277 HQ998294
Ardeola rufiventris	3	1	HQ998317
Batis erlangeri	4	4	HQ998150 HQ998267 HQ998302 HQ998305
Batis minor	1	1	HQ998315
Batis molitor	3	3	HQ997992 HQ997993 HQ997994
Brachycope anomala	3	2	HQ998357 HQ998424
Bradypterus cinnamomeus	3	2	HQ997984 HQ997985
Bubulcus ibis	5	1	HQ998116
Buphagus africanus	1	1	HQ998050
Buphagus erythrorhynchus	2	1	HQ998012
Butastur rufipennis	2	1	HQ998257
Buteo buteo	1	0	n.a.
Butorides striatus	2	1	HQ998236
Caprimulgus prigoginei	1	1	HQ998268
Centropus monachus	7	7	HQ997943 HQ997944 HQ997945 HQ997946 HQ997947 HQ997948 HQ997949
Chlorocichla laetissima	4	4	HQ998101 HQ998167 HQ998230 HQ998242
Chlorocichla prigoginei	3	3	HQ998159 HQ998254 HQ998292
Circus aeruginosus	1	0	n.a.
Circus cyaneus	1	0	n.a.
Coracina azurea	2	0	n.a.
Coracina caesia	3	1	HQ998239
Coracina graueri	5	2	HQ997972 HQ997973
Coracina pectoralis	2	2	HQ998130 HQ998220
Cossypha bocagei	3	3	HQ997976 HQ997977 HQ997978
Cuculus canorus	2	2	HQ997941 HQ997942
Dendropicos goertae	5	4	HQ998201 HQ998269 HQ998279 HQ998282
Dendropicos griseocephalus	3	3	HQ998245 HQ998263 HQ998281
Dendropicos sp.	2	2	HQ998136 HQ998189
Estrilda astrild	10	0	n.a.
Estrilda atricapilla	4	4	HQ998333 HQ998335 HQ998407 HQ998411
Estrilda nigriloris	1	1	HQ998013
Euplectes hartlaubi	3	2	HQ998332 HQ998361
Foudia eminentissima	1	0	n.a.

Species	Ns.	Nsq.	Accession numbers
Francolinus afer	14	9	HQ997925 HQ997928 HQ998372 HQ998376 HQ998391 HQ998403 HQ998405 HQ998414 HQ998419
Francolinus albogularis	5	3	HQ997930 HQ997931 HQ997932
Francolinus camerunensis	3	3	HQ998367 HQ998378 HQ998418
Francolinus coqui	6	5	HQ997929 HQ998350 HQ998366 HQ998369 HQ998394
Francolinus kasaicus	2	0	n.a.
Francolinus lathami	7	3	HQ998088 HQ998089 HQ998417
Francolinus levaillantii	6	3	HQ997933 HQ997934 HQ998321
Francolinus nahani	3	2	HQ998326 HQ998380
Francolinus nobilis	1	1	HQ998110
Francolinus ruandae	2	2	HQ998389 HQ998390
Francolinus shelleyi	1	1	HQ997926
Francolinus sp.	1	1	HQ998371
Francolinus squamatus	17	15	HQ997935 HQ997936 HQ997937 HQ998330 HQ998341 HQ998353 HQ998362 HQ998368 HQ998382 HQ998383 HQ998397 HQ998412 HQ998416 HQ998420 HQ998425
Glaucidium albertinum	2	2	HQ998216 HQ998223
Glaucidium capense	2	0	n.a.
Graueria vittata	2	2	HQ998163 HQ998248
Guttera plumifera	1	1	HQ998082
Gymnobucco bonapartei	3	0	n.a.
Gymnobucco calvus	2	0	n.a.
Gymnobucco peli	1	0	n.a.
Gymnobucco sladeni	3	1	HQ998138
Hemitesia neumanni	4	2	HQ998160 HQ998238
Indicator conirostris	4	0	n.a.
Indicator exilis	8	3	HQ997961 HQ997962 HQ997963
Indicator indicator	9	5	HQ997953 HQ997954 HQ997955 HQ998153 HQ998232
Indicator maculatus	8	5	HQ998074 HQ998093 HQ998262 HQ998271 HQ998280
Indicator meliphilus	2	2	HQ998237 HQ998313
Indicator minor	9	3	HQ997964 HQ997965 HQ997966
Indicator pumilio	3	0	n.a.
Indicator sp.	4	4	HQ997960 HQ998076 HQ998083 HQ998105
Indicator variegatus	7	5	HQ997950 HQ997951 HQ997952 HQ998152 HQ998243
Indicator willcocksi	4	4	HQ998077 HQ998133 HQ998284 HQ998309
Ixobrychus minutus	2	2	HQ997927 HQ998081
Ixobrychus sturmii	2	1	HQ997924
Kaupifalco monogrammicus	1	0	n.a.
Laniarius barbarus	2	0	n.a.
Linurgus olivaceus	3	0	n.a.
Lioptilus chapini	4	4	HQ998115 HQ998139 HQ998151 HQ998205
Lioptilus rufocinctus	2	1	HQ998212
Lybius minor	3	3	HQ997969 HQ997970 HQ997971
Malimbus cassini	2	2	HQ998324 HQ998428

Species	Ns.	Nsq.	Accession numbers
Malimbus coronatus	2	2	HQ998334 HQ998355
Malimbus nitens	2	2	HQ998346 HQ998406
Malimbus rubricollis	3	3	HQ998123 HQ998137 HQ998142
Melaenornis ardesiaca	3	3	HQ998161 HQ998162 HQ998240
Melichneutes robustus	2	2	HQ998241 HQ998286
Melignomon eisentrauti	1	1	HQ998274
Melignomon zenkeri	5	5	HQ998103 HQ998128 HQ998141 HQ998247 HQ998307
Micronisus gabar	2	1	HQ998233
Micronisus metabates	2	1	HQ998168
Muscicapa aquatica	6	6	HQ997998 HQ997999 HQ998000 HQ998001 HQ998002 HQ998003
Muscicapa lendu	3	3	HQ998118 HQ998289 HQ998290
Muscicapa olivascens	3	3	HQ998126 HQ998214 HQ998318
Nectarinia congensis	3	0	n.a.
Nectarinia humbloti	3	0	n.a.
Nectarinia rockefelleri	3	0	n.a.
Neolestes torquatus	3	3	HQ998140 HQ998266 HQ998306
Parmoptila woodhousi	5	5	HQ998327 HQ998331 HQ998381 HQ998413 HQ998441
Phedina brazzae	3	1	HQ998255
Phodilus prigoginei	1	1	HQ998210
Phyllastrephus lorenzi	3	3	HQ998127 HQ998198 HQ998273
Pitta angolensis	2	2	HQ998072 HQ998073
Platysteira peltata	3	3	HQ997995 HQ997996 HQ997997
Ploceus albinucha	6	3	HQ998199 HQ998209 HQ998228
Ploceus alienus	3	3	HQ998029 HQ998067 HQ998092
Ploceus angolensis	2	2	HQ998356 HQ998363
Ploceus atrogularis	3	3	HQ998054 HQ998055 HQ998056
Ploceus aurantius	15	10	HQ998276 HQ998283 HQ998300 HQ998365 HQ998399 HQ998408 HQ998409 HQ998410 HQ998422 HQ998427
Ploceus baglafecht	6	5	HQ998323 HQ998328 HQ998421 HQ998433 HQ998439
Ploceus bertrandi	1	1	HQ998049
Ploceus bicolor	6	6	HQ998026 HQ998027 HQ998063 HQ998109 HQ998339 HQ998398
Ploceus bojeri	1	1	HQ998440
Ploceus capensis	1	1	HQ998445
Ploceus castanops	5	4	HQ998046 HQ998170 HQ998181 HQ998312
Ploceus cucullatus	27	14	HQ998034 HQ998035 HQ998044 HQ998045 HQ998085 HQ998086 HQ998096 HQ998097 HQ998250 HQ998260 HQ998301 HQ998358 HQ998393 HQ998437
Ploceus dichrocephalus	2	2	HQ998435 HQ998436
Ploceus dorsomaculatus	2	2	HQ998065 HQ998066
Ploceus flavipes	4	4	HQ998069 HQ998213 HQ998320 HQ998377
Ploceus galbula	1	1	HQ998329
Ploceus grandis	1	1	HQ998360

Species	Ns.	Nsq.	Accession numbers
Ploceus heuglini	3	3	HQ998158 HQ998235 HQ998285
Ploceus insignis	8	7	HQ998014 HQ998061 HQ998062 HQ998211 HQ998308 HQ998348 HQ998396
Ploceus intermedius	4	4	HQ998166 HQ998311 HQ998351 HQ998446
Ploceus jacksoni	4	4	HQ998178 HQ998179 HQ998182 HQ998193
Ploceus katangae	5	5	HQ998037 HQ998038 HQ998154 HQ998155 HQ998187
Ploceus luteola	4	4	HQ998125 HQ998157 HQ998183 HQ998310
Ploceus melanocephalus	10	10	HQ998030 HQ998031 HQ998047 HQ998095 HQ998325 HQ998338 HQ998347 HQ998401 HQ998426 HQ998431
Ploceus melanogaster	5	5	HQ998087 HQ998104 HQ998108 HQ998111 HQ998112
Ploceus nelicourvi	1	1	HQ998039 HQ998040
Ploceus nigerrimus	4	4	HQ998251 HQ998256 HQ998261 HQ998113
Ploceus nigricollis	14	8	HQ998099 HQ998173 HQ998258 HQ998384 HQ998385 HQ998386 HQ998387 HQ998388
Ploceus ocularis	3	3	HQ998098 HQ998342 HQ998395
Ploceus pelzelni	6	5	HQ998028 HQ998059 HQ998340 HQ998364 HQ998430
Ploceus philippinus	1	1	HQ998114
Ploceus preussi	2	2	HQ998064 HQ998429
Ploceus rubiginosus	4	3	HQ998373 HQ998375 HQ998438
Ploceus ruweti	3	2	HQ998144 HQ998447
Ploceus sanctithomae	1	1	HQ998359
Ploceus sp.	4	4	HQ998129 HQ998174 HQ998177 HQ998392
Ploceus spekei	2	2	HQ998349 HQ998434
Ploceus spekeoides	1	1	HQ998379
Ploceus subpersonatus	1	1	HQ998370
Ploceus superciliosus	9	1	HQ998132
Ploceus taeniopterus	6	6	HQ998051 HQ998052 HQ998053 HQ998208 HQ998295 HQ998402
Ploceus tricolor	6	5	HQ998024 HQ998025 HQ998070 HQ998337 HQ998423
Ploceus upembae	3	2	HQ998191 HQ998374
Ploceus velatus	13	12	HQ998032 HQ998043 HQ998149 HQ998171 HQ998172 HQ998188 HQ998207 HQ998249 HQ998343 HQ998442 HQ998443 HQ998444
Ploceus vitellinus	7	7	HQ998041 HQ998042 HQ998078 HQ998079 HQ998080 HQ998169 HQ998195
Ploceus weynsi	3	2	HQ998319 HQ998322
Ploceus xanthops	4	4	HQ998033 HQ998075 HQ998345 HQ998400
Podica senegalensis	1	1	HQ998023
Prionops alberti	1	0	n.a.
Prionops plumata	2	2	HQ998009 HQ998010
Prionops poliocephala	1	1	HQ998011
Prodotiscus insignis	6	5	HQ997956 HQ998119 HQ998217 HQ998291 HQ998314
Prodotiscus regulus	8	7	HQ997957 HQ997958 HQ997959 HQ998131 HQ998147 HQ998231 HQ998264
Prodotiscus zambesiae	4	3	HQ998121 HQ998146 HQ998200

Species	Ns.	Nsq.	Accession numbers
Pseudoalcippe abyssiscicus	3	3	HQ997981 HQ997982 HQ997983
Pseudocalyptomena graueri	2	1	HQ998244
Pseudochelidon eurystomina	3	1	HQ998297
Pteronetta hartlaubii	1	0	n.a.
Pyrenestes ostrinus	3	2	HQ998021 HQ998022
Quelea cardinalis	2	0	n.a.
Quelea erythrops	1	0	n.a.
Quelea quelea	9	6	HQ998019 HQ998020 HQ998068 HQ998102 HQ998352 HQ998354
Quelea sp.	2	2	HQ998084 HQ998094
Riparia congica	2	1	HQ998218
Riparia paludicola	1	0	n.a.
Sagittarius serpentarius	1	0	n.a.
Salpornis spilonotus	2	2	HQ997975 HQ998058
Sarothrura rufa	2	2	HQ997938 HQ997939
Sasia africana	1	1	HQ998100
Schoutedenapus myoptilus	3	0	n.a.
Schoutedenapus schoutedeni	2	0	n.a.
Scopus umbretta	1	0	n.a.
Seicercus laurae	3	3	HQ997989 HQ997990 HQ997991
Smithornis capensis	2	2	HQ997980 HQ998091
Smithornis rufolateralis	1	1	HQ998107
Smithornis sharpei	1	1	HQ998106
Stactolaema anchietae	3	2	HQ997967 HQ997968
Terpsiphone batesi	4	2	HQ998134 HQ998296
Terpsiphone bedfordi	3	3	HQ998229 HQ998265 HQ998270
Terpsiphone mutata	1	0	n.a.
Terpsiphone rufocinerea	2	1	HQ998299
Terpsiphone viridis	3	2	HQ998221 HQ998278
Trochocercus nitens	2	0	n.a.
Turtur brehmeri	1	1	HQ998090
Uraeginthus angolensis	3	2	HQ998015 HQ998017
Uraeginthus bengalus	3	3	HQ998016 HQ998018 HQ998060
Urotriorchis macrourus	1	0	n.a.
Zoothera graueri	1	0	n.a.
Zoothera guttata	1	0	n.a.
Zoothera oberlaenderi	2	1	HQ998165
Zoothera piaggiae	2	0	n.a.
Zosterops maderaspatana	3	0	n.a.

APPENDIX. List of all species under study. (Ns) Number of sampled specimens. (Nsq) Number of sequences with minimum 99 bp overlap with the universal mini-barcode. Highlighted species names may differ from one reference to another.

FRANCES'S SPARROWHAWK *ACCIPITER FRANCESIAE* (AVES: ACCIPITRIDAE) RADIATION ON THE COMORO ISLANDS

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ABSTRACT

The nominate subspecies of Frances's Sparrowhawk *Accipiter francesiae* lives on Madagascar, while three of the Comoro Islands have distinct subspecies. Morphological variation among these four populations is peculiar: whereas on Madagascar a sexual difference in color pattern occurs, plumage differences are small in the Comoros populations, with masculine females (on Grand Comoro, Anjouan) and feminine males (on Mayotte), and there is also a juvenal plumage (*sensu* Palmer 1972) on Mayotte which does not exist in any other population. The Comoran endemics also show important differences between islands in density and habitat preference. DNA sequence analysis of the mitochondrial cytochrome oxidase 1 gene shows that they are characterized by closely related but distinct mitochondrial haplotypes. Furthermore, the phylogeographic pattern indicates that these islands were colonized in the same historical timeframe. We cannot date this event as yet, although considering the age of the archipelago (*ca.* 3.9 Myr) it must have been relatively recent. The discrepancy between molecular and ecological results indicates rapid, divergent morphological and ecological evolution of the insular populations.

Key words: Madagascar, Comoros, cytochrome oxidase 1, Aves, Accipiter*, phylogeography.*

INTRODUCTION

The Comoro Islands are situated on a NW-SE axis between the African continent and Madagascar. The archipelago consists of four large volcanic islands (Grand Comoro, Moheli, Anjouan, and Mayotte: see geographical position on Fig. 1), and was never connected to any of the two neighboring old land masses. Volcanic activity is still ongoing after a complex history (Emerick & Duncan 1982). Grand Comoro is dated at 0.5 Myr BP (Nougier *et al.* 1986). This date corresponds to the oldest age that would allow the colonization by birds (Pasquet *et al.* 2007) but the three other islands are *ca.* 3.9 Myr old (Nougier *et al.* 1986). However, island-hopping and local extinctions could have occurred more recently. The present-day avifauna of the Comoros comprises 59 breeding species and approximately 49 species of migrants and vagrants; 17 species are endemic and another 19 breeding species are shared with Madagascar (and are absent from the African continent) (Louette *et al.* 2008).

One case of the latter category is Frances's Sparrowhawk *Accipiter francesiae* (for the nomenclature we follow BirdLife International 2009), a mainly reptile-eating raptor, the nominate subspecies of which lives throughout Madagascar. It also occurs on three of the four Comoro Islands (it is absent from Moheli), where it is the only representative of the raptor genus *Accipiter*. It is clear from morphological and ecological differences that populations are resident and isolated. Based on their morphology, the populations on each of these islands are thus considered as different subspecies (Benson 1960, Louette

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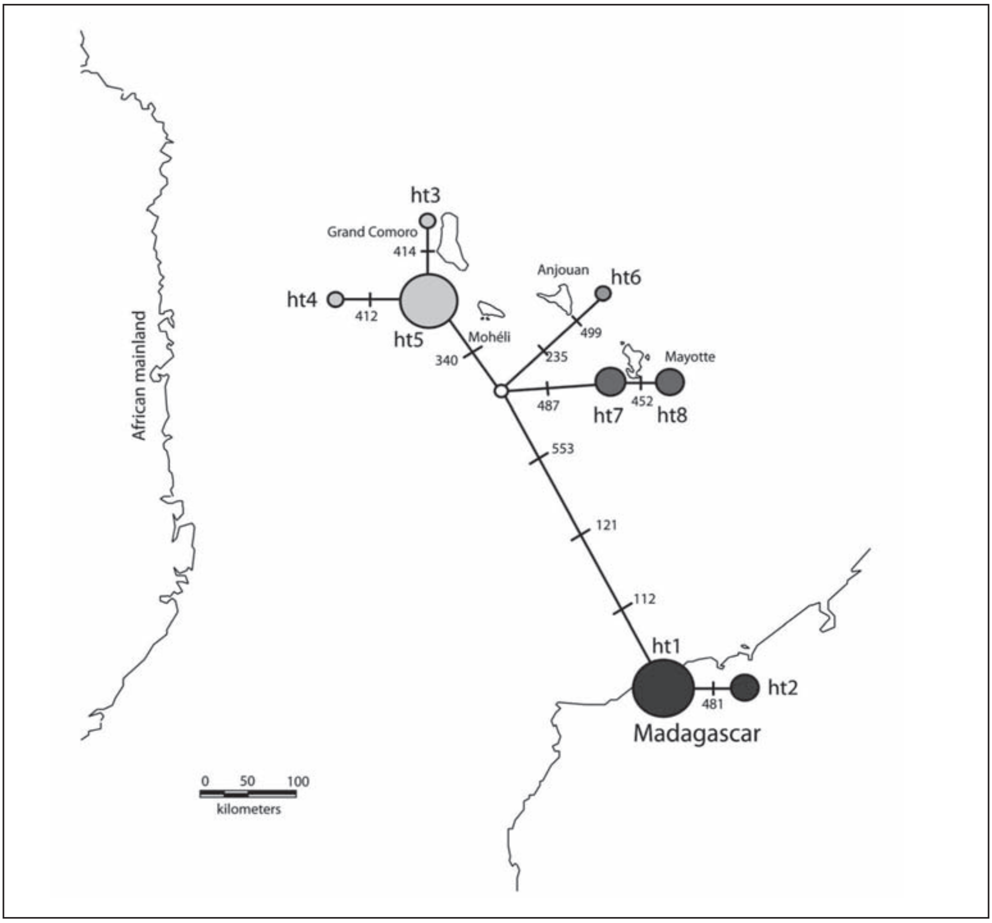

FIG. 1: Median-joining network of the eight haplotypes (h1-h8) of *Accipiter francesiae* superimposed on a map of the Comoros and Madagascar. Circles (i.e. haplotypes) do not represent geographical sampling coordinates (see Table 1 for the coordinates). Numbers indicate nucleotide substitution positions and perpendicular lines indicate one nucleotide substitution in the COI sequence. The open circle represents a hypothetical ancestor for the Comoran subspecies.

1988, Ferguson-Lees & Christie 2001). It is assumed that the three Comoran taxa are derived from Madagascar stock (Louette 2004). Sexes on Madagascar (*A. f. francesiae* Smith, 1834) have well-differentiated plumages. Adult males are dark gray above with a paler head, the underside is white and thinly barred rufous to gray-brown on breast and upper flanks. Adult females are larger and browner above than males, with broader and much more profuse barring below. Juveniles resemble the female but are a richer and more rufous-brown above, and have broader and browner bars below. The sexual dimorphism in plumage pattern is much less pronounced in the three Comoran subspecies, which are also slightly smaller than *A. f. francesiae* (del Hoyo *et al.* 1994, Herremans *et al.* 2001, unpublished data from ML: material at NHM, Tring, UK). On Grand Comoro (*A. f. griveaudi* Benson, 1960) and Anjouan [*A. f. pusillus* (Gurney, 1875)], *A. francesiae* is morphologically similar to male *A. f. francesiae*, in both sexes. The subspecies from Grand Comoro has a salmon flush on the breast. In the subspecies from

Anjouan the contrast of black and white plumage is particularly strong (Benson 1960, Ferguson-Lees & Christie 2001). On Mayotte, in *A. f. brutus* (Schlegel, 1866), both sexes resemble the female of the Malagasy subspecies in having brown upperparts and in being heavily barred brown underneath (Ferguson-Lees & Christie 2001, Herremans *et al.* 2001). *A. f. brutus* has a juvenal plumage which does not exist in any other population (Herremans *et al.* 2001, Herremans *et al.* 2011). Compared to the nominate form from Madagascar, *A. f. brutus* on Mayotte is thus partially neotenic (Herremans 1990). A relationship between neotenic evolution (reflected for example in plumages) and reduced territoriality and increased densities has been shown on the Comoros as one of the "insular syndromes" shared by several bird species (Louette *et al.* 1993).

The foot apparatus of a mainly reptile-eating *Accipiter* species has the peculiarity of a short middle toe (Wattel 1973). The Comoro birds differ in having a somewhat longer middle toe which is, relative to tarsus length, in *A. f. griveaudi* males 0.48, females 0.54; in *A. f. brutus* males 0.51, females 0.49; in *A. f. pusillus* males 0.54, females 0.55, compared with *A. f. francesiae* on Madagascar: males 0.43, females 0.44 (calculated from Rene de Roland & Thorstrom 2003, Herremans *et al.* 2011, and new calculations from measurements in the NHM by ML). These figures are still very much within the "normal" values for reptile-eaters (Herremans *et al.* 2011).

Bill length has also changed somewhat after the colonization process. Bill length (to cere) relative to wing length is in *A. f. griveaudi* males 0.090, females 0.090; in *A. f. brutus* males 0.089, females 0.091; in *A. f. pusillus* males 0.092, females 0.094 (calculated from Herremans *et al.* 2011, and new calculation from measurements in NHM by ML), compared with *A. f. francesiae* on Madagascar: males 0.085, females 0.088 (calculated from Rene de Roland & Thorstrom 2003). A long bill is a specialization for forest habitat, according to Wattel (1973).

Apart from the morphological differences, these subspecies also show remarkable differences with respect to habitat preference and population densities. The Malagasy race occurs "fairly commonly in various original forest types and degraded woodlands… from sea level to 2000 m" (Langrand 1990). On Mayotte, *A. francesiae brutus* prefers degraded habitats and attains record breeding densities in the agricultural landscapes of the western part of the main island at moderate altitudes (Herremans *et al.* 2001), whereas on Grand Comoro *griveaudi* is curiously restricted to the rainforest belt on the flanks of Mount Karthala and the immediate adjacent zones with lush vegetation, being absent from the northern volcano, La Grille (Louette *et al.* 2008). On Anjouan, due to the heavy degradation of the original vegetation, it is difficult to say which habitat is preferred, but all recent observations are from the central part of the island (Louette *et al.* 2008).

The species is the most common *Accipiter* on Madagascar (Langrand 1990, Rene de Roland & Thorstrom 2003) occurring throughout this large island, but is rarer in the xeric south. Whereas the subspecies *brutus* is numerous on Mayotte, with an estimated number of 7225-10 960 breeding pairs on less than 350 km² (Herremans *et al.* 2001), the subspecies *griveaudi* is restricted to an area of *ca.* 400 km² on Grand Comoro. Although still "relatively common" it reaches only ca. 10% of the density shown by *brutus* in prime habitat on Mayotte (Herremans *et al.* 2001, Louette *et al.* 2008). The subspecies *pusillus* on Anjouan is "rare" in an area of *ca.* 200 km²; at one time it was even thought that this subspecies was close to extinction, but there are signs of recent recovery (Louette *et al.* 2008). It is possible that these differences in numbers between the islands are due to differences in the level of human persecution between the islands and not necessarily to intrinsic differences between the taxa. We do know that the species commonly uses exotic trees in open positions for nest building on Mayotte; in contrast, on Grand Comoro the only two nests ever found were built in closed forest at moderate altitude, and no nest has ever been found on Anjouan, which no doubt indicates that all nests are built in closed forest on those two islands (Herremans *et al.* 2001).

Here, we study the phylogenetic relationships between the different subspecies of *A. francesiae*, using the mitochondrial cytochrome oxidase 1 gene (COI) to elucidate their colonization history. In order to have a clue to the relationship with close relatives, we include in our analysis two other reptile-eating *Accipiter*, the Levant Sparrowhawk *A. brevipes* and the Chinese Sparrowhawk *A. soloensis*. Both breed in the Palearctic Region and are strongly migratory to Africa and Asia respectively (Ferguson-Lees & Christie 2001). The two other *Accipiter* species occurring in Madagascar, the Malagasy (Madagascar) Sparrowhawk *A. madagascariensis* and Malagasy (Henst's) Goshawk *A. henstii*, belong to other *Accipiter* clades (Wink & Sauer-Gürth 2004, JEMU unpublished).

MATERIAL AND METHODS

Collection and selection of samples for the molecular study (see Table 1).

During our ecological study of birds, blood samples of *A. francesiae* were obtained on Madagascar by L-AR, on Grand Comoro by MH, and on Mayotte by ML and MH. Feather samples were obtained on Mayotte by ML. Fresh tissue samples from Anjouan were not obtained because the subspecies is very rare. Toe pads were sampled for all races from specimens stored in the RMCA and RBINS collections. For the tissue material obtained from the two related *Accipiter* species, see the Acknowledgments section.

Laboratory methods

Total genomic DNA was extracted from the toe pads of museum specimens, and from blood samples or feather shafts of living specimens, using the NucleoSpin Tissue Kit (Macherey-Nagel, Germany) following the manufacturer's protocol. Overlapping fragments of approximately 100, 300, or 700 bp length of the COI gene were PCR-amplified. PCR was carried out using a TProfessional thermocycler (Biometra) in a reaction volume of 30 µl, containing 2 µl of genomic DNA , 3µl of 10X PCR buffer, 0.2 mM dNTPs, 0.8 µM of each primer, 2.0 mM MgCl$_2$, 0.5 U of Platinum Taq DNA polymerase (Invitrogen) and mQ-H$_2$O. The PCR profile was: 4 min at 94°C followed by 35 cycles of 30 s at 94°C, 30 s at 50°C and 45 s at 72°C; with a final extension of 7 min at 72°C. Museum samples that failed in a first PCR attempt were redone with 4µl of DNA added to the reaction mix and with 40 PCR cycles. In order to avoid contamination, aerosol barrier tips and different rooms for pre- and post-PCR steps were used. All PCR products were visualized with the E-Gel Electrophoresis System (Invitrogen). PCR products were purified using the NucleoFast 96 PCR Plate kit (Macherey-Nagel, Germany) and sequenced using the BigDye Terminator v1.1 chemistry on an ABI 3130xl automated capillary DNA sequencer (Applied Biosystems). Sequences were checked, assembled, and aligned in SeqScape v2.5 (Applied Biosystems).

Whenever possible we used the BirdF1d and BirdR1d degenerated primers modified after Hebert *et al.* (2004) and Lohman *et al.* (2008) for the standard DNA barcode region (694 bp in birds) (Table 2). For museum specimens, we used BirdF1d and BirdH351d to amplify a 298 bp DNA fragment corresponding to the first half of the standard DNA barcode, and BirdF1d and BirdH153d to amplify a 100 bp DNA fragment representing the first part of the standard DNA barcode (Table 2). This "mini-barcode" region corresponds to the first 100 bp of the universal DNA mini-barcode (128 bp) proposed by Meusnier *et al.* (2008). For the second half of the DNA barcode we used the primers L288_310dt or L501_523dt with BirdR1dt amplifying a 434bp and 224 bp fragment with the same PCR protocol as for the other primer combinations.

TABLE 1. Samples of *Accipiter francesiae* and both outgroups used in this study with geographical coordinates. Geographical coordinates marked with an asterix are estimated from locality names on collection labels. #: partial sequence obtained, sample not used in the analyses; ##: migratory bird, no information on source or destination population.

(Sub)species	Country/island	Haplo-type	GenBank accession number	Geographical coordinates	Tissue used
A. f. francesiae					
RBINS35415	Madagascar	ht1	JF312086	18°55'S_47°33'E*	toepad
RBINS35416	Madagascar	ht1	JF312104	18°55'S_47°33'E*	toepad
RMCAA90380001	Madagascar	ht1	JF792344	14°19'42"S_48°34'54"E	blood
RMCAA90380002	Madagascar	ht1	JF792345	15°28'42"S_48°28'00"E	blood
RMCAA90380003	Madagascar	ht1	JF792346	15°28'42"S_48°28'00"E	blood
RMCAA90380004	Madagascar	ht1	JF792347	15°59'00"S_47°56'18"E	blood
RMCAA90380005	Madagascar	ht2	JF792348	15°37'48"S_49°58'30"E	blood
RMCAA90380006	Madagascar	ht1	JF792349	18°15'06"S_49°17'54"E	blood
RMCAA90380007	Madagascar	ht1	JF792350	18°13'24"S_49°18'48"E	blood

(Sub)species	Country/island	Haplotype	GenBank accession number	Geographical coordinates	Tissue used
A. f. brutus					
RMCAA8_17_A_1	Mayotte (Comoros)	ht7	JF312162	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_2	Mayotte (Comoros)	ht7	JF312172	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_3	Mayotte (Comoros)	ht7	JF312174	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_5	Mayotte (Comoros)	ht7	JF312175	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_6	Mayotte (Comoros)	#	JF312176	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_7	Mayotte (Comoros)	ht8	JF312177	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_8	Mayotte (Comoros)	ht7	JF312178	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_9	Mayotte (Comoros)	ht7	JF312179	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_10	Mayotte (Comoros)	ht8	JF312163	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_11	Mayotte (Comoros)	ht7	JF312164	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_13	Mayotte (Comoros)	ht7	JF312165	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_14	Mayotte (Comoros)	ht7	JF312166	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_15	Mayotte (Comoros)	ht8	JF312167	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_16	Mayotte (Comoros)	ht8	JF312168	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_17	Mayotte (Comoros)	ht7	JF312169	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_18	Mayotte (Comoros)	ht7	JF312170	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_19	Mayotte (Comoros)	ht8	JF312171	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_20	Mayotte (Comoros)	ht7	JF312173	12°49'30"S_45°08'00"E	feather
A. f. griveaudi					
RMCA8343A199	Grand Comoro	ht5	JF312093	11°39'17"S_43°19'13"E*	toepad
RMCAAfran006	Grand Comoro	ht5	JF312100	11°48'S_43°16'E	blood
RMCAAfran007	Grand Comoro	ht5	JF312101	11°48'S_43°16'E	blood
RMCAAfran008	Grand Comoro	ht5	JF312102	11°48'S_43°16'E	blood
RMCAAfran009	Grand Comoro	ht5	JF312103	11°48'S_43°16'E	blood
RMCAAcc006	Grand Comoro	ht5	JF312096	11°48'S_43°16'E	blood
RMCAAcc007	Grand Comoro	ht5	JF312097	11°48'S_43°16'E	blood
RMCAAcc008	Grand Comoro	ht4	JF312098	11°48'S_43°16'E	blood
RMCAAcc010	Grand Comoro	ht3	JF312099	11°48'S_43°16'E	blood
RMCAAcc011	Grand Comoro	#	JF312189	11°48'S_43°16'E	blood
A. f. pusillus					
RMCA8343A358	Anjouan (Comoros)	ht6	JF312094	12°12'49"S_44°26'13"E*	toepad
LI1941/662	Anjouan (Comoros)	#	JF312095	12°12'49"S_44°26'13"E*	toepad
RBINS8867	Anjouan (Comoros)	#	JF312089	12°11'S_44°43'E	toepad
A. brevipes					
RMCAAcc235	Israel	##	JF312109	bird migrating	blood
A. soloensis					
RMCAA90081	South Korea		JF312181	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90082	South Korea		JF312182	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90083	South Korea		JF312183	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90084	South Korea		JF312184	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90085	South Korea		JF312185	37°26'42.37"N_127°16'34.39"E	feather

TABLE 2. Primer combinations used in this study.

Primer combination	Forward primer sequence	References forward primer	Reverse primer sequences	References reverse primer	Fragment length (bp)
BirdF1d+Bird_H153_175d	TCAACCAACCACAAAGAYATYGGYAC	modified from Hebert *et al.* 2004, Lohmann *et al.* 2008	ACGATTACRTTGTARATYTGRTC	This study	100
BirdF1d+Bird_H351_370d	TCAACCAACCACAAAGAYATYGGYAC	modified from Hebert *et al.* 2004, Lohmann *et al.* 2008	CCTGCTCCWGCTTCTAYDGT	This study	298
BirdF1d+birdR1dt	TGTAAAACGACGGCCAGTTCAACCAACCACAAAGAYATYGGYAC	modified from Hebert *et al.* 2004, Lohmann *et al.* 2008	CAGGAAACAGCTATGACACGTGGGAGATGATTCCGAAKCCKGG	modified from Hebert *et al.* 2004, Lohmann *et al.* 2008	694
Aves_L288_310dt+birdR1dt	TGTAAAACGACGGCCAGTCGCATAAAYAACATAAGCTTYTG	This study	CAGGAAACAGCTATGACACGTGGGAGATGATTCCGAAKCCKGG	modified from Hebert *et al.* 2004, Lohmann *et al.* 2008	424
Aves_L501_523dt+birdR1dt	TGTAAAACGACGGCCAGTACCGCCATCAACATAAAACCNCC	This study	CAGGAAACAGCTATGACACGTGGGAGATGATTCCGAAKCCKGG	modified from Hebert *et al.* 2004, Lohmann *et al.* 2008	224

For all samples, except RBINS 8867 (100 bp fragment only), we successfully sequenced at least the 298 bp fragment. Sequences are available in GenBank (see Table 1).

Phylogenetic inference and network analysis
Neighbor-Joining (NJ) analysis on K2P distances (Kimura 1980) and parsimony analysis were run using PAUP* v.4b10 (Swofford 2002). One thousand bootstrap replicates served for testing branch support. Maximum likelihood analysis was conducted in Garli v0.96 (Zwickl 2006), running two searches and with 200 bootstrap replicates. Nucleotide substitution models for parsimony and maximum likelihood analyses were selected in jModelTest (Posada 2008) applying the AIC(c) and BIC criteria. Two other reptile-eating raptors, *A. brevipes* (Acc 235) and *A. soloensis* (RMCA A90082, RMCA A90083, RMCA A90084, RMCA A90085), were used as outgroups; *A. soloensis* is the closest relative (unpublished data) of *A. francesiae* and *A. brevipes* is an African representative of the genus.

Because part of the material was old (> 20 years) the full (694 bp) barcode fragment could not be sequenced. Therefore the analyses were performed on a data set of the first 572 bp of the barcode fragment. A median-joining haplotype network was constructed using Network v4.5.1 (http://www.fluxus-engineering.com) with default settings (Bandelt *et al.* 1999).

RESULTS

Including both outgroups, the 572 bp fragment yielded 87 variable sites, of which 41 were parsimony informative. Within *A. francesiae* there were 14 variable sites, of which eight were parsimony informative. Eight haplotypes were found in *A. francesiae* which appeared to be monophyletic (Fig. 2). Within *A. francesiae* two groups were found, although one group only showed high bootstrap support for the NJ analysis. One group comprises the two haplotypes of *A. f. francesiae* from Madagascar, one of which is probably common (eight individuals) and widespread whereas the other haplotype was found in a single individual in our data set. The second group comprises the haplotypes from the Comoros. Two out of the three haplotypes of *A. f. griveaudi* were single individuals and six other specimens belonged to a third haplotype. Also two haplotypes were found in *A. f. brutus* (Table 1). Despite the limited number of sampling localities on both Grand Comoro and on Mayotte (their coordinates are given in Table 2), specimens with different haplotypes were found syntopically on both islands. For *A. f. pusillus* we could only successfully sequence the long fragment from a single individual (toe pads from other specimens yielded short fragments; Table 1). Even though the haplotypes of *A. f. brutus* and *A. f. griveaudi* grouped together, the nodes had low bootstrap support (i.e. between 60 and 70%) (Fig. 2). A median-

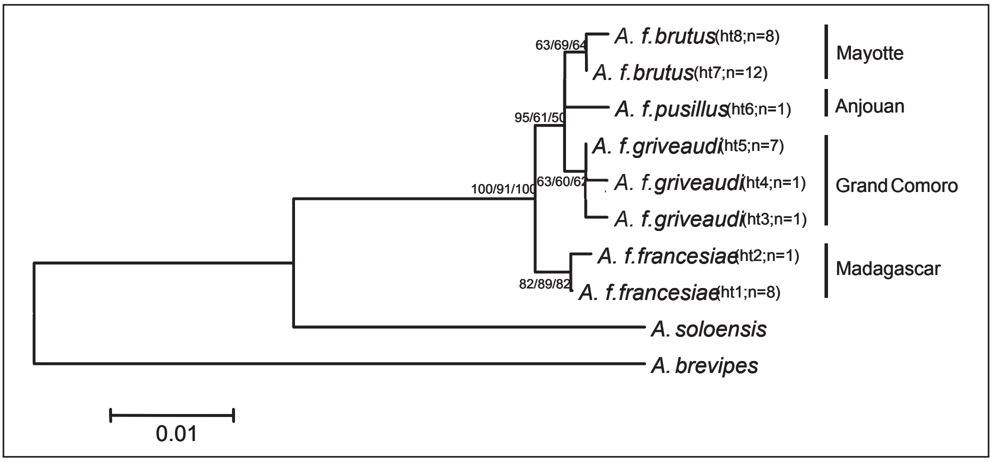

FIG. 2. Phylogenetic tree with indication of major lineages of eight COI haplotypes (ht1–ht8; n = number of individuals) of *Accipiter francesiae* and two outgroup taxa. Bootstrap values for node support are shown on the branches: neighbour-joining (1000 replicates) / maximum likelihood (200 replicates) / parsimony (1000 replicates). Bootstrap values ≥50% are shown. Branch lengths are according to the NJ tree.

joining haplotype network is presented in Fig. 1 and shows that all islands have different haplotypes of *A. francesiae*.

DISCUSSION

Our phylogeographic analysis based on the COI gene shows that *A. f. francesiae* from Madagascar appears well-differentiated from the other subspecies and that these other subspecies are less differentiated. Yet even though the genetic differences between the Comoran subspecies are very small, each subspecies corresponds to one or more unique mitochondrial haplotypes and none of the haplotypes is shared between subspecies. It may thus also be assumed that there is little, if any, exchange of individuals between different islands. Surprisingly, on the one hand, the two well-studied *A. francesiae* Comoro populations (Mayotte and Grand Comoro), resident on small oceanic islands, show some within-island molecular variation, notwithstanding rather small potential and actual (confirmed in the case of Grand Comoro) population sizes. On the other hand, we only found two haplotypes (h1: eight individuals; h2: one individual) in *A. f. francesiae* on Madagascar, despite the larger geographical sampling (Fig. 3).

Interestingly, in contrast to the limited molecular differentiation, the subspecies differ markedly in morphology. In birds, isolation on islands is known to lead to rapid changes in morphology when compared to their mainland source population (Burns *et al.* 2002, Mathys & Lockwood 2009). This finding could be due to different (or new/absent) selection pressures such as the absence of (or the presence of other) predators, competitors and pathogens, and/or the availability of new niches in the new habitat (Ricklefs & Birmingham 2007, Clegg *et al.* 2008), or it may be the result of founder effects due to limited genetic variability in (presumably small) founder populations.

Accipiter francesiae is listed in the category "least concern" according to the IUCN Red List (BirdLife International 2009). However it is current practice to also consider intraspecific variation in conservation strategies. Because the subspecies of *A. francesiae* i) are morphologically differentiated, ii) each consist of a number of unique mitochondrial haplotypes, and iii) appear strongly isolated from each other, they may each represent independent evolutionary units. In that case, conservation efforts should focus on each of the subspecies. This focus should apply to *A. f. pusillus* in particular, which is very rare. Extinction of this subspecies would result in a significant loss of intraspecific genetic variation (i.e. a unique mitochondrial haplotype and morphological variation) in this sparrowhawk.

The small genetic differences suggest a relatively recent colonization of the Comoros. Furthermore, the molecular pattern indicates that these islands were colonized within the same historical timeframe. It can tentatively be assumed that the colonization occurred from north Madagascar, which is a scenario that has been found in several terrestrial vertebrate taxa such as night-geckos (Jackman *et al.* 2008), day-geckos (Rocha *et al.* 2009), and frogs (Vences *et al.* 2003). Louette (2004), in an overview of colonization patterns for the birds of the Comoros, sug-

FIG. 3: Map of Madagascar. Black pins indicate sampling localities of individuals with haplotype 1 (ht1). Note that at some localities more than one individual was sampled; the white pin indicates the sampling locality of the individual with haplotype 2 (ht2). For the geographical sampling coordinates we refer to Table 1.

gested that birds evidently disperse more readily than geckos and frogs, as indicated by the number of bird taxa shared among the islands, although the direction of colonization has not been proven. The same holds for *A. francesiae*. For instance, there is a minimum of four mutational steps between *A. f. francesiae* (Madagascar) and *A. f. griveaudi* (Grand Comoro) or *A. f. brutus* (Mayotte), but the same number of mutational steps occurs between haplotypes from the Comoro subspecies. Nevertheless, the Comoran subspecies probably share a common ancestor (Fig. 1) that is younger than the common ancestor of the Malagasy and Comoran clades. However, the limited number of specimens for some of the subspecies, and the limited variation in the COI gene, do not allow speculation on the exact colonization route or divergence times, although the low variation suggests a recent split between the subspecies.

A large-scale molecular analysis of the genus *Accipiter* is currently ongoing. Preliminary results show that, in general, genetic divergences of mitochondrial gene markers among *Accipiter* species are small (Van Houdt *et al.* 2009, JEMU unpublished data) suggesting a rapid radiation within this genus. Nevertheless, the analysis will shed light on the relationship between *A. francesiae* and the other *Accipiter* species and provide information on the colonization of western Indian Ocean islands (e.g. Comoros and Madagascar) by this species. The western Indian Ocean islands have been considered as part of the African realm (see Newton 2003), but the fauna on these islands is in fact a mixture of both old African and Asian clades (Keith 1980, Louette 1996, Hawkins & Goodman 2003). This situation has been demonstrated in detail for the bulbul genus *Hypsipetes*, which is shared with, and derived from, Asia (Louette & Herremans 1985, Warren *et al.* 2005). However, this is not a general rule. Warren *et al.* (2003) concluded an African origin for the genus *Nectarinia*. For other genera, such as *Zosterops, Dicrurus*, and *Otus*, Warren *et al.* (2006), Pasquet *et al.* (2007), and Fuchs *et al.* (2008) respectively postulate complex dispersal histories from both continents. These authors even mention the possibility of an island being a source for the colonization of a continent. Bellemain & Ricklefs (2008) have discussed cases of continents being colonized from islands in other parts of the world. Although we do not consider this possibility likely in the *A. francesiae* Madagascar ("continent") - Comoros (island) case, we cannot refute it.

Interestingly, in our analyses of *Accipiter* data sets (containing the vast majority of the African representatives, JEMU unpublished), *A. soloensis* from Asia groups as the closest relative of *A. francesiae*. It is thus a possible scenario that the ancestor of *A. soloensis*, which occurs on migration in SE Asia (del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001), made an overshoot migration to Madagascar in the distant past and may have settled in the Madagascar area after loss of migratory behavior. This theory was hypothesized for some related buteonine hawks, in which a number of island colonizators turned sedentary (Raposo do Amaral *et al.* 2009). Another famous example among raptors is the Palearctic migrant Short-toed Eagle *Circaetus gallicus* that settled in Wallacea (White 1976).

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THE FETISH CULTURE IN WEST AFRICA: AN ANCIENT TRADITION AS A THREAT TO ENDANGERED BIRDLIFE?

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ABSTRACT

The persistent traditional use of bird fetishes for various purposes in some West African countries poses a considerable threat for certain bird species. In countries such as Nigeria or Benin there is still a strong demand for such items and high prices are realized for some species. This market is often served by trading over long distances. For some species this development has seriously aggravated the threat situation on a continental scale.

Key words: Fetish culture, bird conservation, West Africa.

INTRODUCTION

The traditional use of wildlife items for medicine is found in almost every country in West Africa. There are a few countries like Ghana and Guinea where such practices have become uncommon, but in countries such as Benin they still are a strong cultural tradition supported by the government. Such traditions can have severe consequences for wildlife where intensive land use, overpopulation, biofuel production, and other anthropogenic activities have already strongly modified the natural environment.

MATERIAL AND METHODS

This study, aimed at investigating the potential effect of fetish culture on endangered wildlife in West Africa, started in Nigeria in 1999 in collaboration with the Nigerian Conservation Foundation by monitoring several of the biggest fetish markets in the country. In addition, people were asked about the traditional use of different bird species in popular beliefs (for details on methods and results, see Nikolaus 2001). Additional surveys were undertaken in 2001 (Nigeria), 2002 (Ghana, Togo, Benin, Niger, Burkina Faso, Ivory Coast), 2003 and 2005 (Morocco), 2007 (Mali, Burkina Faso, Benin), 2008 (Nigeria, Benin, Republic of the Congo [Brazzaville], Democratic Republic of the Congo [Kinshasa]), and in 2009 (Burkina Faso, Benin). Guinea (Conakry) was visited in 1996/7 for some months, but here the fetish tradition using wild birds or mammals is strictly forbidden by law and no relevant data could be collected.

RESULTS

The current state of fetish culture as observed in markets selling wildlife items

Morocco: There are a few traders having birds or parts of them among their items. Hoopoes and Griffon Vultures *Gyps fulvus* are often displayed openly in the shops. It seems that many of the larger birds for sale were killed by electrocution or collision with electric power lines (Nikolaus 2006).

Guinea (Conakry): Very little is left of this culture, at least as observed in the open public markets. Most of the traditional doctors selling their medical products have only a few feathers, bits of skins or bones on display.

Ghana: This tradition was forbidden under the country's former British colonial rule. There are relatively few markets where wildlife items for traditional medicinal purposes are sold. Relevant items on the market are sold by Yoruba women traders from Nigeria and most of the items are known to be imported from Nigeria.

Nigeria: The fetish tradition has remained strong in the country because, unlike in Ghana, the country's former British colonial rulers could not constrain it substantially. Most of the pertinent trading is handled

FIG. 1. The fetish market at Cotonou, Benin

by Yoruba women, mainly in the southern part of the country.

Mali, Niger, Ivory Coast: Fetish markets in larger towns are often found in scattered small shops where traders sell whole animals or parts of them. They probably receive their products from local hunters and traders.

Burkina Faso, Togo, Benin: In almost all larger towns traders sell birds/bird items (often complete body parts), heads of mammals, snakes, scorpions, and other animals valuable for traditional medicines (Fig. 1).

Republic of the Congo (Brazzaville), *Democratic Republic of the Congo* (Kinshasa): Fetish traditions persist, but mainly using plants. Wildlife items are rare, at least in both capitals.

Medical and/or beneficial effects ascribed to bird species in traditional African medicine

The information detailed below regarding effects ascribed to particular species/species groups is based on interviews in Nigeria (Nikolaus 2001).

All birds of prey: help against weakness of the body

Large vultures: help against mental disturbance, epileptic problems, bad eyesight

Hooded Vulture: brings good luck when buried in the ground before building a new house

Abdim's Stork: brings fertility

Cattle Egret: brings money and good luck

Black Crowned Crane: guarantees a lucky wedding and family future

Francolin: helps against fever

Stone Partridge: stops children from being afraid

Parrots: give intelligence

Coucals: entail blessing (Senegal)

Cuckoo: if the bird calls in the forest, a close relative or friend will die

Owls, Nightjars: provide protection from witchcraft

Great Blue Turaco: protects from poverty

Turacos: attract customers

Rollers: give beauty

Ground Hornbill: helps the hunter to get very close to the game because the game cannot see the hunter

Hornbills: give protection and security (e.g., for the house or farm)

Pygmy Kingfisher: attracts customers to a shop

Woodpeckers: improve business

Yellow-fronted Tinkerbird: helps if a woman cannot have children

Snowy-headed Robin-Chat: acts against examination stress in students

Tchagra: imparts its muscial talent

African Pied Wagtail: gives security

Swallows, Swifts: are used for blessing

Weavers: are used for blessing

Pied Crow: gives protection from witchcraft.

Species and Numbers of Birds

More than 370 different bird species were recorded on West African markets during this survey (Nikolaus, personal database) Some are very valuable in the traditional medicinal culture, especially nocturnal birds such as nightjars, owls and snake eagles *Circaetus* (looking like owls). The most valuable bird species are vultures (with prices of up to 100 US$ per specimen), African Pied Wagtail *Motacilla aguimp*, and male Paradise Flycatcher *Terpsiphone viridis* (costing about 40 US$ each per specimen). Other valuable birds include hoopoes, birds of prey, flufftail crakes, Black Crowned Crane *Balearica pavonina*, cuckoos, turacos, hornbills, tinkerbirds, Cattle Egret, Pygmy Kingfisher *Ceyx picta*, rollers, Stone Partridge *Ptilopachus petrosus*, francolins, Grey Parrot *Psittacus erithacus*, Snowy-headed Robin-Chat *Cossypha niveicapilla*, African Thrush *Turdus pelios*, Black-crowned Tchagra *Tchagra senegalus*, Yellow-billed Shrike *Corvinella corvina*, and Village Weaver *Ploceus cucullatus*.

The following numbers of birds/bird items were counted in fetish markets in various West African countries and years: Benin (2002: 1700; 2007: 1200; 2008: 2005; 2009: 2500); Burkina Faso (2002: 400; 2007: 360; 2009: 320); Democratic Republic of the Congo (Kinshasa): (2008: 7); Ghana (2002: 100); Ivory Coast (2002: 100); Mali (2007: 220); Morocco (2003: 210; 2005: 150); Niger (2002: 180); Nigeria (1999: 2250; 2001: 1400; 2008: 3500); Togo (2001: 460); Republic of the Congo (Brazzaville) (2008: 22). These numbers show that of the countries surveyed this culture is most commonly practised in Nigeria and Benin. Cocker (2000) assessed the number and species of birds affected by the fetish culture and estimated that possibly millions of birds are killed annually because of it. Based on the present investigation I estimate the number of birds used in this tradition to be in the range of tens of thousands up to hundreds of thousands. However, calculating the market turnover rate of these items based only annual visits in certain months is rather difficult.

The origin of the bird items in fetish markets

Hausa traders regularly visit small villages to buy bush meat remains, like the dried heads and feet of hunted birds and other animals, which they take to the big fetish markets, where these are sold as traditional medicinal items. However many of the bird items observed in the fetish markets were probably not killed primarily for this particular purpose. Casualties from electric power lines/masts (as observed in Morocco) or road casualties also end up there. Only "real" fetish birds are hunted for this purpose (but are often eaten as well). Predominantly only parts of birds like heads (sometimes with feet in addition) are presented or offered on markets. A smaller proportion of bird items are complete body parts preserved by using salt, kerosene, or fire drying. Some of these bird items are likely to have been transported over long distances to reach the markets, mainly to Nigeria. However, most birds are said to be locally harvested, hunting being a common practice all over West Africa (Martin 1991).

Long-term changes in the markets and in bird species offered

While the number of birds offered seems to increase in Benin and Burkina Faso, the situation in Nigeria is different. In Nigeria, most birds and some mammals like chimpanzee are not on open display for sale. Only when clear interest is shown, pots and boxes containing wildlife items are opened for sale. During the last 10 years some of the important markets in southern Nigeria, such as Abeokuta, Ijebu-Ode, and Oshogbo, and even Onitsha, have shown a substantial decrease in the number of wild animals presented for sale. Other markets, like Ilorin and Ibadan, have become much more important.

The governments of Benin and Burkina Faso support the old fetish tradition, so many birds are shown on display for sale. But some of the valuable birds like vultures and eagles, which are almost extinct in most parts of Africa now, are not found in the markets any more, except in Nigeria, where people have a lot of money and can afford to buy them. In some cases, traders now even pull out the headfeathers of Black Kites to make them look like Hooded Vultures, and so hope to obtain a better price for the item. As mentioned above, vultures and eagles have almost completely disappeared from the markets except in Nigeria, where their numbers have more than doubled since the early surveys. There is very high hunting pressure on Palm-nut Vulture *Gypohierax angolensis* now. The price for this species reaches *ca.* 100 US$ per bird! Due to hunting pressure, Crowned Eagle *Stephanoaetus coronatus*, Martial Eagle *Polemaetus bellicosus*, and snake (harrier-) eagles *Circaetus* are also likely to head for extinction. Large owls have also become rare on fetish markets, and even the formerly common Red-necked Buzzard *Buteo auguralis* has become very uncommon on these markets, as have falcons, storks, Black Crowned Crane, and bustards. Numbers of large vultures offered were very small (see Table 1); while the numbers of Hooded Vultures increased. Recently the number of Black Kites used in the tradition has increased. Grey-throated Rail and White-spotted Flufftail are very rare in the region but are offered on fetish markets nevertheless.

During visits to the market in Bohicon (Benin) large numbers of carcasses of freshly killed Barn Owl and White-faced Scops Owl were seen laid out to dry (Table 2). This observation raises the question as to where so many owls can be "harvested" and which consequences these activities have on the species and other wildlife.

The African Barred Owlet is restricted to Liberia and Ivory Coast, yet the species was recently found in small numbers on markets in Benin (Table 2). Unpublished isotope studies suggest that it may occur in small numbers in this region.

Future prospects

A good example to assess the threat the fetish culture in West Africa might pose for the endangered birdlife is the case of the Crowned Eagle. This bird of prey has a distribution range restricted to the African forest ecosystem. Twenty-six birds were counted on

TABLE 1. Selected bird species counted in large Nigerian fetish markets in different years.

Species	Locality				
	Ilorin		Onitsha		Ibadan
	1999	2008	1999	2008	2008
Cattle Egret *Bubulcus ibis*	3	60	12	20	30
Hooded Vulture *Necrosyrtes monachus*	2	18	1	30	50
White-backed Vulture *Gyps africanus*	1			8	8
Rüppell's Griffon *Gyps rueppelli*		3	2	2	7
Lappet-faced Vulture *Aegypius tracheliotus*				3	12
White-headed Vulture *Aegypius occipitalis*				1	2
Short-toed Eagle *Circaetus gallicus beaudouini*				2	
Brown Harrier-eagle *Circaetus cinereus*					
Banded Harrier-eagle *Circaetus cinerascens*			2		4
Double-spurred Francolin *Pternistis bicalcaratus*	15	200	22	10	
Barn Owl *Tyto alba*		20	7	5	3
African Scops Owl *Otus senegalensis*		2	2		
Northern White-faced Scops Owl *Ptilopsis leucotis*	2	5	12	10	8
Verreaux's Eagle Owl *Bubo lacteus*		1			
Greyish Eagle Owl *Bubo cinerascens*	1	1	4	2	
Pearl-spotted Owlet *Glaucidium perlatum*	1		11		1

TABLE 2. Selected bird species counted in large Benin fetish markets in different years.

Species	Locality							
	Cotonou				Bohicon			
	2002	2007	208	2009	2002	2007	2008	2009
Black Kite *Milvus migrans*	15	20	50	100	3	4	30	67
Hooded Vulture *Necrosyrtes monachus*	24	15	40	10	1		15	
White-backed Vulture *Gyps africanus*								
Rüppell's Griffon *Gyps rueppelli*		1						
Lappet-faced Vulture *Aegypius tracheliotus*			1	1				
White-headed Vulture *Aegypius occipitalis*								
Short-toed Eagle *Circaetus gallicus beaudouini*								
Brown Harrier-eagle *Circaetus cinereus*						1		
Banded Harrier-eagle *Circaetus cinerascens*	2		1					1
Grey-throated Rail *Canirallus oculeus*	4		2	6				
White-spotted Flufftail *Coturnicops pulchra*	2	7	5	7	10	2	4	1
Violet Turaco *Musophaga violacea*	14	10	100	7		1	25	5
Barn Owl *Tyto alba*	33	50	100	25	26	100	40	22
Northern White-faced Scops Owl *Ptilopsis leucotis*	40	30	40	50	42	28	50	95
Verreaux's Eagle Owl *Bubo lacteus*			1					
Greyish Eagle Owl *Bubo cinerascens*	1		4		1	1		
Pearl-spotted Owlet *Glaucidium perlatum*	28	6	30	25	5	13	10	8
African Barred Owlet *Glaucidium capense etchecopari*			8				2	1
African Wood Owl *Strix woodfordii*	2	4	15	3		1	5	2
Yellow-fronted Tinkerbird *Pogoniulus chrysoconus*	37	5	20	65	10	50	80	1

fetish markets during this study. Taking the turnover rate in markets and the limited time these were visited into account, ten times more individuals of this species may have been sold during the last ten years, bringing the total to about 250 birds killed in the region under study and possibly elsewhere! Crowned Eagles need five years to become mature and breed only every other year. This gives an idea of the influence of hunting for the traditional fetish market on the survival of this and other bird species.

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RANGE CHANGE AMONG NEW WORLD TROPICAL AND SUBTROPICAL BIRDS

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This paper is dedicated to the memory of our dear friends and colleagues, Gary Waggerman, 1942-2009, and James Cox, 1952-2008

ABSTRACT

Range change is occurring at a rapid rate for tropical, subtropical, and warm desert birds in Texas. Comparisons between former (1974) and current avian distributions for the region show significant breeding range extension of 40-220 km to the N, NE, or E for at least 68 species, many of which cross major biogeographic boundaries. Fieldwork at the northern end of the subtropics along the coastal plain of the Gulf of Mexico has provided extensive documentation of breeding populations in new areas (e.g., nests, eggs, nestlings, fledglings, pairs, singing males on territory, and response to playback) for nine subtropical species (e.g., Green Jay *Cyanocorax yncas* and White-tipped Dove *Leptotila verreauxi*), as well as photographic evidence of seasonal persistence derived from use of a novel, web-based collaborative online robotic wildlife camera. Poor previous documentation, population change, habitat loss in the former range, and habitat change in the new range are considered as possible explanations. We conclude that change in key parameters of habitat, e.g. seasonal food availability, as affected by factors related to climatic change, e.g., mean annual precipitation, temporal distribution of precipitation (monthly means), or monthly means for nighttime-low temperatures during the breeding season, provide the most likely explanations for observed range extensions. At present, movement of a large segment of the subtropical avian community into temperate habitats has not been met with a corresponding shift of temperate species as had been predicted by a number of models; rather the communities now overlap, creating, in effect, novel communities. Results of this overlap are likely to produce profound changes that may first be evident in the genetics of subtropical/temperate species pairs, e.g., Black-crested Titmouse *Baeolophus atricapillus* and Tufted Titmouse *Baeolophus bicolor*.

Key words: Biogeography, biome, breeding ecology, climate change, novel communities, range shift, wildlife camera.

INTRODUCTION

Range shift in a number of organisms in apparent response to climate change has been treated in an increasing number of studies (e.g., Parmesan 2006) since a seminal paper in Nature provided prominent documentation for the phenomenon in English avian communities (Thomas & Lennon 1999). Based almost entirely upon anecdotal information derived from observations by amateur naturalists, avian data sets have served as the core for a number of modeling papers, several of which predict the shrinking and eventual disappearance of ecological communities at higher latitude or elevation (Jetz *et al.* 2007, Sekercioglu et al. 2008).

Texas has unique properties that make the study of the process and effects of range change especially informative, e.g., relatively abrupt boundaries between major biogeographic realms and historically well-documented avian species distributions (Cope 1880, Strecker 1912, Blair 1950, Oberholser 1974, Lockwood & Freeman 2004, Rappole *et al.* 2007). The purpose of this study is to use recently-published information along with fieldwork to test whether or not substantial changes in avian breeding ranges have

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occurred over the past four decades in Texas, and, if present, to consider what the long-term effects of such changes on existing communities might be.

METHODS

Oberholser's *The Bird Life of Texas* (1974), provided a thorough summary of the distribution of Texas birds as of 1973, including highly detailed maps of breeding distribution. The Texas Ornithological Society published updated maps for Texas breeding birds in 2004 (Lockwood & Freeman 2004). For each species in which range change was evident, we used the mapping program DeLorme (2007) to plot the northern, northeastern, or easternmost breeding record by county from Oberholser (1974) and the northern, northeastern, or easternmost extent of breeding range according to Lockwood & Freeman (2004). We then measured the distance between these points (to the nearest 10 km) and the approximate cardinal or intermediate direction from the Oberholser point to the Lockwood & Freeman point.

In addition to examining data in the literature, we conducted a three-year field study on ranch land of the Welder Wildlife Refuge along a 30-km stretch of the Aransas River (15 km on a straight west-to-east line) from the bridge across U.S. Highway 77 (28° 7' 37.69" N, 97° 25' 39.85" W) east to within 5 km (by air) from the river's mouth in Copano Bay (28° 6' 31.92" N, 97° 18' 57.24" W) in San Patricio and Refugio counties, at the northern end of the New World subtropics (Fig. 1).

The principal habitats surveyed included mesquite chaparral, oak chaparral, coastal prairie (maintained by fire and cell grazing by cattle), riparian forest, bridge abutments (for swallow nesting), vertical stream and river banks (for kingfisher nesting), and fresh and brackish water (tidal influence) marshes (Box & Chamrad 1966, Rappole & Blacklock 1985). Audiovisual surveys were conducted during 16 Apr - 14 May 2007, 3-10 Jun 2007, 4-30 Sep 2007, 13-19 Jan 2008, 28 Mar - 5 May 2008, and 18 Mar - 4 May 2009. Surveys were conducted at least once each year in April or May on all roads or trails on foot or on bicycle and on the Aransas River and Moody Creek by canoe. Sites where singing males or flocks of target species were found by surveys were visited repeated times each season to search for additional evidence of breeding (female, agitated pair, nests, fledged young, adults carrying food or nesting material, response to playback). The data gathered included GPS (Garmin 76) localities for displaying

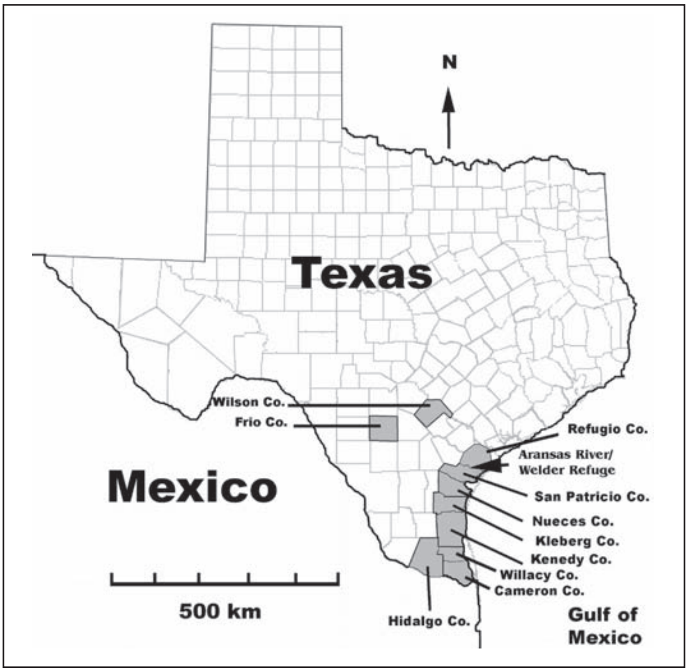

FIG. 1. US state of Texas, with the location of the Aransas River and Welder Wildlife Refuge (arrow) and the counties (shaded) mentioned in the text.

Please email support cone.welder@gmail.com with problems/suggestions/etc.
(please note which browser version and operating system you are using)

FIG. 2. Interface of the website (http://cone.berkeley.edu) for the collaborative telerobotic wildlife camera system, CONE Welder. The top panorama illustrates the camera field of view, which allows users to draw rectangles to control the camera. The camera window on the right side of the frame shows the live view. Each user can capture a picture by clicking on the camera button to the right of the live view. The image is then stored and displayed in the list at the left side of the live view, where users can enter their comments to annotate the image or comment on photos taken. Each user logs on to the system to draw rectangles on the panorama to indicate where they want the camera to observe. Details regarding camera operation can be found in Song (2009).

or singing males or birds responding to playback of recorded song, pairs, flocks, nests, eggs, fledglings or juveniles accompanied by adults. Exemplary nests, eggs and/or nestlings were collected and preserved as museum specimens (stored in the collection of the Welder Wildlife Foundation), and photos were taken of all nest sites discovered. *Ad hoc* mist-netting was done in attempts to capture specific individuals or species representatives. Mist nets were 12 m x 2.6 m of various mesh sizes (24 mm, 30 mm, 36 mm, 61 mm, or 121 mm) depending on the target species (AFO Mist Nets, Manomet, Massachusetts). Captives were banded with USFWS numbered bands and color-banded for individual recognition. Blood was drawn from the brachial vein using a small syringe to be used to determine whether birds captured earlier in the study were parents of birds captured in subsequent years. These data will be presented in a later paper. GPS localities were plotted and displayed on maps of Welder and vicinity using DeLorme Topo USA, version 6 (DeLorme 2006).

Seasonal persistence for several species was documented by means of a networked telerobotic camera set up at a lighted feeding and watering site established in mesquite chaparral about 100 m NW of the Welder Headquarters building. Online public access to the camera is controlled through a website titled "CONE-Welder" (CONE-Welder 2011) (Fig. 2). Building on the recent system and algorithmic development of collaborative observation (Song 2009), this novel web-based wildlife camera system was deployed on 12 May 2008, and has engaged citizen scientists to take photos of birds (and other animals) visiting the site 24 hours a day, seven days a week, except for brief downtimes for occasional maintenance and repair. Photos taken are logged automatically as to date, time, and photographer, and the users vote to classify each photo according to species (Faridani *et al.* 2009).

The conclusions in this paper are based on presence/absence data. Presence of breeding populations of target species is documented by the methods described above. It is not possible to document the historical absence of breeding populations with the same level of certainty. However, in addition to thorough documentation of the historical ranges of the species under consideration presented in the distributional literature (Strecker 1912, American Ornithologists' Union 1957, 1983, 1998; Packard 1951, Oberholser 1974, Rappole & Blacklock 1985, 1994; Vega & Rappole 1994), as well as in the appropriate species accounts from the *Birds of North America* (Poole 2011), there is extensive information on the historical bird community, and specifically for the area along the Aransas River, based on ornithological work done by several generations of researchers dating back over half a century (Roth 1971, Cottam & Blacklock 1972, Emlen 1972, Woodard 1975, Rappole 1978, Blacklock 1984, Blankenship & Glasscock 2007). Data in Oberholser (1974) are the principal source used for comparison of former nearest known breeding sites with current localities. These data are based on Oberholser's notes, published literature, major museum collections, personal fieldwork, observations by the senior editor of the volume (E.B. Kincaid, Jr.) and his associates, and thousands of records from Audubon Field Notes, Spoonbill (newsletter of the Houston Outdoor Club), *Bulletin of the Texas Ornithological Society*, and local and regional checklists and reports.

For bird taxonomy and species sequence we followed the *Check-List of North American Birds* (American Ornithologists' Union 2011).

RESULTS

For 68 species a considerable change in Texas range over a 35-year period is evident (Appendix 1). Recent documentation by photo of a Texas breeding record for the Mangrove Warbler (*Dendroica petechia erithachorides*), a tropical taxon (Lowther *et al.* 1999) is exemplary (Fig. 3).

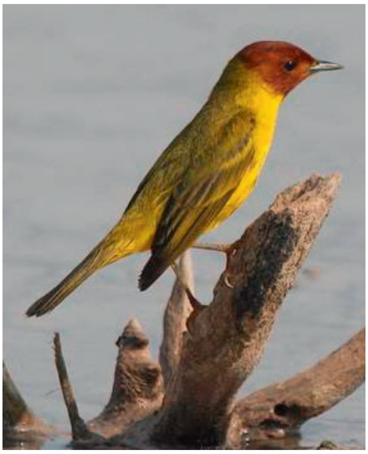

FIG. 3. Male member of a breeding pair (nest photographed) of Mangrove Warblers at the mouth of the Rio Grande River in South Texas. Photo by Scarlet Colley.

National Breeding Bird Survey data trends for 1966-2007 (Sauer *et al.* 2008) show that populations of 20 species increased, eight of which increased significantly; 13 decreased, one significantly; three show no change; and there are no data for 32. The mean distance of range expansion was 205 km. The approximate direction of furthest expansion was N for 31, NE for 28, E for 7, and NW for 2 species.

Data documenting presence of new breeding populations in San Patricio and Refugio counties and vicinity at the northern end of the subtropics are summarized below by species.

White-tipped Dove *Leptotila verreauxi* - Evidence of breeding for this species was observed at 21 new localities, 190 km N of the nearest known breeding area in the region (Cameron County) according to Oberholser (1974: 428) (Fig. 4). The majority of these were singing birds (> 500 m apart or birds heard simultaneously); however, at two sites (#7 and 5, Fig. 4) birds responded to playback (approach to < 10 m) and were captured and banded; one site (#13) was an observation of two adult birds with a juvenile; and one site (#9, Fig. 4) was a singing bird sitting on a nest. In addition, White-tipped Doves were photographed at the CONE feeding site in March of 2008 and May and June of 2009 (Table 1), although it is a woodland species that only rarely feeds at such open sites.

Buff-bellied Hummingbird *Amazilia yucatanensis* - Males were observed calling and displaying at four localities (Fig. 5), three of which were in the vicinity of feeders. Extensive photo evidence documents presence of this species at the CONE site during Apr-Oct 2008 and Apr-Oct 2009 (Table 1). The absence of records from Nov 2008 - Mar 2009 and 1-30 Nov 2009 (up to date of manuscript submission) likely

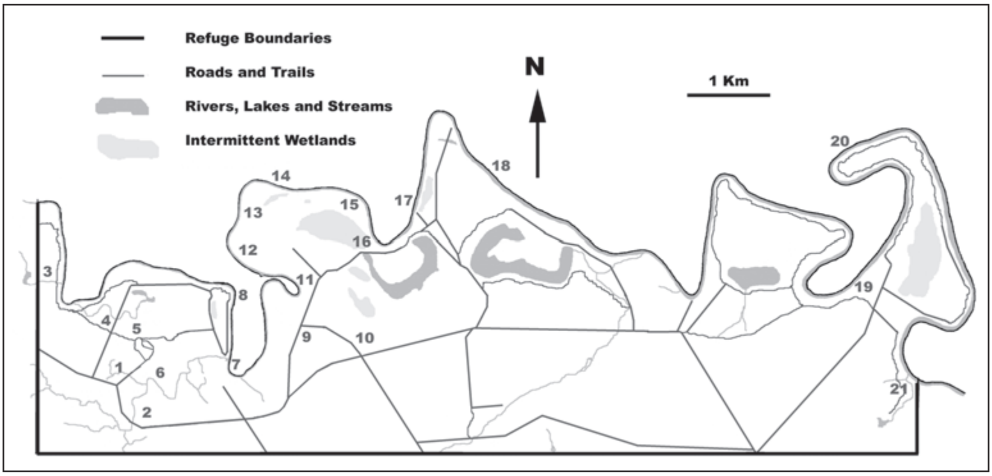

FIG. 4. White-tipped Dove *Leptotila verreauxi* localities in the main study area in the vicinity of the Aransas River and Welder Wildlife Refuge in San Patricio and Refugio counties, showing rivers, streams, roads, and trails where surveys were conducted, 2007-2009.

indicates migration for the majority of the population of this species.

Green Kingfisher *Chloroceryle americana* - Pairs of this species were observed at five localities on the Aransas River and two on Moody Creek (a tributary of the Aransas) (Fig. 5). In addition, a pair was seen on a creek in Sinton (#6, Fig. 5) and at Paradise Pond (#7, Fig. 5) in Port Aransas. Both members of one of the pairs on Moody Creek (#2, Fig. 5) were captured and banded; the female was captured and banded on 22 Apr 2007 and recaptured on 10 Apr 2009 at the same locality. Active nest holes (adults entering carrying food) were located at #1 and #4 (Fig. 5).

Great Kiskadee *Pitangus sulphuratus* - Pairs were observed at 22 separate localities in 2007-2009, 21 of which were along the Aransas River or nearby wetlands, and one in Sinton, 7 km S of the Aransas; active nests (adults constructing or visiting) were found at 12 sites (Fig. 6) most of which were over or near open water. Eggs were collected from site #2 (Fig. 6). Birds responded to playback (calling, approach) at two sites (#13 and 17, Fig. 6). Photos were recorded at the CONE site during several months in 2008 and 2009 (Table 1), although the only attractions at the site were bathing areas and foraging perches.

TABLE 1. Number of days by month on which photos were recorded by CONE website visitors for species new to the Welder avifauna. during 20 April 2008 – 30 November 2009. Photos can be viewed at http://cone.berkeley.edu.

	Month																			
	2008									2009										
Species	A	M	J	J	A	S	O	N	D[1]	J[1]	F	M[2]	A[2]	M	J	J	A	S	O	N
White-tipped Dove	0	3	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0	0	0	0
Buff-bellied Hummingbird	0	26	21	21	28	26	13	0	0	0	0	0	19	31	30	31	27	29	13	0
Great Kiskadee	0	0	5	5	2	0	9	6	2	2	13	1	0	0	15	11	6	2	0	0
Couch's Kingbird	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
Green Jay	4	29	18	27	31	29	31	30	16	11	26	2	18	22	10	9	18	30	13	12
Audubon's Oriole	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0

[1] Camera was not functioning during 17 Dec 2008 - 14 Jan 2009.

[2] Camera was not functioning during 4 Mar - 3 Apr 2009.

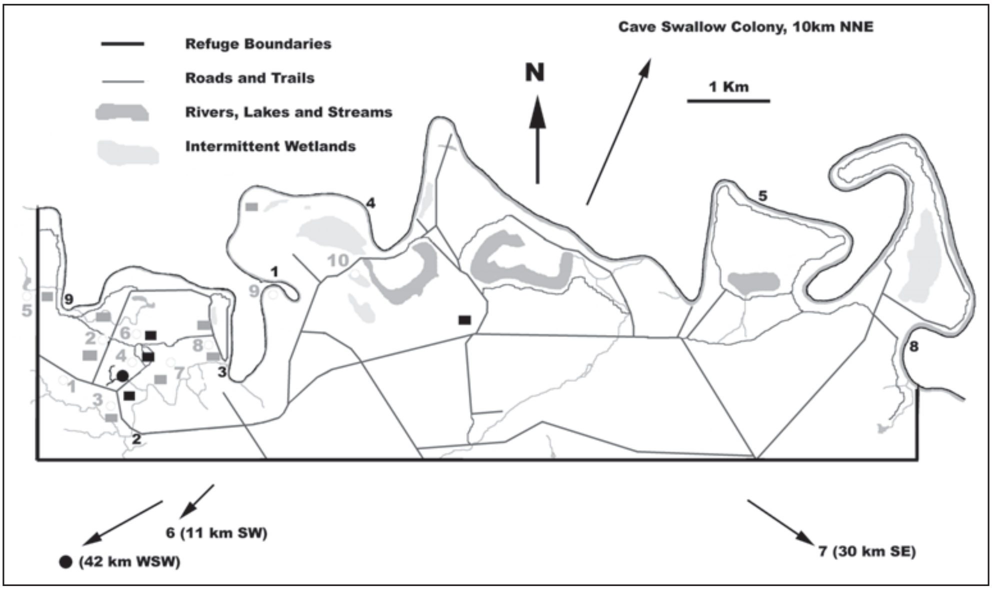

FIG. 5. Buff-bellied Hummingbird *Amazilia yucatanensis* (black rectangles), Green Kingfisher *Chloroceryle americana* (black numbers), Couch's Kingbird *Tyrannus couchii* (gray numbers), Tropical Parula *Parula pitiayumi* (black circle and arrow), Audubon's Oriole *Icterus graduacauda* (gray rectangles), and Cave Swallow *Petrochelidon fulva* (arrow) localities in the main study area (see Fig. 4 for details).

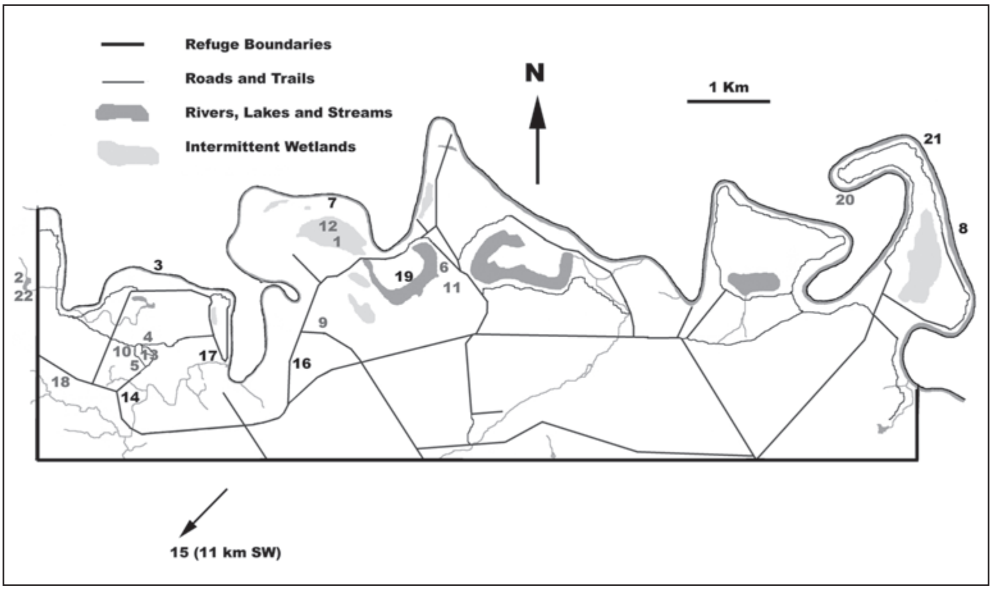

FIG. 6. Great Kiskadee *Pitangus sulphuratus* localities in main study area (see Fig. 4 for details). Black numbers are localities for calling birds; gray numbers are nest sites.

Couch's Kingbird *Tyrannus couchii* - Ten localities were found over the course of the study, five of which (#1,3,4,9,10, Fig. 5) were occupied by pairs in 2007, 2008, and 2009. Both members of one pair (#4, Fig. 5) were banded in 2008 and observed again in 2009. Individuals responded to playback (call, approach) at sites #3 and #4. Photos were taken at the CONE site in April 2008 and 2009 (Table 1).

Green Jay *Cyanocorax yncas* - Groups of this species were seen or heard at 25 separate localities in 2007-2009, 22 of which were in riparian forest, oak chaparral, or mesquite chaparral near the Aransas River (Fig. 7). In addition, groups were heard at Sous Creek (#23), Aransas National Wildlife Refuge (#24), and Paradise Pond at Port Aransas (#25). Most of the Aransas River area localities had Green Jay groups during all three field seasons. Green Jays were among the most common and regular visitors to the CONE feeding site, where they were photographed almost every day during every month of the year when the camera was operating (Table 1). A total of 17 jays was banded with both USFWS bands and color bands for individual recognition over the course of the study. Several of the color-banded birds were regular visitors to the CONE feeding site, where they were easily identified from photos. Both members of two pairs (from localities #4 and #5) were banded and color-marked. These birds were observed carrying food (cicadas mostly) in early May 2007, presumably to nestlings or recently-fledged young. The male from the pair captured and banded at locality #4 on 14 May 2007 was recaptured near that site 31 Mar 2009.

Cave Swallow *Petrochelidon fulva* - A nesting colony of this species was discovered under a bridge on Sous Creek in Refugio Co., 10 km NNE of Welder on 28 Apr 2007 (Fig. 5).

Tropical Parula *Parula pitiayumi* - Skoruppa & Blacklock (2007) reported pairs of both Tropical and Northern Parula warblers at Hibernia, San Patricio Co., 42 km SW of Welder. We found a pair of Tropical Parulas at Welder in May 2010 (Fig. 5), and also heard and saw a singing male of Northern Parula on several occasions during April and May 2010 in the vicinity of the Administration Building (28° 6' 48.86" N, 97° 25' 1.31" W) and at the south end of Hackberry Motte (28° 6' 42.54" N, 97° 24' 22.56" W).

Audubon's Oriole *Icterus graduacauda* - Eight localities for singing Audubon's Orioles were recorded during the course of the study, at least six of which were occupied during all three years (Fig. 5).

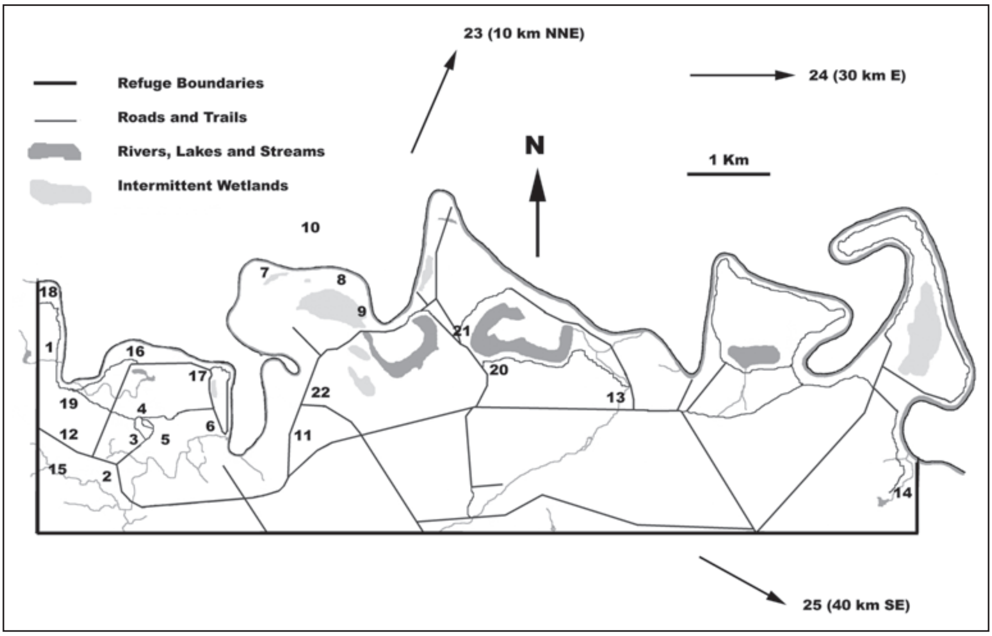

FIG. 7. Green Jay *Cyanocorax yncas* localities in the main study area (see Fig. 4 for details).

Males responded to playback (singing, approach) at two sites. Photos at the CONE site recorded presence of Audubon's Orioles during three months (Table 2), although no attraction other than water can be found at the site for this species.

Additional Species - Seven other subtropical, warm desert, or tropical birds were seen on or near the Welder Refuge within the past four years, but data are insufficient at present to document breeding: Groove-billed Ani *Crotophaga sulcirostris* - sightings at three localities in 2007 and 2008; Black-throated Sparrow *Amphispiza bilineata* - sighting in Apr 2009; Green-breasted Mango *Anthracothorax prevostii* - seen at SG's feeder each year from 2003-2008; Hooded Oriole *Icterus cucullatus* - male sighted on 18 Apr 2009; Gray Hawk *Buteo nitidus* - sightings at three localities by three different observers in 2007, 2008, and 2009; Lesser Nighthawk *Caprimulgus acutipennis* - seen and heard vocalizing on 17 Apr 2009, responded to playback (approach, call); Ringed Kingfisher *Megaceryle torquata* - seen on the Aransas River, E of Welder in 2006 by SG.

DISCUSSION

In this study, we document shift of breeding range for 68 species of birds, most of which fall into one of three major biogeographic categories in terms of their ecological communities: subtropical, tropical, and warm desert. The direction of range shift for nearly all of these species is into regions that historically were cooler and wetter than their original range (as of 1974) (Norwine & John 2007). Several reasons have been proposed for these or similar range changes that have occurred in other regions or taxa, which we discuss below:

1. Poor Historical Data - As Lockwood (2001: 108) has stated regarding the Gray Vireo, whether evidence of breeding populations from areas where they were not previously recorded "...is a result of an actual range expansion or if they were simply overlooked is open to speculation". Fall (1973) makes a case for "overlooked" for 10 subtropical species that he found on a huge private ranch (King Ranch) in Kenedy County, well north of their previously known ranges. Perhaps this explanation has some validity in situations where evidence of a range extension is based on observations of a few individuals at a few sites, but when the extension is documented for several individuals at several sites, the idea that a significant portion of the range was missed by earlier workers seems unlikely for one species let alone 68, at least in Texas where ornithological exploration has been conducted for well over a century (see review in Oberholser 1974). The ornithology of northeastern Mexico is less well-documented, making it difficult to assess the distances and rate of tropical species' range extensions. Nevertheless, the broad outlines of historical species distribution are well understood for the region (Friedman *et al.* 1950, 1957; Howell & Webb 1995), and certainly, the appearance of tropical bird species in Texas has been thoroughly recorded (Oberholser 1974, Lockwood & Freeman 2004).

2. Population Change - Populations of a species introduced to a new, suitable environment will expand to fill that environment, providing births exceed deaths. Rate of expansion will depend on factors affecting the relative rates of birth, e.g., food availability, and death, e.g., predators or disease (Wilson & Bossert 1971). For instance, since its introduction into the western hemisphere in 1851, the House Sparrow has expanded its range to include nearly all of North America south of the Arctic Circle, although in this case population increase and range expansion appear to have been a result of introduction into a suitable, vacant environment rather than a cause (Lowther & Cink 2006). Examples of species whose populations fill a new environment simply because of population pressure within their former environment are less obvious. Fretwell (1972) proposed that population density alone could affect habitat suitability. He argued that given two habitats, A and B, in which A has the higher quality for species X, the quality of habitat A can be reduced below that of habitat B simply by increasing the number of individuals occupying habitat A. Thus it is at least theoretically possible for population change within a species's existing range to force occupation of neighboring habitats formerly outside the range, providing these habitats are at least marginally suitable.

If avian range extension in Texas were a function of population change, a logical prediction would be that range would expand in some years for some species for those with increasing populations, contract in other years for those with decreasing populations, while showing no change for those with stable populations. However, this is not the pattern that has been recorded (Appendix 1). Rather, rapid range extension has occurred over a 30-year period for species in which some populations are decreasing, some are increasing, and others are showing no change. Therefore we conclude that population change does not provide an adequate explanation for the observed range expansions.

3. Habitat Destruction Within the Former Range - Replacement of large amounts of native habitat by agriculture is well documented for the northeastern Mexican state of Tamaulipas as well as for large parts of south Texas, particularly Hidalgo and Cameron counties of the Lower Rio Grande Valley (Dinnerstein *et al.* 1995: Map 6). This destruction has been suggested as a cause for the appearance of tropical species in Texas, e.g., Green Parakeet *Aratinga holochlora* and Red-crowned Parrot *Amazona viridigenalis* (Lockwood & Freeman 2004: 91), and might be considered as an explanation for range expansion in other species as well. However, most of this habitat destruction occurred more than 30 years ago (Purdy 1983), predating much of the observed range expansion.

Normal reproduction and dispersal provide sufficient impetus for occupation of nearby suitable habitat, at least in such well-adapted dispersers as birds (Fretwell 1972). In addition, there are many among the species in which range expansion has been observed, specifically those native to warm desert, for which no obvious change in habitat within the former breeding range has occurred. We conclude that habitat destruction in the former range does not provide a sound explanation for observed range expansion.

4. Habitat Creation Within the New Range - There are many examples of situations in which habitat change outside the former range of a species has resulted in expansion of the species into the newly-created habitat. Roberts (1936: 385), for instance, describes range change of the Greater Prairie Chicken *Tympanuchus cupido* in Minnesota as follows: "It entered the state from the east and south some time previous to the middle of the nineteenth century and spread rapidly west and north with the settlement of the country". What is noteworthy about most cases in which a species expands outward from former range into a neighboring new range is that obvious structural change in habitat in the newly colonized portion has taken place. This situation does not explain avian range expansion in Texas. Some small shifts (< 10%) in the relative amounts of native habitats have been documented in the region over the past decade (Wilkins *et al.* 2009), and shrub density has increased significantly in some South Texas prairie and savanna (Glasscock 2001), but for none of the 68 species documented as occupying new range in Texas has any obvious fundamental structural change in habitat within the new range occurred. Although the total amounts have increased for some habitats and decreased in others, all of the habitats into which these species moved were available before the range extensions occurred, even the specialized nesting habitats required by birds like the Cave Swallow (concrete bridge abutments), kingfishers (vertical banks of sandy loam soil), and Hooded Oriole (untrimmed palms with low-hanging fronds).

Despite the lack of obvious structural change in habitats within newly-occupied ranges, we suggest that habitat change remains the most probable explanation for the observed extensions in range for 68 Texas birds. Fretwell (1972: 80) defines "habitat" for a species as, "...any portion of the surface of the earth where the species is able to colonize and live (temporarily or permanently) at some density greater than zero". From an operational perspective, "habitat" for a given species is normally defined based on plant community (Odum 1971: 234), but clearly Fretwell's definition allows for multiple dimensions that relate to the species's niche. We suggest that some factor has influenced one or more critical habitat dimensions other than structure, causing a broad range of Texas habitats to become suitable that were previously unsuitable for a number of bird species.

The most obvious environmental factor associated with avian range shift in South Texas has been change in mean annual temperature (Fig. 8). Norwine & John (2007) provide extensive documentation of this fact, noting that the region is becoming warmer and dryer with a likelihood of longer droughts punctuated by more intense precipitation episodes. We hypothesize that climate change, exemplified by mean annual temperature changes, provides the ultimate cause for avian range change that we have documented in this paper. The proximate cause is unknown. However, we suggest that change in key parameters of habitat, e.g., seasonal food availability, as affected by factors related to climatic change, e.g., mean annual precipitation, temporal distribution of precipitation (monthly means), or monthly means for nighttime-low temperatures during the breeding season, provide the most likely explanations for observed range extensions.

Possible Effects of Range Extension on Avian Communities - In this paper we report on the immigration of 68 species of tropical, subtropical, and warm desert birds into avian communities of which they were not previously members, many of them in the

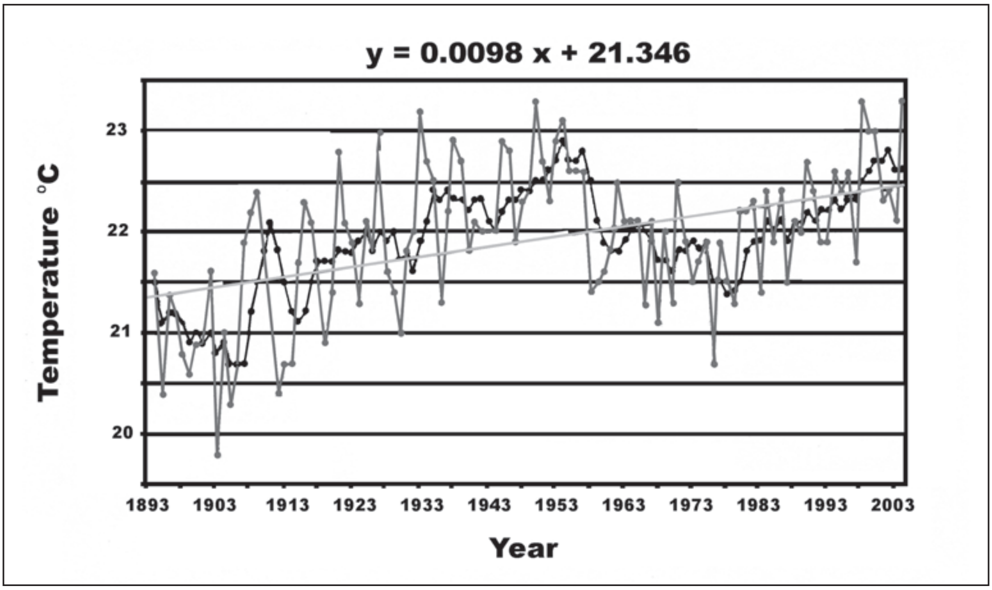

FIG. 8. Mean annual temperature for South Texas, 1893-2003. Dark gray dots = yearly average; black dots = 5-year running average; light gray line = trend line.

temperate biome. Expansion of the ranges of bird species of more "southern" or lower elevation communities into areas occupied by more "northern" or higher elevation communities is happening in many regions, although perhaps not so dramatically as in Texas. For instance, in New York State, publication of two breeding bird atlases at a 20-year interval (Andrle & Carroll 1988, McGowan & Corwin 2008) documents the movement of breeding populations of several species (e.g., Carolina Wren *Thryothorus ludovicianus*, Red-bellied Woodpecker *Melanerpes carolinus*, Tufted Titmouse *Baeolophus bicolor*) native to the Carolinean Zone (elevations < 300 m in southern New York) into breeding bird communities of the Transitional (300-600 m) and even the Canadian Zone (> 600 m) with no obvious change in the distribution or population size for members of the higher elevation communities (McGowan & Corwin 2008). Such range extensions would seem to have obvious implications for existing members of the invaded communities. Several models derived from avian range-shift data predict the disappearance of communities at higher elevation or latitude. For instance, Jetz *et al.* (2007: 1) state, "Even under environmentally benign scenarios, at least 400 [bird] species are projected to suffer > 50% range reductions by the year 2050 (over 900 by the year 2100)". Perhaps such changes will occur over the long term. At present, however, there is no evidence of such effects where subtropical species have invaded temperate bird communities in Texas. The same bird species that were present before the newcomers arrived are still present (Lockwood & Freeman 2004). It could be argued that since the avian range shifts have been so rapid and recent, and have not been accompanied by obvious changes in vegetation distribution, the predicted shift in habitat distribution will, in fact, occur over the years, decades, or centuries to come. However this argument simply begs the questions of how and why these range changes have occurred in the absence of structural change in existing habitat.

The fact that in Texas a major portion of the subtropical avian community now breeds in temperate communities alongside temperate species may indicate that the result of range shift caused by climate change will not be simple replacement of a more "northern" natural community by a more "southern" one. Rather, this mixing of communities could lead to the evolution of entirely new sets of communities (Parmesan 2006). Of course it will likely take decades if not centuries for the community mixing process to evolve, but it may not take long before evidence of profound change can be detected. We propose that initial evidence of how communities will change will come from newly-overlapping pairs of closely-related, and formerly largely allopatric, congeners. For instance, the original northeastern range boundary for the subtropical Black-crested Titmouse *Baeolophus atricristatus* and Golden-fronted Woodpecker *Melanerpes aurifrons,* was the San Antonio River along the northern border of Refugio County (Fig. 1) (Oberholser 1974, Grubb & Pravasudov 1994, Husack & Maxwell 1998, Shackelford *et al.* 2000, Patten & Smith-Patten 2008). There is no evidence that this boundary has expanded northeastward for these species as yet, but some effect on populations or gene pools of their respective temperate congeners, the Tufted Titmouse *B. bicolor* and Red-bellied Woodpecker *M. carolinus* can certainly be expected: (1) one member of the species pair will push the other out of the new community, (2) both will occupy the new community, or (3) genetic mixing will occur. We believe that #3 is the most likely scenario, and we predict that genetic studies comparing DNA of historic specimens from border regions with those from the new region of overlap will show that the process is already well underway for superspecies pairs like the titmice and woodpeckers mentioned above. The Blue-winged Warbler *Vermivora cyanoptera*/Golden-winged Warbler *V. chrysoptera* situation, with *cyanoptera* DNA swamping *chrysoptera* populations (Gill 1997), may be a prototype for what we can expect in the future as more and more southern or low elevation congeners move into the ranges of their northern or higher-elevation counterparts.

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APPENDIX 1. Distance and cardinal or intermediate direction of range expansion[1], preferred habitat in biological region of origin, and evidence of recent population change based on National Breeding Bird Survey (BBS) data for avian species undergoing range expansion in Texas within the past 35 years (1974 - 2009). Species for which there is evidence of breeding within the new range as reported in this paper or the literature are shown in bold.

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Black-bellied Whistling-Duck	*Dendrocygna autumnalis*	300 km N	Tropical and subtropical freshwater wetlands	Increase
Muscovy Duck	*Cairina moschata*	280 km N[2]	Tropical freshwater wetland	No data
Mottled Duck	*Anas fulvigula*	220 km NE	Subtropical freshwater wetland	Decrease
Plain Chachalaca	*Ortalis vetula*	180 km N	Tropical and subtropical woodlands, usually near water	No data
Neotropic Cormorant	*Phalacrocorax brasilianus*	220 km NE	Tropical and subtropical wetlands	No data
White-tailed Kite	*Elanus leucurus*	290 km N	Tropical, subtropical, and temperate savanna, thorn forest, and grassland	No change
Common Black-Hawk	*Buteogallus anthracinus*	410 km NE	Tropical and subtropical lowland woodland	No data
Short-tailed Hawk	*Buteo brachyurus*	370 km N[3]	Tropical savanna	No data
Crested Caracara	*Caracara cheriway*	220 km NE	Tropical and subtropical savanna, thorn forest and scrub	Increase[4]
White-winged Dove	*Zenaida asiatica*	480 km N	Tropical and subtropical thorn forest	Increase[4]
Inca Dove	*Columbina inca*	360 km N	Tropical and subtropical savanna and thorn forest	Increase[4]
White-tipped Dove	*Leptotila verreauxi*	190 km N	Tropical and subtropical woodland	No data
Green Parakeet	*Aratinga holochlora*	280 km N[5]	Tropical lowland woodland	No data
Red-crowned Parrot	*Amazona viridigenalis*	280 km N[5]	Tropical lowland woodland	No data
Greater Roadrunner	*Geococcyx californianus*	340 km NE[6]	Tropical, subtropical, and temperate semi-arid and arid scrub	Increase
Western Screech-Owl	*Megascops kennicottii*	330 km E	riparian woodland in temperate and subtropical semi-arid and arid lands	Decrease
Ferruginous Pygmy-Owl	*Glaucidium brasilianum*	70 km N	Tropical and subtropical riparian woodland	No data
Elf Owl	*Micrathene whitneyi*	300 km NE	Tropical and subtropical desert	No data
Common Pauraque	*Nyctidromus albicollis*	80 km N	Tropical and subtropical thorn forest and riparian woodland	No data
Common Poorwill	*Phalaenoptilus nuttallii*	80 km NE	Temperate and subtropical desert and thorn forest	Increase
White-throated Swift	*Aeronautes saxatalis*	140 km E	Temperate, subtropical, and tropical; aerial over montane and arid lands	Decrease
Buff-bellied Hummingbird	*Amazilia yucatanensis*	190 km N	Tropical and subtropical thorn forest and riparian woodland	No data

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Blue-throated Hummingbird	*Lampornis clemenciae*	290 km NW	Tropical and subtropical montane semi-arid and arid lands	No data
Magnificent Hummingbird	*Eugenes fulgens*	290 km NW	Tropical and subtropical montane and arid woodland	No data
Black-chinned Hummingbird	*Archilochus alexandri*	70 km NE	Temperate and subtropical semi-arid and arid woodland and thorn forest	Increase
Ringed Kingfisher	*Megaceryle torquata*	210 km N	Tropical and subtropical riparian	No data
Green Kingfisher	*Chloroceryle americana*	70 km NE	Tropical and subtropical riparian	No data
Northern Beardless-Tyrannulet	*Camptostoma imberbe*	180 km N	Tropical and subtropical riparian woodlands and thorn forest	No data
Buff-breasted Flycatcher	*Empidonax fulvifrons*	400 km E[7]	Tropical and subtropical pine and pine-oakwoodlands	No data
Vermilion Flycatcher	*Pyrocephalus rubinus*	110 km NE	Temperate, subtropical, and tropical semi-arid and arid lands	Decrease
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	370 km NE[8]	Tropical and subtropical lowland woodlands	No data
Ash-throated Flycatcher	*Myiarchus cinerascens*	90 km E	Temperate, subtropical, and tropical semi-arid and arid lands	Increase
Brown-crested Flycatcher	*Myiarchus tyrannulus*	130 km N	Tropical and subtropical woodlands	Increase[4]
Great Kiskadee	*Pitangus sulphuratus*	80 km NE	Tropical and subtropical freshwater wetlands	No data
Tropical Kingbird	*Tyrannus melancholichus*	110 km NE[9]	Tropical and subtropical savanna	No data
Couch's Kingbird	*Tyrannus couchii*	200 km N	Tropical and subtropical thorn forest and savanna	Increase[4]
Gray Vireo	*Vireo vicinior*	250 km NE	Temperate, subtropical, and tropical semi-arid and arid woodlands and thorn forest	Increase
Hutton's Vireo	*Vireo huttoni*	300 km E	Temperate, subtropical, and tropical pine-oak and juniper woodlands	Increase
Yellow-green Vireo	*Vireo flavoviridis*	30 km NE	Tropical and subtropical lowland woodlands	No data
Green Jay	*Cyanocorax yncas*	80 km NE	Tropical and subtropical savanna and woodlands	Increase
Western Scrub-Jay	*Aphelocoma californica*	310 km N	Temperate, subtropical, and tropical oak woodlands	Increase
Cave Swallow	*Petrochelidon fulva*	510 km NE	Tropical and subtropical open areas and wetlands (with bridge abutments or caves for nesting)	Increase[4]
Black-crested Titmouse	*Baeolophus atricristatus*	110 km N	Temperate, subtropical, and tropical riparian and oak woodlands in semi-arid lands	No data

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Verdin	*Auriparus flaviceps*	120 km NE	Temperate, subtropical, and tropical thorn forest and oak woodlands in arid and semi-arid areas	Decrease
Bushtit	*Psaltriparus minimus*	400 km N	Temperate, subtropical, and tropical thorn forest and oak woodlands in arid and semi-arid areas	Decrease
Cactus Wren	*Campylorhynchus brunneicapillus*	160 km NE	Temperate, subtropical, and tropical thorn forest and desert	Decrease
Black-tailed Gnatcatcher	*Polioptila melanura*	260 km E	Temperate, subtropical, and tropical thorn forest and desert	Decrease
Clay-colored Thrush	*Turdus grayi*	280 km N[5]	Tropical lowland woodland and riparian forest	No data
Long-billed Thrasher	*Toxostoma longirostre*	90 km NE	Tropical and subtropical semi-arid woodlands	Increase[4]
Curve-billed Thrasher	*Toxostoma curvirostre*	310 km N	Temperate, tropical, and subtropical semi-arid and arid thorn forest and woodlands	Decrease
Crissal Thrasher	*Toxostoma crissale*	270 km NE	Temperate, tropical, and subtropical semi-arid and arid thorn forest and woodlands	Increase
Tropical Parula	*Parula pitiayumi*	150 km N[10]	Tropical and subtropical lowland woodlands	No data
Yellow Warbler (Mangrove Warbler race)	*Dendroica petechia erithachorides*	340 km N[11]	Tropical mangroves	No data
Rufous-capped Warbler	*Basileuterus rufifrons*	360 km N[12]	Tropical and subtropical semi-arid and arid woodland and scrub	No data
Olive Sparrow	*Arremonops rufivirgatus*	50 km N	Tropical and subtropical thorn forest and lowland woodlands	No data
Canyon Towhee	*Melozone fusca*	190 km NE	Tropical, subtropical, and temperate arid scrub	Decrease
Botteri's Sparrow	*Peucaea botterii*	90 km N	Tropical and subtropical grasslands	No data
Rufous-crowned Sparrow	*Aimophila ruficeps*	140 km NE	Tropical, subtropical, and temperate arid scrub	Decrease
Black-throated Sparrow	*Amphispiza bilineata*	120 km NE	Tropical, subtropical, and temperate arid scrub	Decrease4
Pyrrhuloxia	*Cardinalis sinuatus*	80 km NE	Tropical, subtropical, and temperate semi-arid and arid scrub	Decrease
Varied Bunting	*Passerina versicolor*	170 km E	Tropical, subtropical, and temperate semi-arid and arid woodlands	No data
Bronzed Cowbird	*Molothrus aeneus*	180 km N	Tropical and subtropical savanna	No change
Hooded Oriole	*Icterus cucullatus*	100 km NE	Temperate, tropical, and subtropical lowlands (with palms for nesting)	Increase

English name	Scientific name	Principal distance and direction of expansion	Preferred habitat in former range	BBS population trend
Altamira Oriole	*Icterus gularis*	80 km N	Tropical and subtropical lowland woodlands	No data
Audubon's Oriole	*Icterus graduacauda*	90 km NE	Tropical and subtropical semi-arid woodlands	No data
Scott's Oriole	*Icterus parisorum*	200 km N	Tropical, subtropical, and temperate semi-arid and arid woodlands	Increase
Lesser Goldfinch	*Spinus psaltria*	90 km N	Tropical, subtropical, and temperate semi-arid and arid woodlands and scrub	No change

[1] Northern or easternmost extent of former Texas range is based on Oberholser (1974) unless otherwise noted. Current northern or easternmost extent of Texas range is based on Lockwood & Freeman (2004) or data presented in this paper. Cardinal and intermediate compass points are used for approximate direction of extension. Distance of extension is given to the nearest 10 km.

[2] Former northern extent of range is based on Friedman *et al.* (1950, 1957).

[3] Former northern extent of range is based on Miller & Meyer (2002).

[4] $P < .05$ based on National Breeding Bird Survey data, 1966-2007, in Sauer *et al.* (2008).

[5] Former northern extent of range based on Gehlbach et al. (1976).

[6] Current northeastern edge of the Greater Roadrunner's range likely is well northeast of the Texas border (Hughes 1996).

[7] Former eastern extent of range based on Bowers & Dunning (1994).

[8] Former northeastern extent of range based on Tweit & Tweit (2002).

[9] Former northeastern extent of range based on Stouffer & Chesser (1998).

[10] Current northern extent based on Skoruppa & Blacklock (2007).

[11] Current northern extent based on Colley (2006); former northern extent based on Lowther *et al.* (1999).

[12] Former northern extent of range based on based on Howell & Webb (1995). There are over 20 Texas records for this species, but no confirmation of breeding to date.

BIRDS AND MAMMALS AS INDICATORS FOR THE CONSERVATION STATUS OF TROPICAL FORESTS IN THE ECUADORIAN CHOCÓ

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ABSTRACT

In 2008 and 2009 I surveyed birds and certain mammals with the 'Multi Time-window Transect-Mapping' (MTW) monitoring protocol sensu Jahn (in press), in order to determine the conservation status of particular sites within the privately-managed Awacachi Biological Corridor, Esmeraldas Province, northwest Ecuador. Here I focus on the bird data for three (of a total of six) transects, whereas the results for mammals are only considered for assessing the impact of hunting. The 1200-m transects were located within forest between 50 and 610 m a.s.l. Field work was performed during the rainy season in March and April 2008 (total effort 173.3 h, 20 man-days). With a total of 8049 observations, I detected 226 avian species, including 43 endemics, 17 globally threatened or near-threatened taxa, and 64 species listed in the same threat categories on the national level. Species richness was much higher in the disturbed lowland forest (AWAC1) than in the pristine foothill forest of AWAC3 and AWAC4, with 158, 125, and 124 bird taxa, respectively. However, the remotest and least species-rich transect (AWAC4) had the highest bird community index value (BCI_{forest} = 2.54) and also the highest proportions of endemics (24.2 %) and threatened species (world: 8.6 %; Ecuador: 35.5 %). In conclusion, avian species richness by itself is a poor indicator for the conservation value of study sites. Instead, the sites should be ranked on the basis of a detailed comparison of the habitat preferences and threat status of their respective bird communities. In addition, the abundance of game species is a good indicator for the impact of hunting at the study sites, with larger mammals, such as *Mazama americana* and *Cebus capucinus*, and some sensitive game birds, viz. *Penelope ortoni*, *Ara ambiguus*, and *Cephalopterus penduliger* only detected at the remote transects of La Carolina ridge.

Key words: Bird community index, birds, Chocó, conservation status, diversity, Ecuador, endemic species, hunting, Multi Time-window Trnsect Mapping, species richness, threatened species, threat status value, tropical forest

INTRODUCTION

Effective and affordable monitoring methods are an important prerequisite for the development of adaptive management strategies for natural resources, the assessment of the status of threatened species, and for studying the impacts of global warming on biodiversity (Jahn in press). Long-term monitoring programs for at least some biological taxa are particularly important for assessing the success of conservation efforts in species-rich tropical latitudes. In this context, birds score very highly on many objective criteria for the selection of indicators for biodiversity patterns and environmental change (BirdLife International 2004). Although they are obviously not perfect indicators, as no single group of organisms is, many characteristics make them perhaps the most appropriate biological indicators in tropical habitats (Stotz *et al.* 1996). Birds are well known in comparison with most other taxa and their populations tend to integrate a number of ecological factors. Consequently, they should always be included as an indicator group in applied conservation-related research and resource management in tropical countries (Jahn in press).

These were my basic considerations for focusing on bird populations in the present study as well as in previous projects (cf. Jahn in press). The aim of the present work was to assess whether conservation efforts in the privately-owned Awacachi Biological Corridor, northwest Ecuador, Esmeraldas, were guaranteeing the survival of threatened, endemic, and otherwise sensitive wildlife. The study was commissioned by the owner, Fundación SIRUA (www.sirua.org), and by Fauna & Flora International (FFI), who co-manage the nature reserve. Due to the fact that illegal hunting by local people is still an important factor in the slow stabilization and recovery of the populations of larger animals, I also decided to assess certain mammal species, which could be surveyed together with the birds. However, here the status of mammals is only addressed at a qualitative level in the context of hunting.

STUDY AREA

The biomes of northwestern Ecuador belong to the Chocó biogegraphic region, which represents an important center of endemism. According to Stattersfield *et al.* (1998) it traverses the length of western Colombia and Ecuador (area: 100 000 km^2, elevational range: 0-3000 m). In southwestern Ecuador it gradually turns into the dry climatic zones of the Tumbesian region. The Chocó is characterized by one of the wettest and most non-seasonal climates on earth. The enormous annual precipitation supports one of the richest forest biotas in the world, with exceptional levels of endemism in a wide range of taxa including plants (Gentry 1986), butterflies (Dinerstein *et al.* 1995), reptiles and amphibians (Lynch 1979), as well as birds (Terborgh & Winter 1983, Stattersfield *et al.* 1998). Not surprisingly, the Chocó region is part of one of the earth's 25 'hotspots' of biodiversity that are urgent priorities for biological conservation efforts – the Chocó-Darién-Western Ecuador hotspot (Myers 1988, Myers *et al.* 2000). Unfortunately the region is increasingly threatened by human activities. In the Ecuadorian Chocó forest loss has accelerated to alarming rates since two important road projects were finished in the mid-1990s (Ibarra – San Lorenzo and Esmeraldas – Mataje); see Jahn (in press) for details.

My study area in Esmeraldas, the 10 200-ha Awacachi Corridor (c. 60-650 m a.s.l.), interconnects two of the largest remnants of Chocoan forest in Ecuador, the 'Awá Reserve' and the Cotacachi-Cayapas Ecological Reserve. The latter is the most important protected area in the region (243 638 ha, 80-4900 m; Esmeraldas, Imbabura) (IUCN 1992, INEFAN-GEF 1998, MAE 2007). Although uninhabited, it has in recent years suffered from increased human activities like illegal hunting, logging, and invasions (Jahn *et al.* 2007). The indigenous territory 'Awá Reserve' (101 000 ha; Esmeraldas, Carchi, Imbabura) is not a nature reserve but was established to maintain the traditional culture of the indigenous Awá people. Hence, the area is inhabited and subsistence agriculture, hunting, selective logging, and even the establishment of oil palm plantations are common and legal (Jahn in press). Together, these reserves form a forest corridor of about 350 000 ha from the lowlands up to at least 3400 m a.s.l., with páramo grasslands replacing woody vegetation above that altitude. Including migrants and vagrants, the potential number of bird species frequenting the entire area is estimated at > 750 species, over 600 of which were already recorded, including 54 species of Neotropical migrants (Jahn 2007). In the following I provide a brief description of the three transects considered here (cf. Table 1):

AWAC1, Río Durango – Río Bogotá area. – The transect was located at the westernmost extreme of the Awacachi Corridor close to the confluence of the Durango and Bogotá rivers. The site was chosen because it represents the lowest elevation (c. 60 m a.s.l.) of the reserve and is affected by the conversion of natural forest into agricultural land in neighboring areas, particularly oil palm monocultures. Therefore strong edge effects exist, making it likely that changes in the composition and structure of the plant and animal communities are in progress. The transect area is intersected by several streams and covered by

TABLE 1: Details on the locality and altitude of the three transects surveyed. The altitudes are based on uncorrected GPS measurements.

		Start		End		Altitude (m)	
Transect	Locality	Latitude	Longitude	Latitude	Longitude	Start	End
AWAC1	Río Durango – Río Bogotá	01°05'00.19"N	78°41'28.11"W	01°04'29.97"N	78°41'06.47"W	65	51
AWAC3	La Carolina ridge	00°53'54.2"N	78°39'27.0"W	00°54'10.3"N	78°38'55.6"W	608	599
AWAC4	La Carolina ridge	00°53'54.9"N	78°39'47.7"W	00°53'32.0"N	78°40'21.6"W	551	600

intensively logged young successional forest, containing numerous recent tree-fall gaps and a presumed natural clearing with shrubby vegetation on swampy ground. It is likely that the site originally fell within the tropical wet forest life zone (sensu Holdridge 1967), but due to recent climate change, caused mostly by the rapid and ongoing deforestation in the entire region, the current bioclimatic conditions probably correspond rather to the tropical humid (moist) forest life zone.

AWAC3 and AWAC4, 'La Carolina' ridge. – Both transects are located close to the northwestern limits of the Cotacachi-Cayapas Ecological Reserve at a ridge, which divides the watersheds of the Río Negro to the southeast and the Río Wimbí to the northwest. The transects are separated by a distance of c. 625 m in a straight line and are covered by primary forest with natural tree-fall gaps of varying size. Forest streams are present only in the close vicinity of AWAC4. The ridge is located in the premontane pluvial forest life zone (sensu Holdridge 1967). In the past only a very few trees were felled in the transect areas.

METHODS

Transect establishment and characterization. – The 1200-m transects were marked with conspicuous distance markers, each 25 m apart, on both sides of the paths. Their orientation, inclination, and altitude were measured and the geographic coordinates of the initial and final points determined with GPS (Global Positioning System).

Transect-mapping surveys. – I surveyed the entire bird communities and selected mammals, using the Multi Time-window Transect-Mapping (MTW) protocol for monitoring studies; cf. Jahn (in press) for methodological details. This standardized audio-visual method allows the detection of species that have their activity peaks at different periods of the day. All transects were surveyed with a set of 24 samples. In the case of AWAC3 and AWAC4 a total of six samples had to be repeated due to rain. The surveys were carried out from predawn to after-dusk periods, with highest effort during early morning hours. For each sample period the mean observer speed was adapted to the activity level of the birds. For optimal efficiency, transects were sampled on the way out as well as on the way back. AWAC3 and AWAC4 were surveyed alternately between 13 and 25 March and AWAC1 between 12 and 19 April 2008. The survey effort per transect was higher for the Río Durango – Río Bogotá area than at 'La Carolina' ridge (Table 2), due to the considerably higher bird activity and abundance at the former transect. The average survey effort was 57.8 ± 5.1 h, equaling 288.8 ± 25.6 min per 100-m transect section and complete survey. The average observer speed was 12.0 ± 1.1 min per 100 m, corresponding to only half the speed of conventional line transect protocols used in temperate zones (cf. Bibby *et al.* 1992). The total survey effort, including samples that had to be repeated, was 20 man-days.

Digitalization and correction of the data. – The field data were transferred to pre-established Excel spreadsheets with an effort of about 14 days per complete survey. Subsequently, I corrected the data with the help of the original transect-mapping forms and the audio recordings of animal vocalizations made during the surveys. In this step, misidentifications and digitalization errors were corrected. Furthermore, I indexed the audio recordings by assigning them to the relevant MTW records in the spreadsheets through specific codes. Records of animals that

TABLE 2: Survey effort and average observer speeds at transects AWAC1, AWAC3, and AWAC4. Abbreviations used: M1A = transect-mapping sample M1A; A2B = transect-mapping sample A2B (cf. Jahn in press); $N_{samples}$ = number of valid samples carried out.

Transect / Survey	Samples	$N_{samples}$	Transect length (m)	Effort (h)	Average observer speed (min/100 m)
AWAC1 / 01	M1A – A2B	24	1200	63.6	13.2
AWAC3 / 01	M1A – A2B	24	1200	53.8	11.2
AWAC4 / 01	M1A – A2B	24	1200	55.9	11.6
Sum		72	3600	173.3	36.1
Average		24	1200	57.8	12.0
Standard deviation		0.0	0.0	5.2	1.1

were overlooked in the field but documented in the audio recordings were also added to the data and marked clearly. This procedure is very laborious, but necessary to guarantee the quality and transparency of the information. It took 42 man-days (c. 12-h workdays), corresponding to 14 days per complete survey. Finally, the corrected data were transferred to a georeferenced SQL Server database, with an effort of about five days per complete survey.

Data analysis. – For practical reasons, I follow Ridgely & Greenfield (2001) for avian taxonomy, family, and species order. However, I implemented recent gender agreements (David & Gosselin 2002a,b) but not the changes at the level of genera (cf. Banks *et al.* 2003, 2006, 2008). For the determination of endemic species I used Stattersfield *et al.* (1998: 199-203, 210-215) and Ridgely & Greenfield (2001: 63-68). For the threat status, I exclusively employed lists based on the official IUCN threat categories (i.e., IUCN 2001, Gärdenfors *et al.* 2001), that is BirdLife International (2009) for the global level and Granizo *et al.* (2002) for the national level. For mammal taxonomy, I follow Tirira (2007), and for the global and national threat status of the species I consulted IUCN (2011) and Tirira (1999), respectively.

I used *EstimateS* 6.0b (Colwell 2000) to extrapolate total species richness; cf. Colwell & Coddington (1994), Keating & Quinn (1998), Colwell (2001), and Herzog *et al.* (2002) for discussions and evaluations of these methods, and Jahn (in press) for the richness statistics computed and the settings used. The estimators were determined for the raw data of each complete survey, for pairs of pooled data sets (e.g., 'AWAC3+4'), and for all three transects together. However, at least two samples are required for the calculation of incidence-based estimators, in contrast to abundance-based statistics. As a result, only ACE and Chao 1 could be computed for all data sets.

I have to emphasize that raw transect-mapping data are not 'valid' samples in the sense of statistical models, as they contain repeatedly recorded individuals. However, Jahn (in press) has demonstrated that some species richness statistics may still produce very realistic estimates even with such 'pseudo-abundance' data.

Using *EstimateS* 6.0b (Colwell 2000) I also determined diversity indices Fisher's α, Shannon's *H'*, and Simpson's *D*, according to the equations stated in Magurran (1988) and Hayek & Buzas (1996); see Colwell (2001) for details. However, the information-theory-based diversity statistics, such as Shannon's *H'* and Simpson's *D*, have been discredited on many occasions (cf. Magurran (1988) and Jahn (in press) and references therein); therefore, they are shown here only for facilitating comparisons with other studies. For a preliminary comparison of bird diversity between transects, I calculated four similarity indices, two qualitative (incidence-based) indices (Jaccard and Sørensen I) and two quantitative (abundance-based) indices (Sørensen II and Morisita-Horn), according to the equations in Magurran (1988: 95), using *EstimateS* 6.0b (Colwell 2001).

In order to demonstrate how the conservation value of study sites can be assessed by analyzing the composition of their avian communities, I looked at the species' habitat preferences, and at the presence/absence of threatened and endemic bird taxa. The sum of 'threat status values' (sensu Jahn in press: Table 53) was calculated on the basis of the number of threatened and near-threatened species times an exponentially increasing factor reflecting the severity of the species-specific extinction risks: NT = 1, VU = 3, EN = 9, and CR = 27. In contrast to the $\log_2$ scale proposed by the aforementioned publication, here I used an even stronger gradient ($\log_3$) in order to pronounce the severity of extinction risk in the higher threat categories. Furthermore, I applied the 'bird community index' approach described by Bradford *et al.* (1998) and Canterbury *et al.* (2000), which analyzes the entire avian community as an indicator of forest condition at the local level; cf. Jahn (in press) for details.

RESULTS

General results of the transect-mapping surveys. – In the standardized study of AWAC1, AWAC3, and AWAC4, I mapped 11 401 birds with 8049 observations. They consisted of 42 families, 170 genera, and 226 species (Table 3). Simultaneously with the birds, I made 112 mammal observations with 108 records, belonging to seven families, eight genera, and eight species (Table 4). In the surveys of AWAC1, I recorded 4732 birds with 3441 observations (0.90 records per minute), representing 158 species. At AWAC3, I noted 3472 birds with 2416 observations (0.75 records per minute) of 125 species. The corresponding figures for AWAC4 were 3197 birds, 2192 records (0.65 observations per minute), and 124 species.

TABLE 3: Taxonomic summary of the bird survey results at AWAC1, AWAC3, and AWAC4.

	Transect			
Taxonomic units	AWAC1	AWAC3	AWAC4	All
Families	40	33	34	42
Genera	125	107	103	170
Species	158	125	124	226

TABLE 4: Taxonomic summary of the mammal survey results at AWAC1, AWAC3, and AWAC4.

	Transect			
Taxonomic units	AWAC1	AWAC3	AWAC4	All
Families	2	6	5	7
Genera	3	7	6	8
Species	3	7	6	8

Avian endemics. – A total of 43 endemic bird taxa were detected during the standardized surveys, representing 19.0 % of all species observed (Appendix 1). Most of them represent the endemic centers 'Chocó Lowlands' and 'Western Andean Slopes' sensu Ridgely & Greenfield (2001). The absolute number and proportion of endemics was considerably higher in the foothill zone than in the lowlands (Table 8). At AWAC4 endemic species represented almost a quarter (24.2 %; n = 30) of the bird community, in comparison with only 12.7 % (n = 20) at AWAC1. At the latter transect at least three taxa of the 'Tumbesian Lowlands' endemics were among the group of range-restricted species.

Threatened bird species. – Not less than 17 (7.5 %) of the bird species recorded are considered to be either threatened or near-threatened at the global level (BirdLife International 2009), whereas 64 (28.3 %) are listed for Ecuador (Granizo *et al.* 2002; Appendix 1). Their numbers were almost identical for AWAC1 and AWAC4, and somewhat lower for AWAC3 (Table 8). However, taking into account the severity of threat, it should be emphasized that globally Endangered species were present only at the foothill transects, viz. *Penelope ortoni* and *Ara ambiguus.* Not surprisingly the threat status values of the latter two transects were higher than those of AWAC1 for both global and national levels. At AWAC3 and AWAC4 I also noted courtship display sites (leks) of *Cephalopterus penduliger* (VU). Two other Vulnerable species were exclusively detected at AWAC4, *Micrastur plumbeus* and *Chlorospingus flavovirens.* Furthermore, La Carolina ridge holds the highest population density of *Pittasoma rufopileatum* (NT) of any of the more than 20 study areas, which I have surveyed in the Ecuadorian Chocó between 1997 and 2009 (total effort > 500 transect-mapping samples). On the other hand, the transect area of AWAC1 is also of key importance for the conservation of various Vulnerable bird taxa, such as *Ortalis erythroptera, Aramides wolfi, Capito quinticolor,* and *Dacnis berlepschi.*

Only one globally threatened mammal was detected (AWAC4), the Bush Dog *Speothos venaticus* (VU). However, this record was exclusively based on tracks crossing the trail (not following it, as would be expected in the case of a domesticated dog, according to local hunters), and thus needs further confirmation. The only primate recorded during the surveys (AWAC3), was the White-throated Capuchin *Cebus capucinus*, listed as Vulnerable at the national level.

Game Species. – The populations of most large mammals and game birds on the survey sites appeared to be depleted or extirpated. The situation was critical in the Río Durango – Río Bogotá area, with only three species of larger mammals detected at low densities. The conditions were considerably better at La Carolina ridge, where populations of some heavily hunted mammals (i.e., *Mazama americana* and *Cebus capucinus*) and some larger species of threatened birds persisted (see previous paragraph). Nevertheless, the lowland site was also an important refuge for some large bird species, particularly raptors (n = 10 species), the threatened cracid *Ortalis erythroptera*, and the heron *Tigrisoma lineatum*. The latter species has been almost extirpated in western Ecuador (Ridgely & Greenfield 2001). That is, the population found in the Awacachi Corridor is of great importance for the species' survival in the country's coastal lowlands. *Tinamus major*, another game bird species, which quickly disappears in over-hunted areas, was also present in at least two territories at AWAC1.

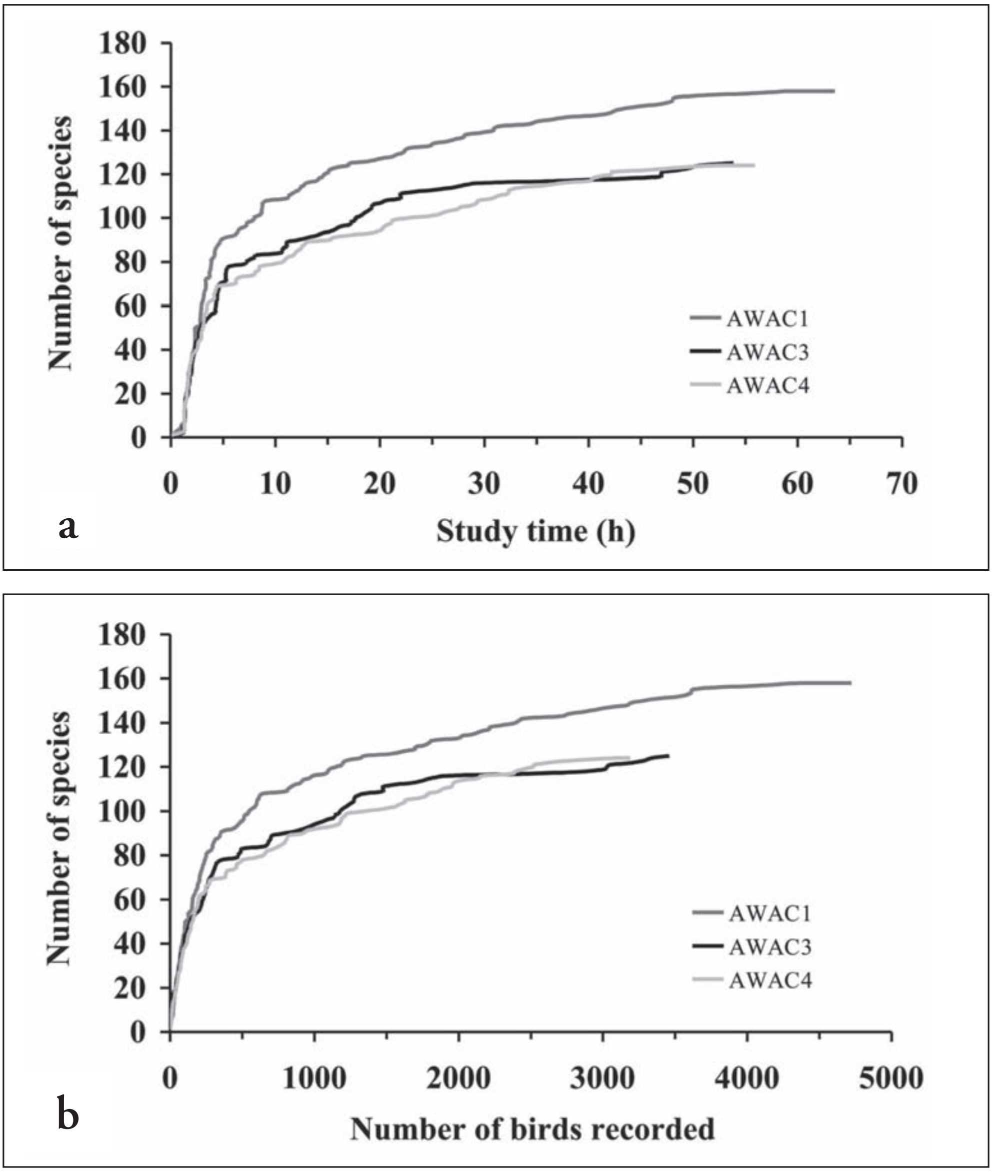

FIG. 1. Comparison of bird species accumulation during standardized transect-mapping (MTW) surveys at transects AWAC1, AWAC3, and AWAC4; (a) number of species versus study time, and (b) number of species versus number of 'birds recorded' (raw data, which include an unknown number of repeatedly observed individuals). AWAC1 represents a disturbed lowland forest in the Río Durango – Río Bogotá area, whereas AWAC3 and AWAC4 were covered by homogeneous primary foothill forest.

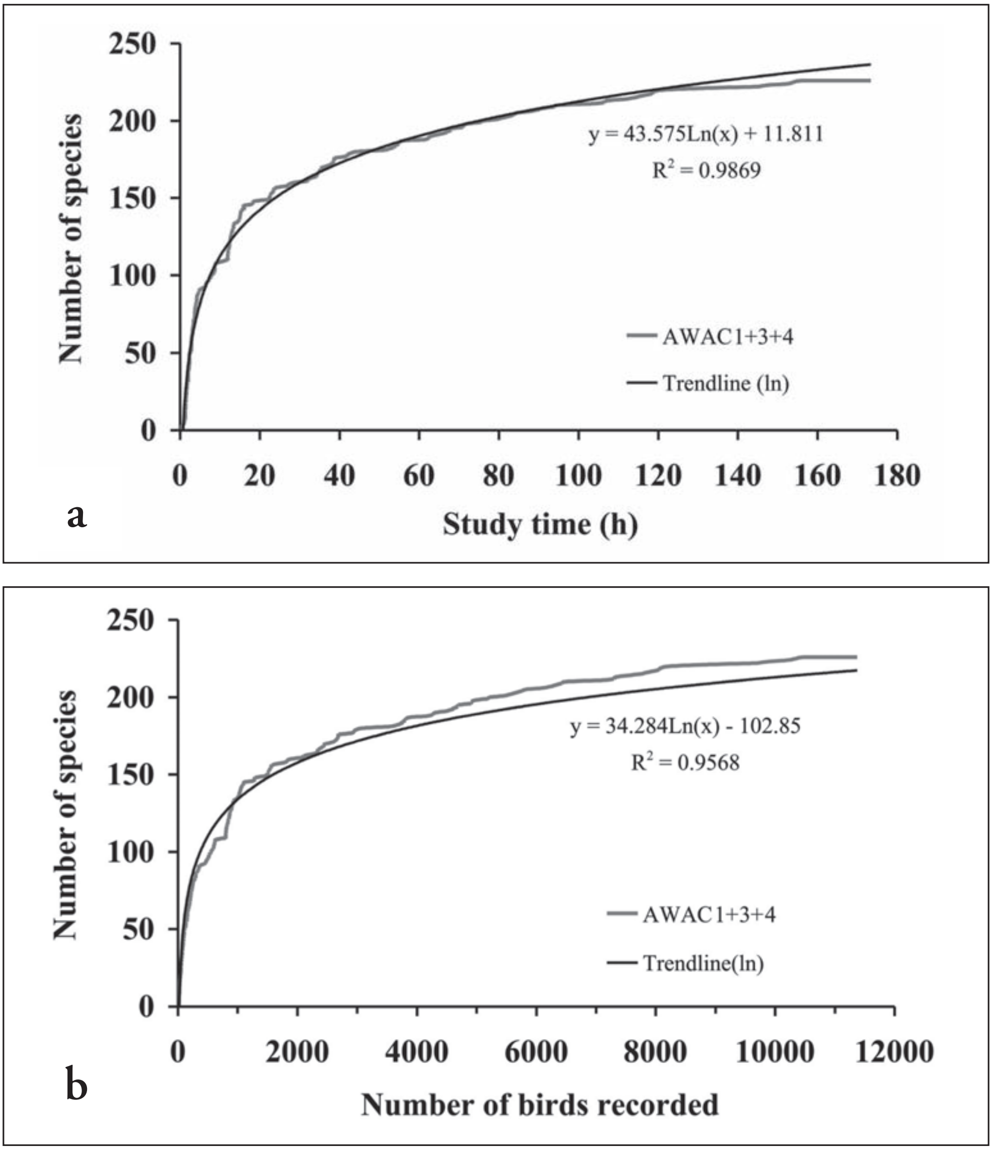

FIG. 2. Bird species accumulation according to the pooled transect-mapping (MTW) data of transects AWAC1, AWAC3, and AWAC4; (a) number of species versus study time, and (b) number of species versus number of 'birds recorded'.

Bird species accumulation. – Species accumulation for the two transects at the Carolina ridge was very similar, with graphs flattening out after about 30-35 h of surveying or 2000-2500 'birds recorded' (Fig. 1a,b). By contrast, at AWAC1 species accumulation continued for about 50 h or 3500 'birds recorded', reflecting the higher species richness and abundance of the lowland transect. It should be emphasized that the 26 % higher species richness at AWAC1, in comparison with AWAC3 and AWAC4, was not the result of the 14 % higher survey effort at the former transect, because only two (1.3 %) additional species were detected there in the last 10 survey hours. For the pooled data set of all three transects the graph flattened out after about 120 h or 9000 'birds recorded' (Fig. 2a,b). Lognormal functions fit the species accumulation graphs of transect-mapping data very well, as demonstrated by the high 'coefficient of determination' values ($R^2 \geq 0.94$) of all the individual and pooled data sets analyzed (cf. Table 5).

Estimation of total avian species richness. – Species accumulation curves (Figs. 1 and 2) and species richness estimators (Table 5) indicate that the bird surveys were almost complete. According to the higher limits of the Chao1 estimates, I detected between 87 and 93 % of all core species (sensu Remsen 1994) present in the transect areas during the survey period. Using the incidence-based statistics MMRuns and MMMean, which require at least two data sets to be computed, the number of core species present at La Carolina ridge can be estimated at 176 bird taxa, of which I detected c. 83 % (n = 146) during the surveys.

Diversity indices and similarity coefficients. – As expected on the basis of species accumulation graphs (Figs. 1 and 2), diversity index Fisher's α was very similar for transects AWAC3 and AWAC4 (Tables 6 and 8), although the number of shared species and similarity coefficients indicate that their diversity was not identical (Table 7). By contrast, diversity was considerably higher in the lowlands than in the foothills and their bird community composition also was very different.

Bird Community Index. – The BCI_{forest} values were highest for transect AWAC4, intermediate for AWAC3, and much lower for AWAC1 (Table 8).

DISCUSSION

Assessment of the conservation status of the transect areas. – According to the standardized transect-mapping surveys, bird species richness and diversity was higher at the lowland transect than in the Carolina-ridge area (Table 8). However, if we look at the habitat selection of the birds, it quickly becomes clear that AWAC1 was more species-rich and diverse only because of the greater extent and variety of disturbed habitats and edge effects there. AWAC3 and AWAC4 held more forest species than AWAC1, whereas the number of forest-edge and open-country taxa was much higher at the latter transect. The disturbed character of the habitats in the Río Durango – Río Bogotá area is clearly reflected by its much lower bird community index (BCI_{forest}) value in comparison with that of the foothill transects. Interestingly, the BCI_{forest} value of AWAC1 was similar to that of two habitat mosaics of semi-open country, forest edges, young successional vegetation, and forest in the Río Santiago floodplain of Playa de Oro (BCI_{MNT1} =

TABLE 5: Observed and estimated avian species richness and number of 'birds recorded' during standardized transect-mapping surveys at AWAC1, AWAC3, and AWAC4. Abbreviations used: (a) data set: xy&yz = 'independent' data sets of the transects; xy+yz = 'pooled' data sets; (b) field data: N_{ds} = number of data sets used for the calculation of the species richness estimators; S_{obs} = number of species observed; N_b = number of 'birds recorded' (raw MTW data, which include an unknown number of repeatedly observed individuals); (c) species richness estimator: see methods for details.

	Field data [b]			Species richness estimator [c]								
Data set [a]	N_{ds}	S_{obs}	N_b	ACE	ICE	Chao1	Chao2	Jack1	Jack2	Bootstrap	MMRuns	MMMean
AWAC1	1	158	4732	171.6		169.4 ±7.7						
AWAC3	1	125	3472	135.4		136.0 ±8.4						
AWAC4	1	124	3197	131.2		128.7 ±4.3						
AWAC1+3	1	218	8204	234.0		228.1 ±6.2						
AWAC1&3	2	218	8204	234.0	654.6	228.1 ±6.2	394.2 ±39.1	294.5 ±16.5	294.5	256.3	591.5	467.3
AWAC1+4	1	210	7929	222.0		216.4 ±4.5						
AWAC1&4	2	210	7929	222.0	543.5	216.4 ±4.5	339.5 ±29.7	279.0 ±17.0	279.0	244.5	491.7	405.6
AWAC3+4	1	146	6669	154.6		161.1 ±12.2						
AWAC3&4	2	146	6669	154.6	185.5	161.1 ±12.2	154.7 ±4.2	167.5 ±0.5	167.5	156.8	176.5	176.4
AWAC1+3+4	1	226	11401	237.5		236.0 ±6.5						
AWAC1&3&4	3	226	11401	237.5	348.2	236.0 ±6.5	309.7 ±22.1	295.3 ±45.6	319.5	259.2	351.5	336.9

TABLE 6: Diversity indices according to the observed avian species richness and number of birds recorded during standardized transect-mapping surveys at AWAC1, AWAC3, and AWAC4. For AWAC3 and AWAC4 values represent within-habitat α (*alpha*) diversity as these transects were located within homogeneous habitat. In the case of AWAC1 values should be regarded as landscape-level γ (*gamma*) diversity, as this transect was located in a habitat mosaic. Finally, the combined data sets of AWAC1 and the Carolina ridge transects represent regional ε (*epsilon*) diversity. Abbreviations used: (a) data set: see Table 5; (b) field data: see Table 5; (c) diversity index: see methods.

	Field data ^{b}			Diversity index ^{c}		
Data set ^{a}	N_{ds}	S_{obs}	N_b	Alpha	Shannon	Simpson
AWAC1	1	158	4732	31.48 ±1.15	4.28	48.56
AWAC3	1	125	3472	25.38 ±1.06	4.01	35.14
AWAC4	1	124	3197	25.66 ±1.09	4.06	38.84
AWAC1+3	1	218	8204	41.13 ±1.23	4.58	63.30
AWAC1&3	2	218	8204	41.13 ±1.23	4.58	63.30
AWAC1+4	1	210	7929	39.59 ±1.21	4.58	64.29
AWAC1&4	2	210	7929	39.59 ±1.21	4.58	64.29
AWAC3+4	1	146	6669	26.37 ±0.94	4.08	37.88
AWAC3&4	2	146	6669	26.37 ±0.94	4.08	37.88
AWAC1+3+4	1	226	11401	39.95 ±1.12	4.56	60.52
AWAC1&3&4	3	226	11401	39.95 ±1.12	4.56	60.52

– 0.049 and BCI_{MNT2} = 0.541; Jahn in press). In the present study, the remotest and least species-rich transect (AWAC4) revealed the highest BCI_{forest} value. The latter transect also had the highest proportion of endemic and threatened species. Although AWAC4's total number of threatened and near-threatened species was almost identical to that found at AWAC1, its 'threat status values' were higher, both on global and national levels. In conclusion, AWAC4 had the highest conservation value of the three transects surveyed. Comparing transects AWAC1 and AWAC3, the latter also had a higher proportion of endemic species and higher threat status values. However, it should be pointed out that the bird species composition and ecological situation of AWAC1 was so distinct from the foothill transects that they are hardly comparable (Table 7). Taking into account that the Chocoan lowland forests of Ecuador have been almost completely destroyed and that altitudes below 100 m a.s.l. represent only a tiny fraction of the Awacachi Corridor and of other protected areas in the region, then the conservation value of the Río Durango – Río Bogotá area must be regarded as extremely high and its status as critical. The presence of some large and sensitive bird species make it likely that the hunting pressure has been declining

TABLE 7: Similarity coefficients comparing avian diversity between transects. The quantitative coefficients are based on 'birds recorded' during transect-mapping surveys. Abbreviations used: (a) data set: mentioned are the transect codes; (b) field data: S_{obs} = number of species observed in samples 1 and 2; shared S_{obs} 1&2 = number of species shared; (c) shared S_{est} 1&2 = coverage-based estimator for shared species (cf. Colwell 2000); (d) similarity coefficients: see methods for details.

Data set ^{a}		Field data ^{b}				Similarity coefficient ^{d}			
				Shared	Shared	(qualitative)		(quantitative)	
1	2	S_{obs} 1	S_{obs} 2	S_{obs} 1&2	S_{est} 1&2 ^{c}	Jaccard	Sørensen I	Sørensen II	Morisita-Horn
AWAC1	AWAC3	158	125	65	73.9	0.30	0.46	0.28	0.32
AWAC1	AWAC4	158	124	72	73.4	0.34	0.51	0.29	0.36
AWAC3	AWAC4	125	124	103	110.6	0.71	0.83	0.79	0.93

there in recent years, making it possible that populations of overhunted mammals (e.g., sloths, monkeys, deer, and peccaries) might also experience a slow comeback in the future. In general, all sites studied in the Awacachi Corridor have the potential to maintain and recover populations of large mammals and birds, whenever hunting can be effectively controlled and the area's forest cover maintained.

Effectiveness and efficiency of transect mapping in bird surveys. – Previous studies demonstrated that Chao1 (and ACE) tend to underestimate true species richness of tropical bird communities (Herzog *et al.* 2002, Jahn in press). Thus, the high single-survey detection rates found in the present study are not conclusive. However, Jahn (in press) also showed that the incidence-based statistics MMRuns and MMMean produce very accurate estimations when calculations were based on at least two data sets of 24 MTW samples per transect. Similar ecological conditions of the study sites are another important prerequisite for obtaining reliable estimates with so few replicates (see next subchapter). As these conditions were fulfilled for AWAC3 and AWAC4, it seems likely that I really detected over 80 % (n = 146) of the total bird species richness present at the Carolina ridge with a survey effort of only 13 man-days (109.7 h). However, additional core species, particularly altitudinal and latitudinal migrants, should be expected to visit the ridge during other months of the year. In consequence, total species-richness estimates are likely to increase with future surveys.

Interestingly, Salaman and co-workers recorded almost the same number of avian taxa (n = 141) in a premontane Chocoan forest at Patio (500 m), Junín, Nariño Dept., southwestern Colombia (Salaman 1994). Their survey methods included mist netting and non-systematic observations. However, in comparison with the present work their study effort in order to accumulate this number of species was 5.4-fold higher (70 man-days). For instance, with a mist-netting effort of 44 708 MNH (= Mist-Net Hours), corresponding to a survey period of about two to four weeks, they detected the presence of 80 taxa, that is, only 55 % of the species richness reported in this study. Although other time-efficient bird survey methods do exist, namely the 'random-walk' approach in combination with 5-, 10- or 20-species lists (Fjeldså 1999, Herzog *et al.* 2002), Jahn (in press) pointed out that the latter method only produces species lists as well as rough estimates of relative abundance and total species richness. By contrast, transect mapping allows the estimation of absolute population densities and biomass with a field effort of approximately one week per transect (Jahn in press). Furthermore, MTW survey data can be georeferenced with minimal effort, revealing the precise distribution patterns of the birds in the transect areas. However, it must be emphasized that any survey method can capture only the situation at the moment when the samples are carried out. Thus for monitoring purposes it should be taken into account that even in the 'stable' humid tropics the detectability of species and territories fluctuates in time due to various factors (cf. Stutchbury & Morton (2001) and Jahn (in press) and citations therein): (a) lunar cycles (i.e., most nocturnal species are easier recorded during nights around full moon); (b) weather (e.g., poor climatic conditions decrease the detectability of most species); (c) seasonal movements influence the presence/absence and abundance of migrants; (d) asynchronous breeding may cause different territories of the same species to have unequal chances of being detected; and (e) unusual reproduction periods (some synchronous breeding birds tend to reproduce during periods when most other species do not breed). In conclusion, at least two complete MTW monitoring surveys per year and transect should be carried out, one in the rainy season and another in the dry season.

Assessment of the total bird species richness of the Awacachi Biological Corridor. – Evidently it is not possible to estimate the total species richness of the study area with only two transects, even if they represented the ecological extremes of the reserve (i.e., disturbed humid tropical forest vs. primary pluvial premontane forest), like the transect pairs 'AWAC1&3' and 'AWAC1&4' (Table 5). The variance of the richness estimates is clearly too high to be conclusive. This holds true even for the MMRuns and MMMean estimates, which fluctuated between 406 and 592 core species. In contrast to the equal-habitat pair 'AWAC3&4' for which the Michaelis-Menten statistics produced identical estimates (Δ = 0.1 species), the difference for the aforementioned unequal-habitat pairs was very large, with 124 and 86 species, respectively. Interestingly, the difference was much lower when the estimates were based on all three transects together (Δ = 15 species). Assuming that the latter estimates come much closer to reality than those obtained with only two unequal-habitat transects, the total avian diversity of the reserve can be roughly estimated at 337 to 352 core species. According to Jahn (in press), core species represented about 87 % of the bird species recorded in Playa de Oro, an intensively studied area, which is located only a few kilometers to the south of the Awacachi Corridor. That is, including non-core taxa (vagrants) the total species richness of the Awacachi Corridor can be estimated at c. 387 to 405 bird taxa. However, it is likely that somewhat higher estimates will be obtained when transects from additional life zones (e.g., wet premontane forest) and habitats (e.g., roadside habitats) have been considered in the analysis. All in all, these numbers are very similar to those reported from Playa de Oro, where 344 avian species were recorded until 2009 and total richness is estimated to be > 400 bird species (Jahn in press).

Animal community characteristics that should be monitored in the long term. – One of the principal objectives of nature reserves is to maintain their biodiversity. Consequently, threatened species are of key importance for monitoring the success of conservation actions. Transect mapping not only facilitates the effective assessment of the presence of red-listed species but also of their absolute population densities (Jahn in press). Thus, even if the total number of threatened species were stable over certain time periods, changes in their conservation status still can be detected by monitoring their population sizes. 'Threat status values' can be used for comparing the importance of particular transects for threatened species and the bird community index (BCI_{forest}) for assessing changes in the sites' general habitat quality (Table 8). For example, if the forest cover at transect AWAC1 slowly recovered in coming years, its BCI_{forest} values should also increase. Likewise, if local people began to illegally extract timber at 'La Carolina' ridge the area's BCI_{forest} values should decrease considerably, because forest-edge and non-forest species would start to colonize the newly created gaps and clearings. Finally, changes in hunting pressure can be assessed by observing the presence/absence and population densities of larger mammals and birds.

The number and especially the proportion of endemic taxa should also be monitored. Although past studies have demonstrated that the presence of endemic taxa is a poor predictor for the conservation status of habitat mosaics (Jahn in press), their proportion of the bird community still could be an important indicator for the status of pristine habitats, given that most range-restricted taxa of the Chocó region are also forest inhabitants. For instance, the proportion of endemic bird species at La Carolina ridge, particularly AWAC4, might decrease with increasing disturbance. Likewise, at AWAC1 the ratio between Tumbesian and Chocoan endemics could considerably change over time, with ongoing shifts in regional and global climate patterns to drier conditions and more pronounced seasonality of precipitation.

In general, changes in absolute population densities of all species that occur at a sufficient number of transects ($n \geq 4$) and at different densities (avoiding tied ranks in nonparametric tests) should be monitored. In order to facilitate statistical testing of changes in key characteristics of the animal communities, the number of survey units in the Awacachi Corridor should be increased to at least eight transects. Additional transects should be established in the Cotacachi-Cayapas Ecological Reserve and Awá Reserve to get comparative data on the conservation status of these important remnants of Chocoan forest, which, doubtlessly, are the main sources for the recolonization of the Awacachi Corridor with locally extinct species, particularly game birds and mammals. In this context, transect mapping might be the best option for applying not only a valid statistical design but also for collecting long-term data for a large number of species (Jahn in press).

Conclusive remarks on assessing the conservation status of tropical forests. – At the local level, bird species richness and diversity indices are poor predictors of habitat quality and conservation status. Whereas birds that depend on mature forest tend to decrease considerably after changes in the forest structure, forest-edge and open-country species might colonize the disturbed habitat. Depending on the biogeographic region or biome, the latter group may mask or outnumber species loss suffered by habitat specialists (Jahn in press). One important lesson learned from the example presented here is that the conservation value of study sites should be ranked on the basis of a detailed comparison of the habitat selection and threat status of the bird species. The central questions of environmental assessments should not be, "How many bird species? / How many individuals?" but, "Which species? / How regularly in which habitats and at which sites? / How sensitive in the face of habitat alteration and human disturbance?" and, "How threatened at regional and global levels?" (Flade 1994, Jahn 2001). Whenever feasible, the entire bird community should be taken into account, instead of only one or a few indicator species, like flagships and umbrellas, which might be doubtful surrogates for the integrity of ecosystems and the

TABLE 8: Assessment of the conservation status of transects AWAC1, AWAC3, and AWAC4, based on transect-mapping data. Number of avian species (N_{spp}) and proportion of total species richness recorded in different classes of main habitats, endemic bird areas, as well as international threat status categories (IUCN 2001). 'Threat status values', diversity index Fisher's α, and the bird community index (BCI_{forest}) are also stated; see methods for details. Note: some of the taxa listed here according to Ridgely & Greenfield (2001) as restricted-range species were not regarded as endemic species by Stattersfield *et al.* (1998).

	AWAC1		AWAC3		AWAC4	
Categories	N_{spp}	%	N_{spp}	%	N_{spp}	%
Species richness	158	100	125	100	124	100
Main habitat						
- Forest	89	56.3	112	89.6	113	91.1
- Forest edge	41	26.0	13	10.4	8	6.5
- Open country	15	9.5				
- River and stream edges	11	7.0			3	2.4
- No preferences	2	1.3				
IUCN threat status category						
World (BirdLife International 2009)						
- Endangered (EN)			2	1.6	2	1.6
- Vulnerable (VU)	4	2.5	1	0.8	3	2.4
- Near Threatened (NT)	5	3.2	2	1.6	5	4.0
Sum	9	5.7	5	4.0	10	8.6
'Threat status value'	17		23		32	
Ecuador (Granizo *et al.* 2002)						
- Critically Endangered (CR)			1	0.8	1	0.8
- Endangered (EN)	6	3.8	6	4.8	6	4.8
- Vulnerable (VU)	19	12.0	15	12.0	20	16.1
- Near Threatened (NT)	18	11.4	16	12.8	17	13.7
Sum	43	27.2	38	30.4	44	35.5
'Threat status value'	129		142		158	
Endemic species						
sensu Stattersfield *et al.* (1998)						
- Chocó	11	7.0	15	12.0	20	16.1
- Tumbesian region	1	0.6				
Sum	12	7.6	15	12.0	20	16.1
sensu Ridgely & Greenfield (2001)						
- Chocó lowlands	17	10.8	14	11.2	18	14.5
- West slope of Andes			12	9.6	12	9.7
- Tumbesian lowlands	3	1.9				
Sum	20	12.7	26	20.8	30	24.2
Ecological indices						
- Fisher's α	31.5 ± 1.6		25.4 ± 1.1		25.7 ± 1.1	
- BCI_{forest}	0.457		2.088		2.539	

ecological functioning of landscapes (Jahn in press). Range-restricted taxa and threatened species themselves perform well as indicator groups. Consequently, these species should be integrated into any approaches of habitat management and landscape planning procedures. Additional information on the impact of hunting can be obtained by assessing larger mammals together with the birds.

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APPENDIX 1: Endemic and threatened bird species of transects AWAC1, AWAC3, and AWAC4 (n = 80 of 226 species). Abbreviations used: (a) Endemic bird area: Cho1 = Chocó EBA 041 sensu Stattersfield *et al.* (1998); Cho2 = Chocó lowlands (Ridgely & Greenfield 2001); Tum1 = Tumbesian region EBA 045 sensu Stattersfield *et al.* (1998); Tum2 = Tumbesian lowlands (Ridgely & Greenfield 2001); RM2 = Río Marañón valley (Ridgely & Greenfield 2001); wAnd2 = western Andean slope (Ridgely & Greenfield 2001); eAnd2 = eastern Andean slope (Ridgely & Greenfield 2001); (b) Threat status: threat status categories sensu IUCN (2001): NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; Ecuador = national threat status (Granizo *et al.* 2002); World = global threat status (BirdLife International 2009). Note: some of the taxa listed here according to Ridgely & Greenfield (2001) as restricted-range species were not regarded as endemic species by Stattersfield *et al.* (1998).

		Threat status ^{b}		Transect		
Scientific name	Endemic bird area ^{a}	Ecuador	World	AWAC1	AWAC3	AWAC4
Crypturellus berlepschi	Cho1, Cho2	EN			1	1
Leucopternis plumbeus		VU	NT	1	1	1
Leucopternis semiplumbeus		EN		1		
Leucopternis princeps		VU			1	1
Micrastur plumbeus	Cho1, Cho2	EN	VU			1
Ortalis erythroptera	Tum1, Tum2, RM2	VU	VU	1		
Penelope ortoni	Cho1, Cho2	EN	EN		1	1
Odontophorus erythrops		VU		1	1	1
Rhynchortyx cinctus		EN		1	1	1
Aramides wolfi	Cho2	EN	VU	1		
Columba goodsoni	Cho1, Cho2	VU		1	1	1
Leptotila pallida	Cho2			1		
Geotrygon purpurata	Cho2	VU			1	1
Geotrygon veraguensis		EN		1		
Ara ambiguus		CR	EN		1	1
Touit dilectissimus		NT			1	
Pionopsitta pulchra	Cho1, Cho2	VU		1	1	1
Pionus chalcopterus		VU		1	1	1
Amazona autumnalis		EN		1	1	
Otus centralis		NT		1	1	1
Glaucidium griseiceps		VU				1
Nyctiphrynus rosenbergi	Cho1, Cho2	VU	NT	1		1
Phaethornis yaruqui	Cho2			1	1	1
Androdon aequatorialis		NT			1	1
Amazilia rosenbergi	Cho1, Cho2			1	1	1
Chalybura urochrysia		VU			1	1
Coeligena wilsoni	Cho1, wAnd2					1
Boissonneaua jardini	Cho1, wAnd2				1	
Trogon comptus	Cho1, Cho2	NT			1	1
Capito squamatus	Cho1, Cho2	NT	NT	1		
Capito quinticolor	Cho1, Cho2	EN	VU	1		
Pteroglossus sanguineus	Cho2	VU		1	1	1
Ramphastos brevis	Cho1, Cho2	VU		1	1	1
Ramphastos swainsonii		VU		1	1	1
Piculus litae	Cho1, Cho2	VU		1		
Celeus loricatus		NT		1	1	1
Veniliornis chocoensis	Cho1, Cho2	VU	NT			1
Campephilus gayaquilensis	Tum2	VU	NT	1		
Hyloctistes virgatus		NT		1	1	1
Dendrocolaptes sanctithomae		VU		1		
Xiphorhynchus lachrymosus		VU		1		
Xiphorhynchus erythropygius		NT		1	1	1
Dysithamnus puncticeps		NT			1	1

		Threat status [b]		Transect		
Scientific name	Endemic bird area [a]	Ecuador	World	AWAC1	AWAC3	AWAC4
Hylophylax naevioides		NT		1		
Myrmeciza immaculata		NT		1	1	1
Myrmeciza nigricauda	wAnd2				1	1
Myrmeciza berlepschi	Cho1, Cho2	NT		1		1
Phaenostictus mcleannani		VU		1	1	1
Pittasoma rufopileatum	Cho1, Cho2	VU	NT		1	1
Hylopezus perspicillatus		VU				1
Scytalopus chocoensis	wAnd2	EN			1	1
Rhynchocyclus pacificus	Cho2	NT		1		
Myiophobus phoenicomitra	wAnd2, eAnd2				1	
Contopus cooperi			NT			1
Rhytipterna holerythra		NT		1	1	1
Conopias albovittatus		NT		1		1
Tyrannus niveigularis	Tum2			1		
Lipaugus unirufus		VU			1	1
Cephalopterus penduliger	Cho1, Cho2	EN	VU		1	1
Machaeropterus deliciosus	Cho1, wAnd2				1	1
Thryothorus leucopogon		NT		1	1	1
Cyphorhinus phaeocephalus		NT		1		
Polioptila schistaceigula		VU		1		1
Basileuterus chlorophrys	wAnd2				1	1
Dacnis venusta		NT		1		
Dacnis berlepschi	Cho1, Cho2	VU	VU	1		
Erythrothlypis salmoni	Cho1, wAnd2	NT			1	1
Tangara rufigula	wAnd2				1	1
Tangara palmeri	wAnd2	NT			1	1
Tangara johannae	Cho1, Cho2	VU	NT	1		
Tangara lavinia		NT		1	1	1
Bangsia rothschildi	Cho1, Cho2	VU			1	1
Bangsia edwardsi	Cho1, wAnd2				1	1
Chlorothraupis stolzmanni	wAnd2				1	1
Heterospingus xanthopygius	Cho2	NT		1	1	1
Chlorospingus flavovirens	Cho1, Cho2		VU			1
Chlorophonia flavirostris	Cho1, wAnd2				1	1
Euphonia fulvicrissa		NT		1		
Cacicus microrhynchus		NT		1	1	1
Zarhynchus wagleri		VU		1		
Total = 80	43	64	17	47	49	56

NESTING OF THE WHITE-RUMPED SHAMA (*COPSYCHUS MALABARICUS*) IN SOUTHERN VIETNAM

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ABSTRACT

We describe nesting of the White-rumped Shama (*Copsychus malabaricus*) in artificial and natural nest cavities in lowland tropical forest and seral stage habitats at Cat Tien National Park and Biosphere Reserve in southern Vietnam. The data was collected from March 7 until July 7 in 2008 in Cat Tien National Park, South Vietnam, on 168 artificial nesting boxes. All taken nest boxes were occupied only by White-rumped Shama. It took up boxes in all studied habitats: in the Lagerströemia forest 61.5% of nest boxes was occupied, in shrub habitat (low brush and bamboo tangles) 55.8%, and in forest edges 44.1%. Clutches were found in 73 boxes (43.4%). The full clutches contained 1–4 eggs, most of them (62%) had three eggs. In average, the hatching was observed 13.4 days after egg-laying. The size of Shama male's territory was 0.3 ha. Nest-building, brooding, feeding of young, nest predation, interspecific competition for breeding sites in native natural habitat are described.

Key words: White-rumped Shama, Copsychus*, artificial nest boxes, hole-nesting birds, southern Vietnam.*

INTRODUCTION

This study forms part of a major ecological research effort conducted by the Joint Russian-Vietnamese Tropical Research and Technological Centre. The main goal for the scientific program of this Institute is to study the diversity, structure and dynamics of Vietnam's forest ecosystems. Ornithological research was begun in 1989. During the early period of operations, most of the work involved short-term visits to selected forest sites. Later we had the opportunity to broaden our surveys to include all major forest habitats throughout the country. As a result of this work, we now have a solid understanding of the diversity of ornithological communities in different forest types of Vietnam and pilot data on trophic niches and other aspects of the biology for most Vietnamese forest birds. With this sound foundation, we are now prepared to focus our attention on long-term investigations of the biology of individual bird species or small ecological or systematic groups on selected forest plots. One of these plots was established in Cat Tien Biosphere Reserve in the southern part of Vietnam.

Nesting in holes is an interesting phenomenon, especially in tropical forest where predation pressure and competition among hole-users is assumed to be high. Most hole-nesters in southeast Asian lowland tropical forest are nonpasserines: woodpeckers, barbets, hornbills, parakeets, owls and trogons. Most of these species nest in holes that are in high in the forest canopy (> 10–15 m), so detailed study of the nesting habits of these birds is not possible without the use of special techniques. Hole-nesting passerines of the area of study include two rather uncommon species of forest starlings (Common Hill-Mina *Gracula religiosa* and Golden-crested Myna *Ampeliceps coronatus*), the Velvet-fronted Nuthatch (*Sitta frontalis*) and two species of the genus *Copsychus*: the White-rumped Shama (*C. malabaricus*), one of the most common bird species in forests and forest

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edges in Vietnam; and the Oriental Magpie-Robin (*C. saularis*), a locally common bird of forest borders.

The White-rumped Shama and the Oriental Magpie-Robin are both insectivorous, middle-sized birds (Muscicapidae). Under natural conditions, shamas build cup-shaped nests in natural holes in tree trunks, tips of stumps, or in the basal stem clumps of bamboo. Magpie-robins also prefer hollows in the trunk of a tree trunk, but often use different kinds of fissures, e.g., interstices in cliffs or ricks of aerial roots (Collar 2005: 765–766; Siddique 2008). We chose hole-nesting birds for this initial study because they present three advantages over open-nesting species: 1) they often will accept artificial nest sites, allowing the researcher to set the parameters for nest location; 2) no nest-search is required; and 3) it is relatively simple to associate a particular pair with a specific nest site.

The main purpose of our study was to try to understand what features of the biology of these two model species favor hole-nesting in this rich tropical forest ecosystem. To this end, we placed nest-boxes in different habitats around the study area.

MATERIALS AND METHODS

The data were collected from March 7 until July 7 in 2008 in Cat Tien National Park and Biosphere Researve, Vietnam. Cat Tien is located 160 km NE from Hochimin City, Dongnai Province, 11°25'N, 107°25'E, c. 300 m above sea level. Climate is typically monsoon, with a wet season that usually includes the period from May or June to October or November. Mean annual temperature exceeds 18°C.

Our study plot was situated in an eastern part of the reserve in an area that is a mosaic of tall forest, different types of forest edges, shrub habitat (low brush and bamboo tangles), and grasslands with a few remaining forest trees, which was created by logging in the 1970s and 1980s. Several small depressions on the study area are flooded during the wet season from July to October.

Artificial nest boxes provide enhanced opportunities for intensive studies of hole-nesting species (Hume 1890; Gibson *et al.* 1982), and previous work has indicated that our study species would use such sites (Aguon & Conant 1994, Lock Nga Yi 2000, Yip 2006). Therefore, we determined to use artificial nest boxes in this study. In March of 2008, we distributed 158 nest boxes along 5 transects in different habitats (FIG. 1): 91 nest boxes in Lagerströemia forest, a habitat in which the dominant tree species include *Lagerströemia* sp., *Tetrameles nudiflora*, *Afzelia xylocarpa* and characterized by some disturbance by logging, a largely closed canopy, and considerable undergrowth; 43 boxes in shrubby, tree-less habitats with bamboo tangles (dominated by Poaceae and Zingiberaceae); and 24 boxes in forest edges, gardens, and overgrown Cashew and Grewia plantations with little closed-canopy. Later, at the end of May, another 10 boxes were placed in the territory of a pair of Magpie Robins located in forest edge.

We used black wooden nest boxes, 28 cm high and 15 cm square. The hole diameter was 5.5 cm; distance between it and top of the box was 11 cm. Boxes were placed on middle-sized trees, 1.5–3 m above ground. Distance between boxes normally 50 m, but sometimes less.

Nest boxes were regularly checked. All animals and their nests except the study species were removed. During the nest examination, all bird nests, clutches and young were described and measured, fledglings were ringed by metallic and colored plastic rings as well as adult birds which were trapped by mist-nets near the nest boxes (mainly females) or sometimes distant their nests (birds of both sexes).

We made observations near the nests and from different distances to collect data about bird's behavior but it was seen that our presence made some artificial impact in it, and this part of the work will be modified in future studies. Also observations on 45 h of behavioral observations were accumulated on males of three different pairs, at times supplemented by the stimulus of song playback.

RESULTS

During our first year of work, nest boxes were occupied only by one of the study species, the White-rumped Shama so our data on the Magpie-robin were limited to several observations of adult birds and one record of a fledgling. For the shama, we were able to ring and make observations on 28 adult females, 18 adult males, and 154 nestlings. Shamas used nest boxes in all types of habitat with evidence of some preference for tall forest (Fig. 2). The rather high breeding density in open areas was a surprise for us. One possible reasons for this behavior could have been our provision of nesting sites. Nest box occupancy rate was rather high: 95 of 168 boxes or 56.5% were used by birds for nest building, and clutches were found in 73 boxes (43.4%). The difference in boxes used for nest construction as opposed to those used for egg-laying occured because adult males

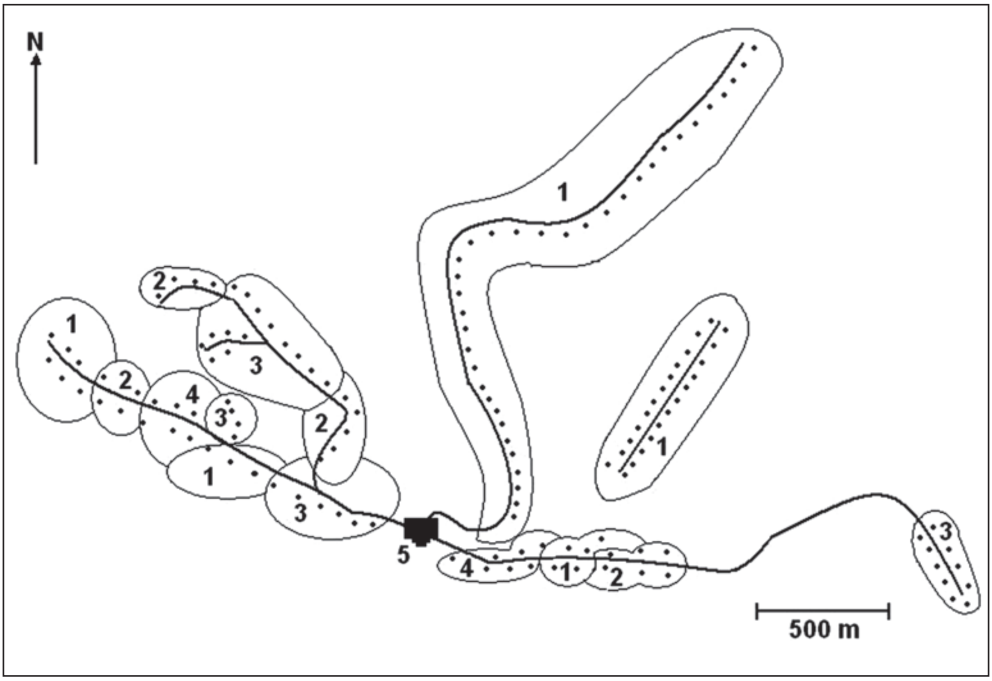

FIG. 1. Scheme of boxes distribution over different habitats. 1 – forest, 2 – bamboo, 3 – forest edges («garden»), 4 – shrub habitat (low brush and bamboo tangles), 5 – Reserve office

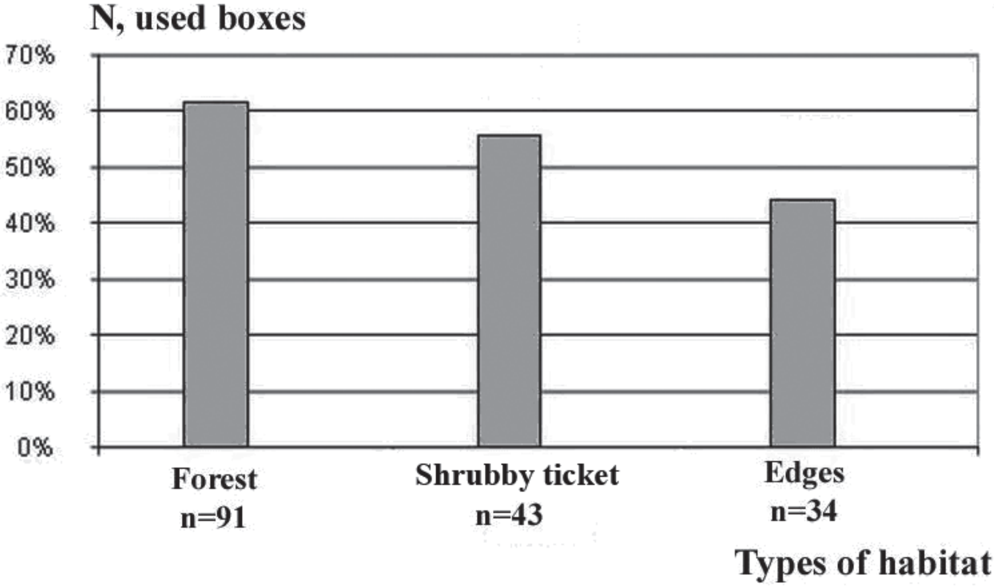

FIG. 2. Degree of box colonization by White-rumped Shama in different types of habitat

initiated nest construction in more than one box, among which females would select one to complete nest building and laying of the clutch (Aguon & Conant, 1994). Second clutches were observed in 19 nests (26 %), and in two cases third clutches of the same pairs were registered.

The density of shama nests was highest in the Lagerströemia forest and shrub habitats. Majority boxes in the «garden» habitat were not used (Fig. 2). In the Lagerströemia forest, shamas occupied 61.5% of nest boxes (56 of 91), in shrub habitats – 55.8 % (24 of 43), and in forest edges – 44.1% (15 of 34).

The first clutches were documented on March 25, shortly after the boxes were put in place (8–20 March). We don't know the end date of nest-box use for shama reproduction because the study was terminated on 7 July at a time when two new nests had recently been completed and one box still contained a 7-day old brood (Fig. 3). The minimal interval between nest box hanging and occupation was 14 days in the «garden» habitat, 17 days in the forest habitat, and 19 days in shrub habitats.

Most of the full clutches contained 3 eggs (62%, n=58), 31% clutches (n=29) had 4 eggs, 4 clutches (5%) – 2 eggs, and 3 (2%) clutches – one egg (Fig. 4). The female lays one egg per day. Permanent incubation started after the last egg was laid. During this time the male doesn't feed the female, but he spends his time not far from the nest. In one case a male visited his nest box 4 times during hatching when a female was absent. The male spent from 40 s to 4 min 50 s in the box, an average of 3.0 min (n=4). Presumably he visited a nest box for assisting in the hatching process.

On average, hatching occurred 13.4 days after egg-laying (n=8). Observations of three nests (4 hours per day) showed that the female did not take part in the feeding of young during the first five days after hatching. She spent almost all her time during this period brooding her young, whereas the male brought food for the chicks and, probably, for the female. After the fifth day, the female helped in the feeding of the young, and was just as active in this role as the male. The duration the nestling period was 12–13 days, and then young birds left the nest. Fledglings spent some time together with parents: we registered a case of feeding the young one month later fledging.

For three shama couples, the nesting cycle lasted for 33-34 days (the time from beginning of nest building till fledgling). The time period from the end of fledgling care until the laying of the first egg of the

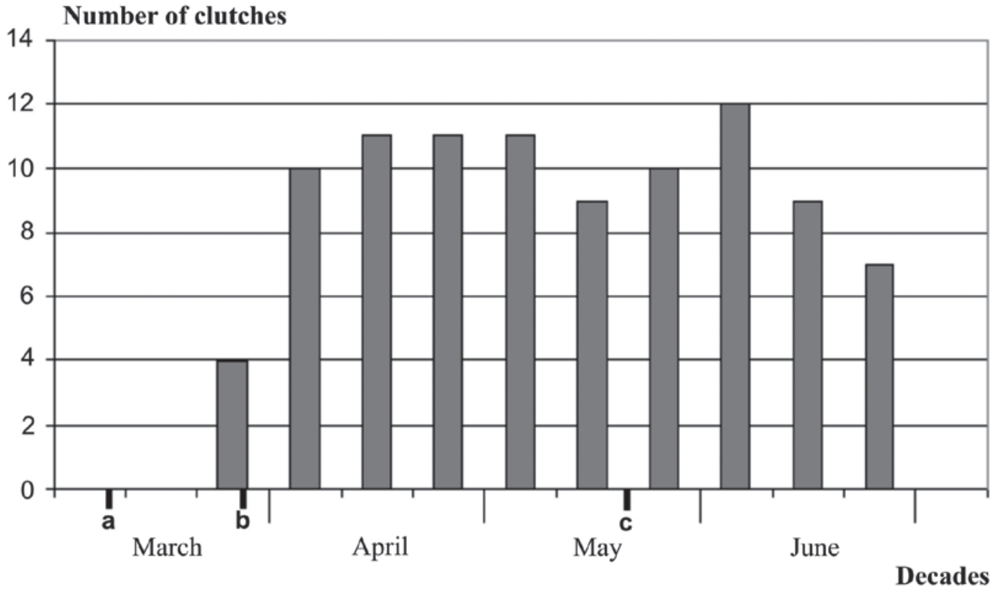

FIG. 3. Quantity clutches distribution during breeding season. «a» – start (8 March 2008) and «b» – end (26 March 2008) of boxes displacing, «c» – 10 boxes added.

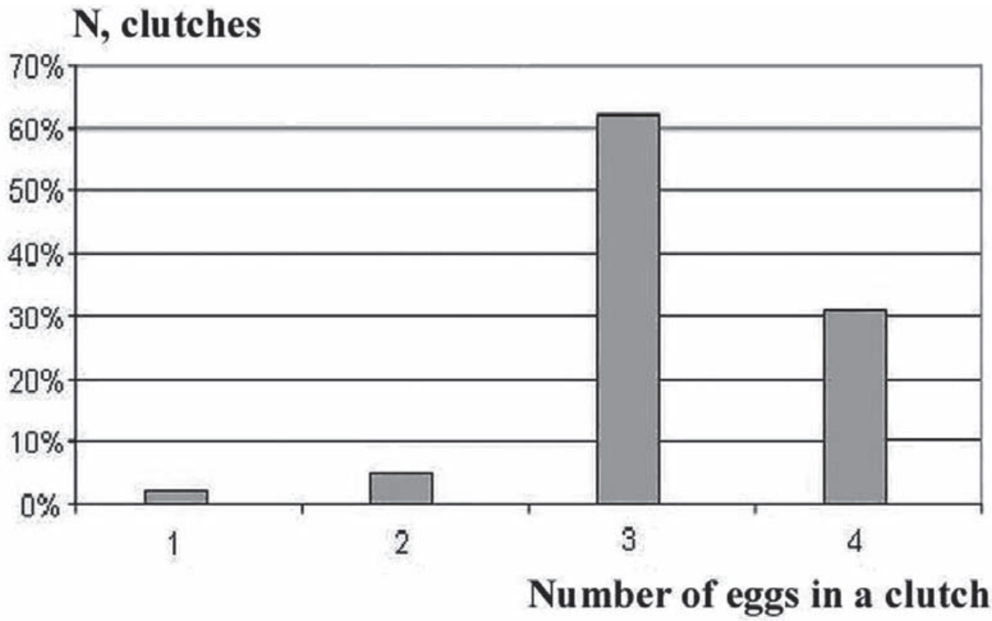

FIG. 4. Number of eggs in a clutch White-rumped Shama in 2008

second clutch for these couples lasted for 22, 24, 24 and 25 days. Intervals between the second and the third clutches were 14 days and 15–16 days.

Clutch mortality was low: 14 of 94 shama clutches were destroyed (14.9%). In two nest boxes, the females had been killed too. Eight clutches were destroyed prior to hatching and 6 during the nestling period. Some nest boxes were used by species that could be predators on, or otherwise harm, shamas including: rats *Niviventer*, tree mice *Chiropodomys gliroides*, tree-shrews *Dendrogale murina*, big spiders, scolopendras and scorpions. In addition, several species of ants occupied various nest boxes as well some other bird species (*Camponotus* sp., *Crematogaster* sp., *Diacamma rugosum*, *Monomorium* sp., *Anoplolepis gracilipes*). Interestingly, big black ants *Polyrhachis armata*, which also occupied nest-boxes, defend them from all other animals including birds. *Polyrhachis armata* was registered in 25 boxes, and may be regarded as a major competitor for shamas in terms of hole use in our study area. Several boxes were also used by bees (three boxes) and wasps (nine boxes).

We tried to keep boxes free from the nesting of insects and mammals as well as from any other competitors. During four months of field work, we removed competitors from 47 boxes (28%). However, the real rate of competition may be lower, because some of competitors were found in boxes after shama breeding was successfully finished. The average breeding territory size (based on three males) was 0.3 ha.

With help from colleagues we found six shama nests in natural cavities. Five of them were found distributed in forest habitat, and one in a housing area of the national park. Of these natural nests, we were only able to study one in detail. This nest was built in a tiny hole of a dry fallen branch (3 m in length, 10 cm in diameter) that was drooped over lianas about 1 m above the ground (Fig. 5). The depth of the hollow was 24 cm, distance between the nest and entrance – 18 cm. Other nests were placed in natural holes or cavities in 3–9 m above the ground, and three of them were concealed by epiphytes (*Dendrobium* sp.).

During the nest building the female shamas are cautious (Aguon & Conant 1994). Based on our observations of two males and one female made in Lagerströemia forest the males first builds a platform inside the hole using dry bamboo or tree leaves and other plant materials. In most cases, the males collected materials near the nest, usually within three m. This process was intensive, and lasted for two or

FIG. 5. Shama's nest, built in native cavity; a – general view, b – the nest

three days. When the male was finished, we found that there was a friable leaf cushion on the bottom of the box. After that, the female added some materials to structure, preparing a tray of hyphae (*Marasmius* sp.), dry thin leafstalks and, sometimes, flakes of dry snake skin or polyethylene. She also collected material normally from nearby the nest box (< 5 m), and finished her work in two-three days. In total, nest building takes 4–7 days in shamas.

DISCUSSION

We present data on shama clutch size, adult male and female behavior in different stages of breeding, phenology of breeding, and other features of life history of the species. Previously data on some aspects of its breeding biology were collected for a population introduced to Hawaii Islands (Aguon & Conant 1994). Work on this Hawiian population found that, under natural conditions, birds from O'ahu Island lay only one or two clutches per season, although captive birds could raise as many as five clutches per season. In our research we found only two pairs out of 73 that had a third clutch per season. Presumably this difference in number of clutches per season can be explained by differences in the environment between southern Vietnam and Hawaii.

During the breeding season we found that 19 out of 95 occupied nest boxes contained unfinished nests (consisting of leave cushions only). We suppose that in these cases males built more than one nest for a female to choose from. According to the literature male shamas build several nests simultaneously. A female then chooses the most appropriate place for the nest among them (Aguon & Conant 1994). However, unfinished nests might also belong to unpaired males.

Interestingly shamas initiated breeding activities in the «garden» habitat earlier than in others. The number of clutches increased in the first half of the breeding season and then gradually decreased. The histogram in Fig. 3 shows two small peaks, which may be related with both to initiation of second clutches by some pairs. Probably the high density of nest box occupation is related to birds gradually finding the new breeding sites represented by the placement of the artificial nest boxes.

The density of shama's nest box occupation was quite high. To compare, in the reserve «Bryansky Les» (European Russia) the common hole-nesting passerine, the Pied Flycatcher (*Ficedula hypoleuca*), nested in 50.2% boxes (n=215) in the first year of using nest-boxes (2005; Palko, unpublished data).

We suppose that the whole forest territory of Cat Tien national park is covered by adjoining home ranges of White-rumped Shama males. This assumption is based on visual observations of marked birds, capture data, observation of the high density of this species in forest habitats, frequency of territorial conflicts, and the complicated structure of the environment.

According to our results the home range of shama males averages 0.3 ha in size. This differs significantly from the Hawaiian population, were a male's home range is about 0.09 ha (Aguon & Conant 1994).

We do not know why Oriental Magpie-Robins did not use the artificial nest boxes provided. Possibilities include: 1) population density was significantly lower than that of the shama; 2) nest box construction or placement did not meet the species' requirements; or 3) lack of information on the biology and status of the bird in southern Vietnam.

In conclusion we found that the experiment of hanging artificial nest-boxes in a tropical forest was valuable. In 2008, 56.5% of nest-boxes were occupied by shamas. Next year we will try to include the second species of hole-nesting passerines that we know of in the area, the Oriental Magpie-Robin.

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MORPHO-FUNCTIONAL ANALYSIS OF THE JAW APPARATUS OF SOUTHEAST ASIAN TROPICAL FOREST TIMALIID BIRDS

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ABSTRACT

The biology of many forest birds of Southeast Asia is still poorly known, and requires extensive field study. An original method of morpho-functional analysis of the jaw apparatus, used in our research, has proven to be extremely useful in this area. This methodoloy helps to interpret data from the field, as well as to hypothesize certain features of timaliid feeding biology without direct field observations. Our method includes a detailed description of the morphology of the jaw apparatus, with a subsequent biomechanical analysis of its mechanical properties allowing the investigation of the possible evolution of trophic adaptations in selected species. A comparison of several congeneric species provides insight into the feeding adaptations within a genus and – on an even broader scale – within a family. Our data can be used for the prediction of the ecological niches of species and their preferred habitat types, as well as their possible reactions to major changes in the habitat. Here we present some results of our method as applied to seven timaliid species inhabiting the lowland forests of Vietnam.

Key words: Forest bird biology, morpho-functional analysis, jaw apparatus, biomechanics, Timaliidae, Vietnam.

INTRODUCTION

The ecology of tropical forests has been a major focus in recent biological research. One of the most important aspects of such research has been trophic interactions. The feeding adaptations of birds are of particular importance, given the high level of avian metabolic rates. Peculiarities of these adaptations in passerines have been a core objective of my field surveys in Vietnam, which started in 1989 (Kalyakin 2008). The chief aim of this work was to outline specific features in the biology of tropical passerines as key points for understanding the functioning of tropical forest ecosystems. This focus was part of a broader program carried out by the Joint Russian-Vietnamese Tropical and Research Centre, whose goal is the investigation of the diversity, structure, and function of the tropical forest ecosystems of Vietnam as a basis for their protection and sustainable development. Here I present the part of those studies that relate to trophic adaptation in lowland forest timaliids of Vietnam.

I define "trophic adaptations" as a complex of specific morphological, functional, behavioral, and ecological features necessary for the effective processing of food (locating, capture, manipulation, swallowing, etc.). The main themes of this paper are the structure and functional characteristics of the jaw apparatus and their relation to birds' everyday life.

The functional analysis of the avian jaw apparatus has been a popular topic since the middle of the last century. Studies by Beecher, Bock, and Zusi are among the best known. However, the main input in the topic was made by Soviet morphologists. Konstantin A. Judin outlined the basics of the morpho-functional analysis of avian jaw apparatus (Judin 1957, 1965, 1970). Felix Ya. Dzerzhinsky developed his ideas, applying them to the analysis of various

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groups of birds (e.g. Dzerzhinsky 1972, 1977, 1980, 1982, 1997). The method used for morphological studies of the jaw apparatus was developed by Dzerzhinsky (e.g. 1997), and allows a decoding of the mechanical properties of the bill structure.

Passerines are quite suitable for morphological research. Their overall small bill size (except for corvids), along with a high degree of uniformity in the jaw apparatus (Beecher 1953, Kalyakin 2002, 2008), make it possible to select several so-called morphological "syndromes' (more than one feature) (Dzerzhinsky 1997). These can be used for the analysis of each individual jaw apparatus. For example, flycatching presumes a well-developed *lig. postorbitale*, together with a light, thin lower jaw, and long-fibered muscles with simple inner aponeurotic carcasses. Frugivory, in turn, requires long-fibered muscles and reinforcement of the upper jaw against passive protraction – enlargement of muscles (chief among them *m. retractor palatini*), development of new muscular heads, and a special construction of the maxillary joint (Kalyakin 2002, 2003). The adaptation to fix the maxillary joint develops if strong pressure in the bill is necessary to catch large and/or mobile prey. Stronger pressure is also achieved by enlarged jaw muscles with a complex inner structure (the pinnate muscles of laniids and corvids: Dzerzhinsky & Mottowj 1989).

This method of morpho-functional analysis has been successfully applied by F. Dzerzhinsky (see above) and L. Korzoun with co-authors to many non-passerines (Korzun 1978, 1986, 1994, 1996, 1998, Korzoun 1991, Korzun & Trunov 1997, Korzoun *et al.* 2003). Some families of passerines were also included in the scope of their studies (Dzerzhinsky & Yesilevskaya 1986, Dzerzhinsky & Mottowj 1989, Korzoun et al. 2000). My own research started with the study of 16 species of SE-Asian Bulbuls (Pycnonotidae) (Kalyakin1998, 2002, 2003) and later, in the course of preparation for my doctoral thesis, incorporated species from 15 other families (Kalyakin 2007a, b; 2008, Kalyakin & Korzoun 2007). Among the wide spectrum of species, and aspects of ecology and morphology which are discussed in my thesis, timaliids were represented by 11 species in 11 genera. Seven of them inhabit the lowland forests of southern Vietnam. In discussing the morpho-functional peculiarities of their jaw apparatus, data on other species were used, namely that on bulbuls and on one or two species from each of 15 other families.

The main result of the morpho-functional method is an understanding of how a particular jaw apparatus functions and what kind of movements it performs with high, medium, or low effectiveness. This allows us to identify peculiarities in a particular apparatus in its evolutionary development, which brings us close to the reconstruction of real phylogeny. For example, analysis shows that laughingthrushes are members of family Timaliidae, which are, in turn, closely related to parrotbills, regardless of their modern systematic position. The comparison between closely related groups enhances the precision of the approach, refining our knowledge on ecological niches of particular species in stable or changing environment. It is unnecessary to say how important this is for the protection of species and their environment, especially in rapidly vanishing tropical forest ecosystems.

METHODS

Field studies of timaliid trophic behavior were supplemented by investigations into the morphology and biomechanics of their jaw apparatus. The dissections were carried out in the Zoological Museum and Vertebrate Zoology Department of Moscow Lomonosov State University under the kind supervision of Felix Ya. Dzerzhinsky and Leonid P. Korzoun.

Field studies began in 1989, and were organized as a series of short-term visits to several forested areas of Vietnam. The first three years of the studies were dedicated to the investigation of bird ecology in Ma Da Forest Enterprise in southern Vietnam (see below). Later trips involved visits to many different parts of the the country. Field observations were made on plots, along transects, or near fruiting trees, as well as by checking the stomach contents of collected birds. Each field record contained time of observation, locality, habitat, foraging height, number of individuals, and description of their activities (including feeding behavior). These studies brought rich material on the diversity of avian communities, individual trophic niches, and other aspects of biology for many birds of Vietnam (Kalyakin 1995, 2006a, 2007b; Kalyakin *et al.* 1997, Kalyakin & Korzun 1998, 2001). More than 2000 observations were recorded for timaliid species. They were subsequently used for descriptions of their biology (see below).

Most of the field work was done at two sites – Ma Da Forest Enterprise (11°20'N, 107°00'E) and Cat Tien National Park (11°27'N, 107°18'E), both in

Dongnai Province, 55 and 80 kms NE of Ho Chi Minh City (Fig. 1). Despite differing tree composition, both localities have one aspect in common – they were logged at roughly the same time, 30–40 years ago. The logging focused on selective extraction of valuable timber belonging to the families Dipterocarpaceae, Fabaceae, and several others. The Ma Da forest, where investigations were carried out during 1989–1994, is a secondary lowland dipterocarp forest, with *Dipterocarpus dyeri* serving as a dominant canopy species. Average altitude is *ca.* 100 m above sea level; climate is monsoon with a rainy season that lasts from May to October-November. Data on timaliid species were also collected in Cat Tien National Park based on two short visits in 1990 and 1994, and longer ones in 2002, 2003, 2006, 2008 and 2009 (4 months in total). The main habitat studied here was a Lagerströemia forest, a habitat in which the dominant tree species include *Lagerströemia*, *Tetrameles nudiflora*, *Afzelia xylocarpa*, among others) and characterized by some disturbance by logging, a largely closed canopy, and considerable undergrowth. Different kinds of open habitat were also visited including shrubby, treeless habitats with some bamboo. Other characteristics are similar to those for Ma Da forest except periodical flooding of part of its territory.

Field observations of avian behavior, especially those in complex ecosystems such as tropical forests, are not always effective due to the absence of knowledge of the functioning of locomotor and feeding apparatus. The required knowledge can be obtained only through morphological studies. These studies are very sensitive to the minute changes in trophic adaptations as well as to their history. Morphological studies were done together with field observations. Based on the meticulous dissections of the jaw apparatus (Figs. 2 & 3), the method of functional analysis of the jaw apparatus incorporates the biomechanical analysis of a free-body diagram. Forces (represented by vectors)

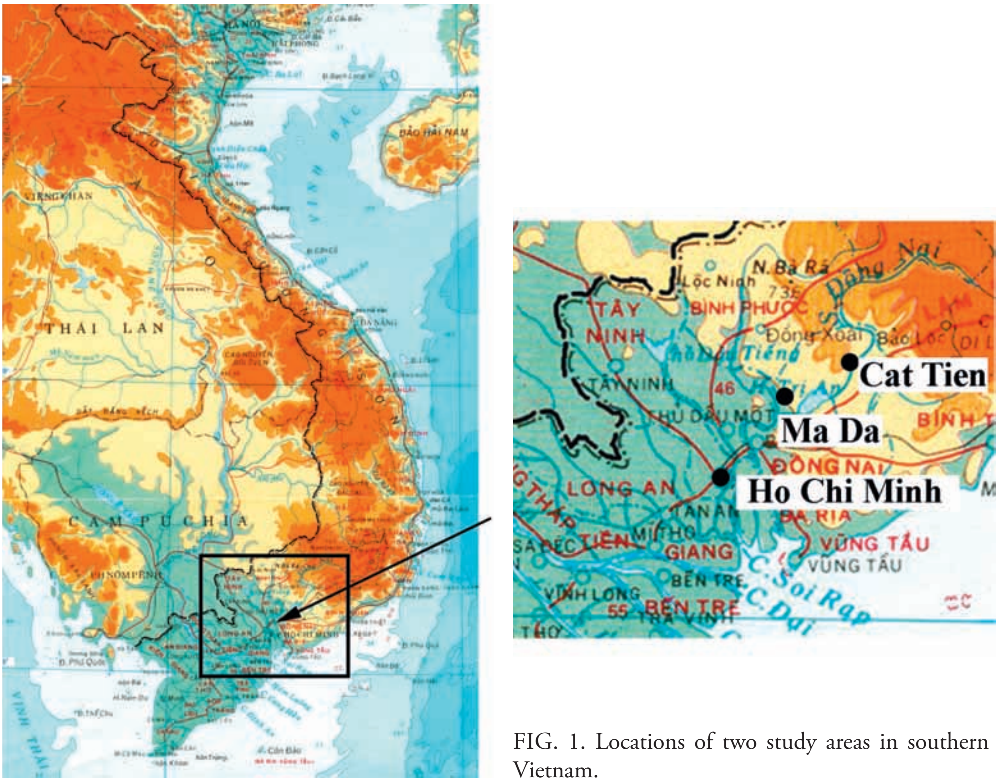

FIG. 1. Locations of two study areas in southern Vietnam.

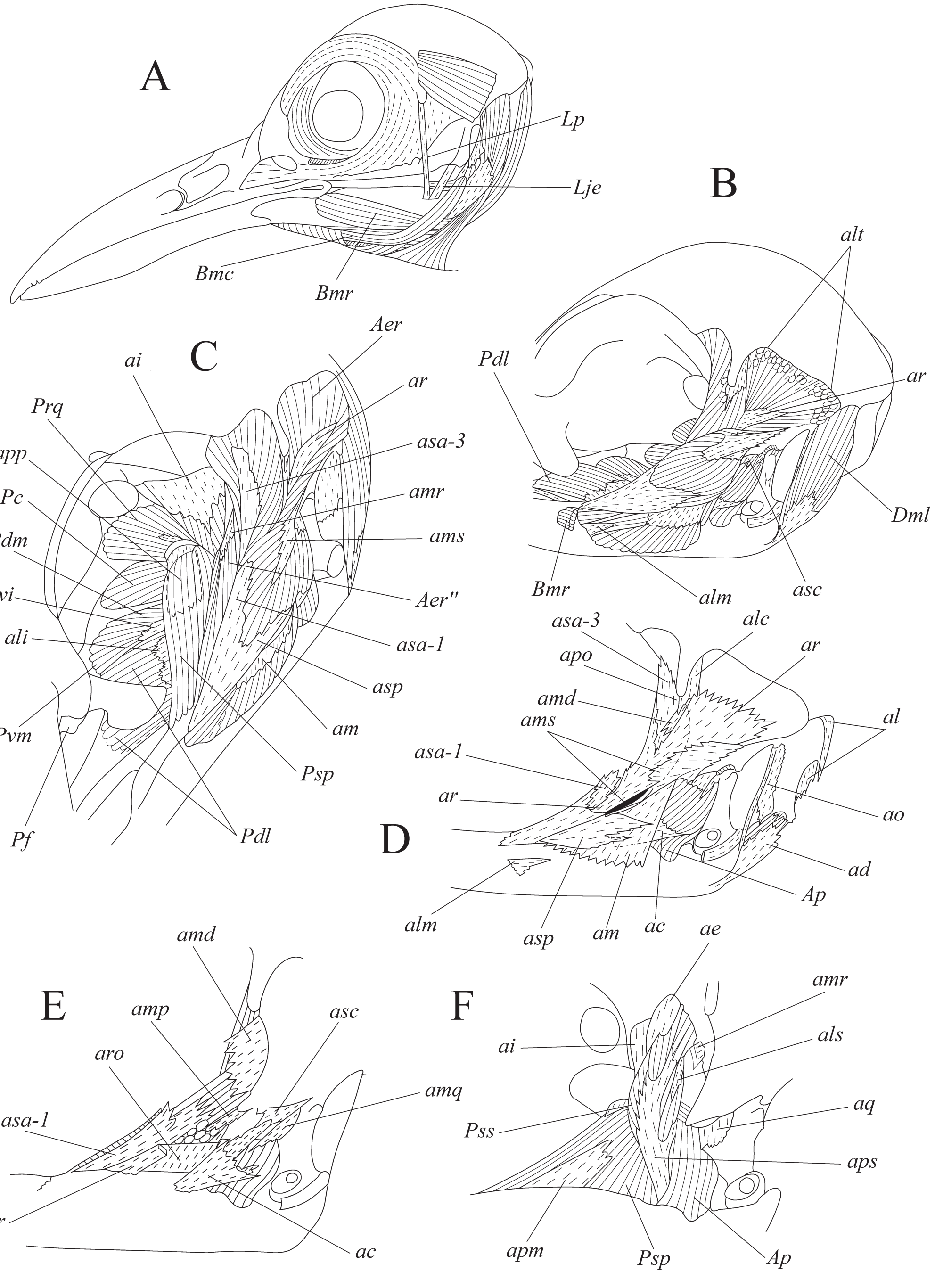

FIG. 2. Morphology of the jaw apparatus of White-crested Laughingthrush *Garrulax leucolophus*: jaw muscles and ligaments; side view; A-F – successive stages of dissection. See Comments in Attachment.

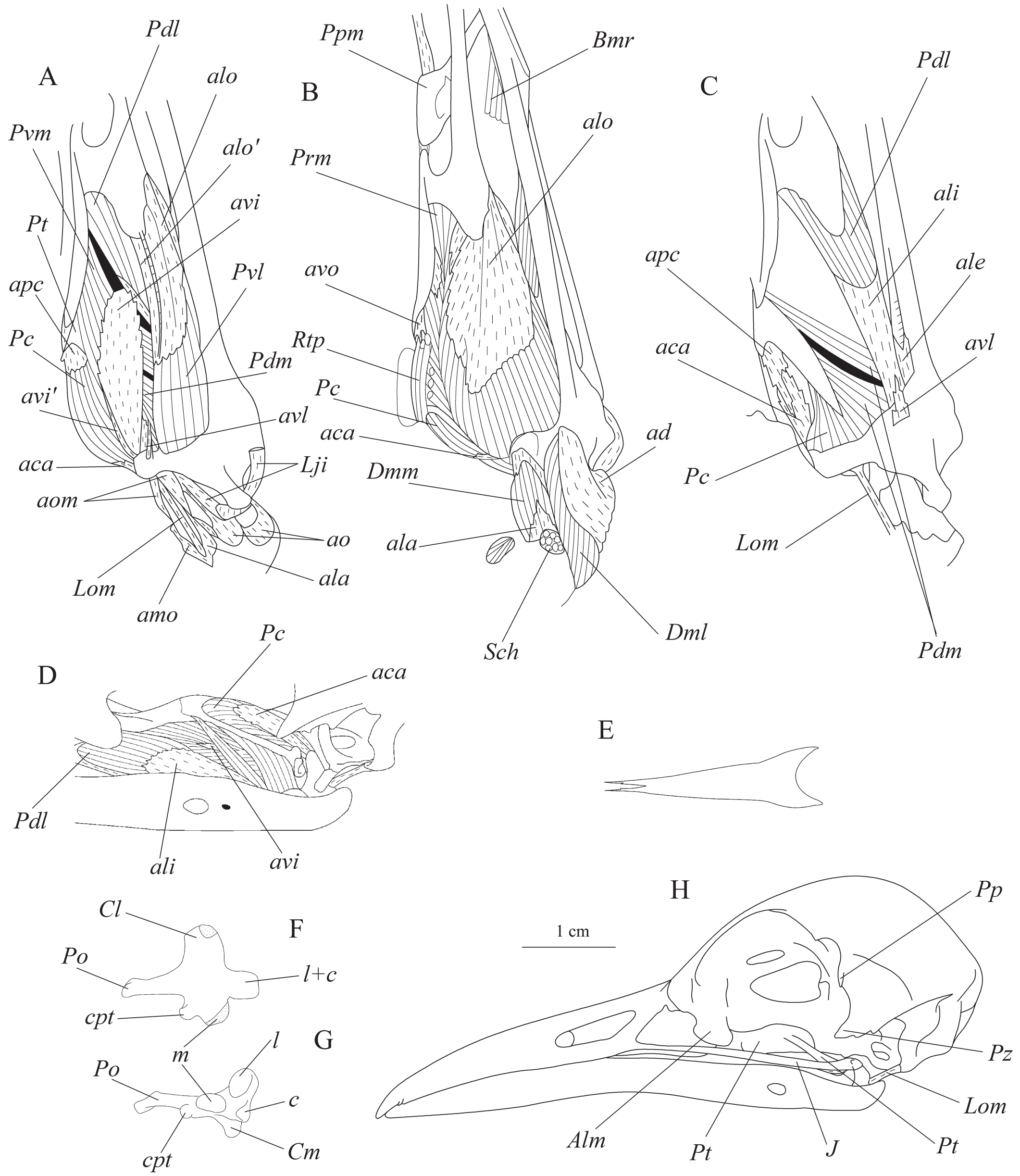

FIG. 3. Morphology of the jaw apparatus of White-crested Laughingthrush *Garrulax leucolophus*: A-C – portions of *m. pterygoideus*, several other muscles, ligaments, and elements of the skull; view from below; successive stages of dissection; D – *m. pterygoideus*, side view after removal of *os quadratum*; E – tongue; F – *os quadratum*, lateral view; G – *os quadratum*, view from below; H – skull, lateral view. See Comments in Attachment.

ATTACHMENT

Legend to the Figures 2 & 3:

Aponeuroses of muscles (*aponeurosis*):

ac – ap. caudalis
aca – ap. accessoria
ad – ap. depressoris
ai – ap. interna
al – ap. lambdoidea
ala – ap. lateralis
ale – ap. lateralis externus
ali – ap. lateralis insertionis
alo, alo' – ap. lateralis originalis
als – ap. lateralis superficialis
alt – ap. lateralis temporalis
alm – ap. lateralis medialis
am – ap. medialis
amd – ap. medialis dorsalis
amo – ap. mandibulooccipitalis
amp – ap. medialis posterior
amq – ap. medioquadrata
amr – ap. mediorostralis
ams – ap. mediosuperficialis
ao – ap. occipitalis
aom – ap. occipitomandibularis
apc – ap. pterygoidea caudalis
apo – ap. postorbitalis
app – ap. pseudotemporalis profundus
aps – ap. pseudotemporalis superficialis
aq – ap. quadrata
ar – ap. rostralis
aro – ap. rostralis originalis
asa-1, asa-3 – ap. superficialis anterior
asc – ap. superficialis caudalis
asp – ap. superficialis posterior
avi, avi' – ap. ventralis insertionis
avl – ap. ventralis lateralis
avo – ap. ventralis originalis

Muscles (*musculus*):

Aer, Aer" – m. adductor mandibulae externus, pars rostralis and pars medialis
Ap – m. adductor mandibulae posterior
Bmr – m. branchyomandibularis rostralis
Bmc – m. branchyomandibularis caudalis
Dml – m. depressor mandibulae pars lateralis
Dmm – m. depressor mandibulae pars medialis
Pc – m. pterygoideus caudalis
Pdl – m. pterygoideus dorsalis lateralis
Pdm – m. pterygoideus pars dorsalis medialis
Prq – m. protractor quadrati
Psp – m. pseudotemporalis profundus
Pss – m. pseudotemporalis superficialis
Pvl – m. pterygoideus pars ventralis lateralis
Pvm – m. pterygoideus pars ventralis medialis
Rtp – m. retractor palatini
Sch – m. stylohyoideus

Ligaments (*ligamentum*):

Lje – lig. jugomandibulare externum
Lji – lig. jugomandibulare internum
Lom – lig. occipitomandibulare
Lp – lig. postorbitale

Elements of the skeleton:

Alm – ala mesethmoidalis
c – condylus caudalis
Cl – condylus lateralis processi otici
Cm – condylus medialis processi otici
cpt – condylus pterygoideus
J – jugale, arcus jugalis
l – condylus lateralis
l+c – condylus lateralis + condylus caudalis
m – condylus medialis
Pf – praefrontale
Po – processus orbitalis quadrati
Pp – processus postorbitalis
Ppm – processus palatinus maxillaris
Pt – pterygoideum
Pz – processus zygomaticus

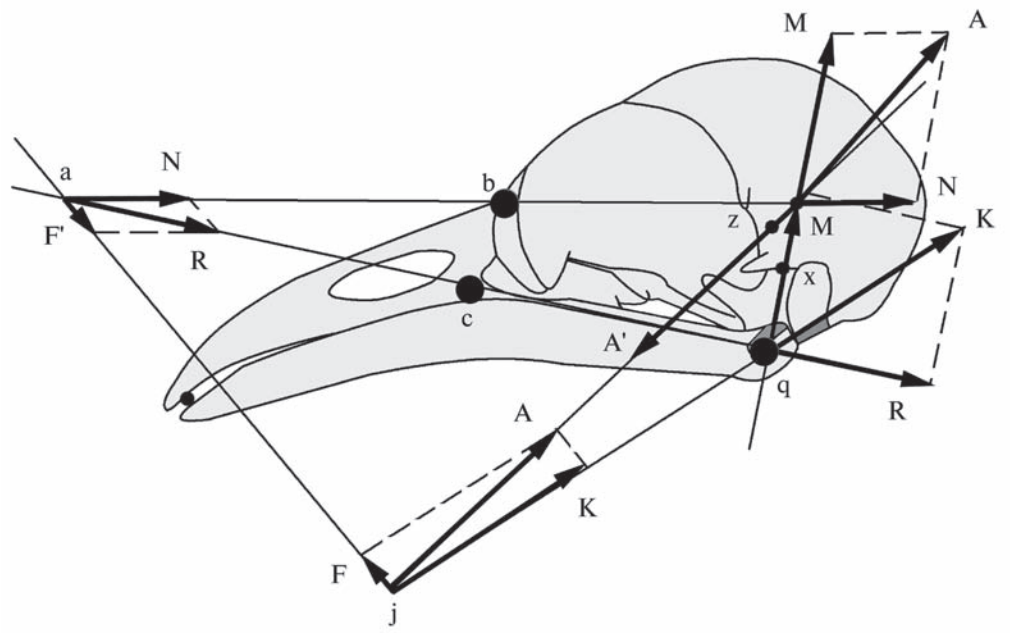

FIG. 4. Free-body diagram of forces acting in the skull during pressure on the small food item (small black dot) near the tip of the bill (after Dzerzhinsky 1972); the jaws are under independent muscle control. A – resulting force of dorsal adductors; F, K, N, M and R – forces of selected jaw muscles in an interaction with the food item reaction force; *c* – point of application of *m. pterygoideus* force to the upper jaw; *x* – rotation point of *os quadratum* against the skull; *q* – rotation point of lower jaw; *b* – rotation point at the base of the upper jaw; *aj* – line of action of forces pressing the food item; *z* – intersection point of lines *ab* and *qx*.

acting on the food item pressed in the tip of the bill are analyzed (Fig. 4). The rotation of individual elements around each other allows identification of the role of each bone, muscle, and ligament in the processing of food items (Dzerzhinsky, 1972).

RESULTS

Ecology of timaliid species

An overview of the ecology and behavior of timaliids from southern Vietnam is necessary in order to interpret the morphological material. The following information is based on the study of a 20-ha plot in Ma Da Enterprise (Kalyakin *et al.* 1997). The composition and structure of the avian community of Ma Da are more closely related to those in Malaysia than to any others in central or northern Vietnam known to me.

There are 12 species in 8 genera of timaliid birds in southern Vietnam. The Chestnut-capped Babbler *Timalia pileata* is excluded from the list as an inhabitant of open grasslands. Eleven species of 7 genera were recorded in Ma Da. Abbott's Babbler *Malacocincla abbotti* was not observed; however it was found in considerable numbers in Cat Tien National Park. Out of the total of 163 species of birds recorded in the study plot in Ma Da, the 11 species of timaliids comprise 6.7%. This percentage is less than is found in several other forested areas of Vietnam, located at higher altitudes, or in more northern regions of the country. Ten timaliid species were resident on the plot, while the Black-throated Laughingthrush *Garrulax chinensis* was a vagrant (Table 1).

TABLE 1. Biological features of forest timaliid species on the study plot in Ma Da forest, Dongnai Province, Vietnam.

Species	Abundance	Habitat	Stories in forest vegetation	Trophic links	Participation in mixed flocks
White-bellied Yuhina *Erpornis zantholeuca*	Rather common	Forest and forest edges, prefer closed-canopy forest	Canopies	Insects	Periodically
Black-browed Fulvetta *Alcippe grotei*	Common	Forest edges	Understory	Insects, small fruits	Stable
Great Scimitar Babbler *Pomatorhinus hypoleucos*	Uncommon	Forest and forest edges	Ground, understory	Insects	Rare
Striped Tit Babbler *Macronous gularis*	Abundant	Forest edges	Understory	Insects, occasionally small fruits	Periodically
Grey-faced Tit Babbler *Macronous kelleyi*	Abundant	Forest and forest edges	Understory, canopies	Insects	Stable
Buff-breasted Babbler *Pellorneum tickelli*	Common	Forest and forest edges	Ground, understory	Insects	Rare
Puff-throated Babbler *Pellorneum ruficeps*	Rather common	Forest and forest edges	Ground	Insects	Rare
Scaly-crowned Babbler *Malacopteron cinereum*	Abundant	Closed-canopy forest	Understory	Insects	No
White-crested Laughingthrush *Garrulax leucolophus*	Very abundant	Forest and forest edges	Ground, understory	Insects, occasionally fruits	Stable
Lesser Necklaced Laughingthrush *Garrulax monileger*	Uncommon	Forest edges	Ground, understory	Insects, possibly small fruits	Stable

Abundance

Most of the timaliid species had rather high population densities in the plot. The White-crested Laughingthrush *Garrulax leucolophus* absolutely dominated – ca. 100 individuals per sq. km – being the most numerous among local species. Playing an important role in forest ecosystems, this laughingthrush is numerous due to the rich forest floor of *Dipterocarpus dyeri* leaves and dense understory as a result of selective logging.

Three other timaliids were among the most abundant birds in a study plot. They are Scaly-crowned Babbler *Malacopteron cinereum*, Grey-faced Tit Babbler *Macronous kelleyi*, and Striped Tit Babbler *Macronous gularis* with around 50 individuals per sq. km. Two species, Black-browed Fulvetta *Alcippe grotei* and Buff-breasted Babbler *Pellorneum tickelli*, were slightly less abundant with 40-50 individuals per sq. km. Thus more than half of the timaliid species can be considered as common and very common for the local forest avian community. White-bellied Yuhina *Erpornis zantholeuca* and Puff-throated Babbler *Pellorneum ruficeps* were also common. The low density was recorded only for Lesser Necklaced Laughingthrush *Garrulax monileger* and Great Scimitar Babbler *Pomatorhinus hypoleucos*.

Habitats

Most of the above-mentioned birds belong to truly forest species, except for Striped Tit Babbler, which inhabits forest edges, and Black-browed Fulvetta plus Lesser Necklaced Laughingthrush, which avoid high forests. Almost all the species, though, can be occasionally observed along the edges of high forest (clearings, roads and paths, partially opened forested areas). Only Scaly-crowned Babbler seems to be confined strictly to the areas of closed-canopy forest; Large Scimitar Babbler and White-bellied Yuhina also show preferences for such habitat type.

Occupation of different stories of forest vegetation

Confinement to certain stories is a very important parameter of ecology of forest species due to the pronounced differences there in temperature, light, and humidity. Timaliids inhabit almost all the forest stories except for the highest ones; they are only rarely recorded in the crowns and canopies of emergents. Only White-bellied Yuhina periodically collects food in lower parts of canopy formed by emergents. The lower we travel the more species of timaliids we meet. Puff-throated Babbler, Buff-breasted Babbler, and Large Scimitar Babbler, as well as two species of laughingthrushes *Garrulax* spp. can be treated as ground birds, partly exploiting lower stories. Scaly-crowned Babbler can also be seen foraging on the ground. Lower parts of emergent crowns are used by White-bellied Yuhina and Grey-faced Tit Babbler, while the understory at various levels is exploited by most of the species mentioned plus Black-browed Fulvetta. Primarily lower stories are occupied by White-crested Laughingthrush, Lesser Necklaced Laughingthrush, Scaly-crowned Babbler, and Striped Tit Babbler.

Trophic links

Timaliid species of lowland forests of southern Vietnam are mainly insectivorous: six species feed only on invertebrates, three others are predominantly insectivorous (see below). Obligate frugivory is reported for Black-browed Fulvetta, which in addition to insects and spiders feeds on fruit pulp. White-crested Laughingthrush, Lesser Necklaced Laughingthrush, and Striped Tit Babbler only occasionally exploit fruits, being facultatively frugivorous birds. Many of the timaliid species of lowland forest of southern Vietnam frequently participate in so-called mixed flocks of insectivorous birds. This is true for all the forest species except for Buff-breasted Babbler and Abbott's Babbler (in Cat Tien Park). The babblers in this study are only rarely seen feeding on the ground or in lower stories in or near mixed flocks. White-crested Laughingthrush, Grey-faced Tit Babbler, and Black-browed Fulvetta seem to be the organizers of such flocks. Scaly-crowned Babbler forms flocks of its own, in which several species of small insectivorous birds only rarely participate. The question of mixed flock formation and the role of timaliids in this process are matters dealt with in a separate study.

Thus forest timaliids of southern Vietnam comprise a group of breeding resident species of small and medium-sized birds, which are more or less abundant and, being predominantly insectivorous, exploit lower stories and forest edges. Only one species can be considered truly frugivorous, while three others can be placed in the subgroup of facultatively frugivorous birds.

Results of morpho-functional analysis and discussion

Morphology and principles of the functioning of the jaw apparatus in the Timaliidae are similar to those in other passerines studied (Figs. 2, 3, 5, 6 & 7). It is adapted to picking a food item by the tip of the bill with subsequent manipulations by the coordinated efforts of muscles, which move the upper and lower jaws. In timaliids, as in other oscines, this coordination is achieved mainly by external adductors and *m. pterygoideus* (Fig. 4).

Despite the general similarity to other oscines, the timaliid jaw apparatus shows some peculiarities. Among them are the small or very small condylus caudalis of quadrate bone and long tiny *lig. jugomandibulare externum* (Fig. 2 & 3). These features, along with the weakness of *lig. postorbitale* indicate the possibility of a simultaneous movement of the jaws when the bill is closed or slightly opened. This is an adaptation for searching in substrate or picking and processing food with a closed or slightly opened bill; an ability to make short vertical and longitudinal movements which help to break up food items.

The other interesting features found in Timaliidae, including parrotbills, is an ability to see food or the substrate close in front of the bill, or even at its tip. All these birds possess very small lateral wings of *mesethmoideum* (Figs. 2, 3, 5, 6, & 7), which usually obscure the field in front of the birds' eyes. This feature, characteristic of Timaliidae and parrotbills, is also described for Sturnidae and Icteridae (Beecher 1951, 1978, Dzerzhinsky 1997). It is considered to be an adaptation for food manipulation in the bill.

The third feature of the jaw apparatus which characterizes its properties is the volume and complexity of the inner structure of the jaw muscles. Timaliidae are in this respect somewhere in the middle among the oscines, being far behind the corvids and laniids. However, there is one lineage in the Timaliidae which shows a trend to reinforcement of jaw musculature. It includes Large Scimitar Babbler and Grey-Headed Parrotbill *Paradoxornis gularis* (Fig. 6). Similar in general, the reinforcements in these two species differ in details due to the difference in bill shape. The reinforcement is necessary to break open the substrate and excavate food items. This habit is observed in parrotbills and was found in several species of scimitar babblers well after our

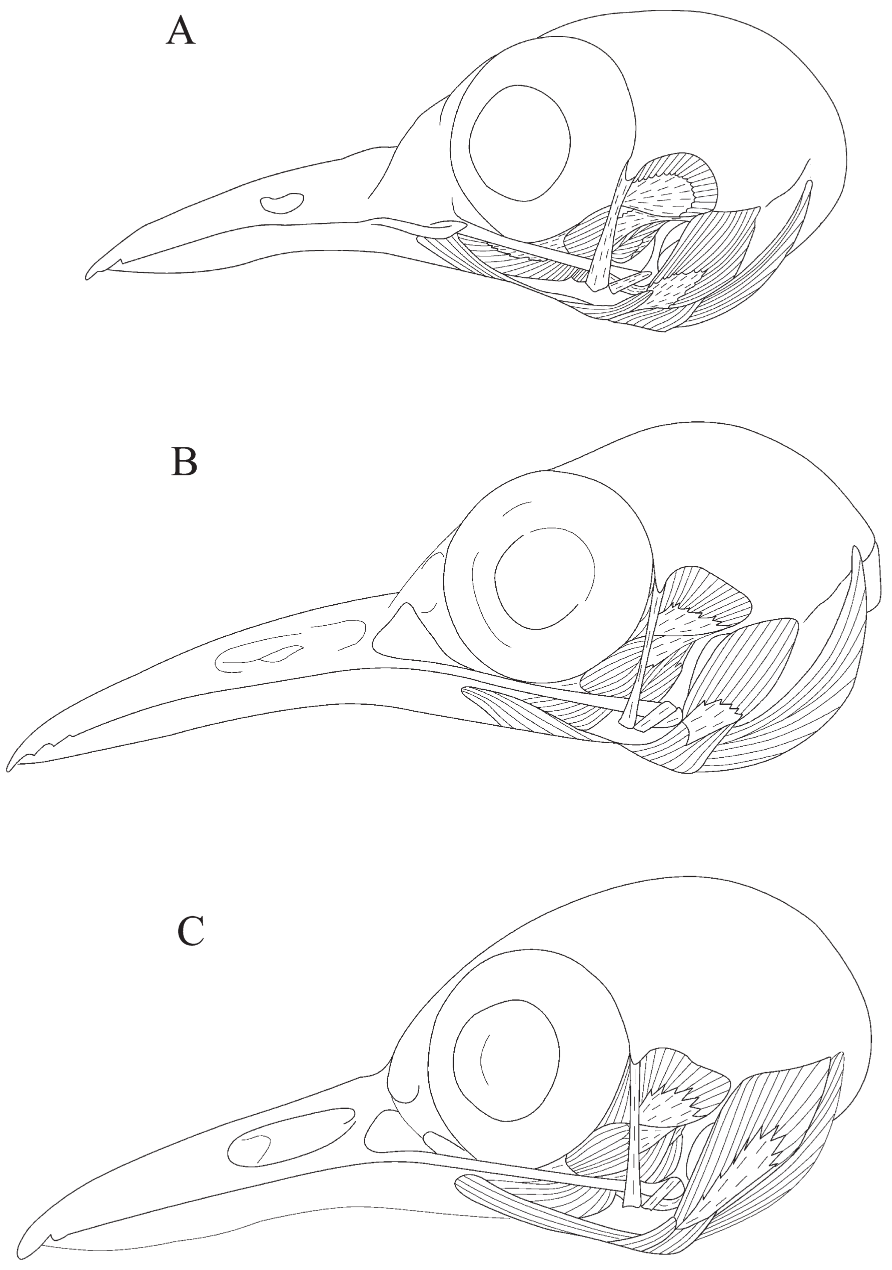

FIG. 5. Morphology of the outer layer of the jaw apparatus muscles in three insectivorous timaliid species, side view: A – Buff-breasted Babbler *Pellorneum tickelli*, B – White-bellied Yuhina *Erpornis zantholeuca*, C – Scaly-crowned Babbler *Malacopteron cinereum*.

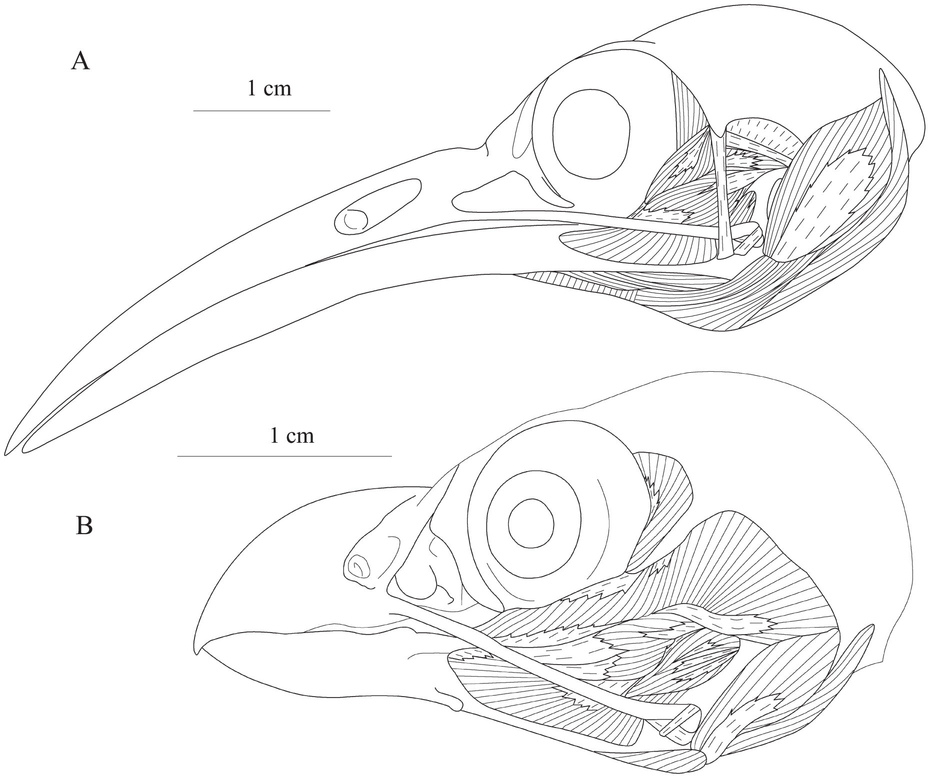

FIG. 6. Morphology of the outer layer of the jaw apparatus muscles in two insectivorous timaliid species, side view: A – Large Scimitar Babbler *Pomatorhinus hypoleucos*, B – Grey-Headed Parrotbill *Paradoxornis gularis*.

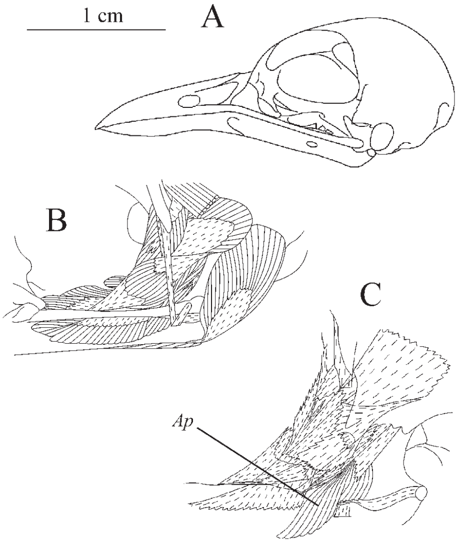

FIG. 7. Morphology of the outer layer of the jaw apparatus muscles in a frugivorous timaliid, Black-browed Fulvetta *Alcippe grotei*, side view.

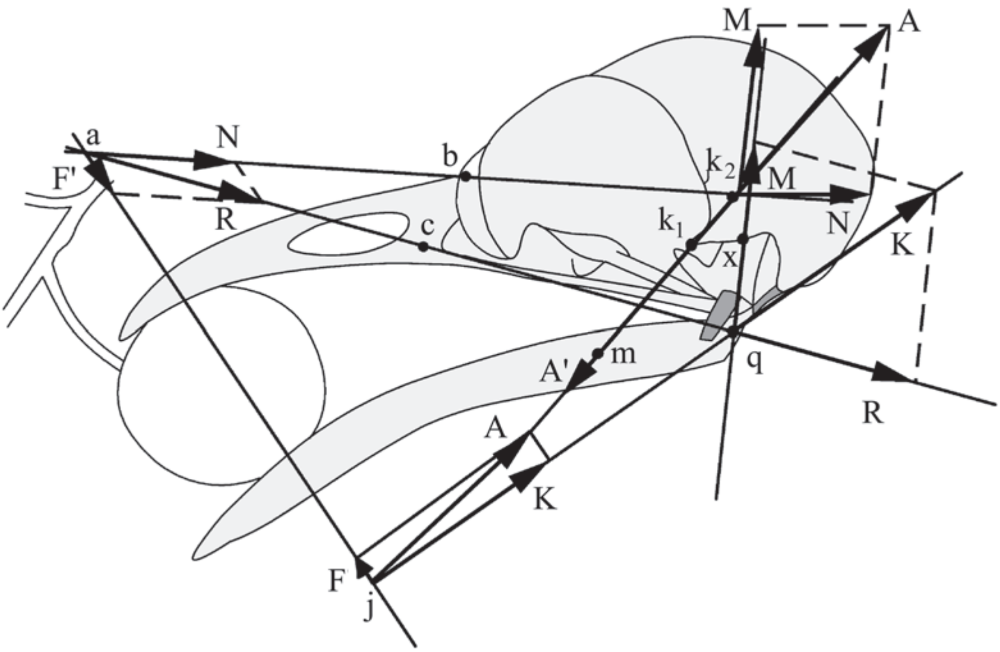

FIG. 8. Free-body diagram of forces acting in the skull during the pressure on the large food item near the tip of the bill (after Dzerzhinsky 1972 and Kalyakin 2002); the jaws are under independent muscle control. k_1 and k_2 – application points of the joint forces of adductors; for other abbreviations see Fig. 4.

morphological studies. Some trends to reinforcement are seen in laughingthrushes. However they are related to the greater body size and do not show any special features, such as higher complexity of aponeurotic carcass or additional muscular heads.

Apart from general insectivorous adaptations of the jaw apparatus, some timaliid species show certain features related to their frugivory. When the bill is widely opened the construction of the maxillary joint provides a slight dominance of the upper jaw over the lower, as has also been described in bulbuls (Kalyakin 2002; Fig. 8). This is an adaptation for an additional pressure of the upper jaw on the fruit picked from the branch. My studies of middle-sized frugivorous passerines, including 16 species of Asian Pycnonotidae, Hill Myna, and Irena (Kalyakin & Dzerzhinsky 1997, Kalyakin 1998, 2002, 2003, 2008), have shown that this reinforcement of the upper jaw in larger birds is sufficient to pick fruit from the branch. However, in the majority of studied timaliid species, *m. retractor palatini* (a very effective retractor of the upper jaw, as only one portion of *m. pterygoideus* has direct contact with the upper jaw and the skull) and some other morphological features related to fruit-picking are not well developed. For these birds we can identify an independent action of muscles controlling the upper and lower jaws (Dzerzhinsky 1997). A well-developed set of fruit-picking adaptations was found only in Black-browed Fulvetta. The special structure of the maxillary joint is accompanied by the reduction of the tongue muscles. The absence of an anterior part of *m. brachyomandibularis* allows the processing of relatively large food items, namely fruits, at the expense of the ability to manipulate small objects, characteristic of insectivorous birds. An extremely enlarged *m. adductor* caudalis greatly adds to the retraction of the upper jaw.

Besides the morphological and functional features common to all studied timaliid species, we found some specificity in the jaw apparatus of selected species that adds some details to characteristics of their trophic adaptations (Table 2).

TABLE 2. Results of study of Southern Vietnam forest timaliid species jaw apparatus and foraging.

Species	Results of dissection	Conclusion about foraging
White-bellied Yuhina *Erpornis zantholeuca*	Quite different from other studied species by general structure, list of muscle portions, abundance of aponeuroses; clearly adopted to gaping (opening beak probing in substrate).	Insectivorous, but on different morphological base; gaping was not observed, but could be using for excavating of food from any substrate, possibly including flowers or buds.
Black-browed Fulvetta *Alcippe grotei*	Simple aponeurotic carcasses, reinforcement of upper jaw, some reduction of tongue muscles.	Insectivorous; features of adaptation to frugivory are very clear due to small body size.
Great Scimitar Babbler *Pomatorhinus hypoleucos*	General structure and composition of muscle portions common are for timaliid species, but volume of muscles are quite more then usual.	Insectivorous with strong reinforcement for probing and exctraction of insects from different shelves.
Striped Tit Babbler *Macronous gularis*	Dissection wasn't done.	Probably similar with Grey-faced Tit Babbler
Grey-faced Tit Babbler *Macronous kelleyi*	Structure and composition of jaw muscles are typical for studied timaliid species, possible are not far from ancestral ones.	Typical insectivorous with orientation on collating of slowly moved or immobile food including examination of cocoons, dry leaves, etc. There are no special signs of adaptation in frugivory.
Buff-breasted Babbler *Pellorneum tickelli*	Only outer layers of muscles were described. Typical picture, wide and strong ligamentum postorbitale helps to open and slum beak quickly.	Typical insectivorous, may be with some tendency to catch mobile insects in dense vegetation more frequently then other timaliid species.
Puff-throated Babbler *Pellorneum ruficeps*	Also outer layers of muscles were examined. No special features were found besides common for other timaliid species.	Typical insectivorous, probably simple collating of insects in style common for small timaliid species.
Scaly-crowned Babbler *Malacopteron cinereum*	Full description of jaw apparatus was done, typical variant of its structure, composition and function was verified.	Typical insectivorous, collating of insects in style common for small timaliid species, no special features shown on orientation on flycatching were found.
White-crested Laughingthrush *Garrulax leucolophus*	Structure and composition of jaw muscles are typical for studied timaliid species, some degree of reinforcement of jaw apparatus is reached due to big body size.	Typical insectivorous, big food items and small fruits are accessible due to general increase of sizes of bird and its jaw apparatus.
Lesser Necklaced Laughingthrush *Garrulax monileger*	Dissection wasn't done.	Probably similar with Grey-faced Tit Babbler

DISCUSSION

The basic morphology of the jaw apparatus, and comparisons with closely-related species, indicate that timaliids are initially adapted to manipulate the substrate or food objects, having prerequisites for fruit processing. The latter ability was used to various degrees by several montane groups, but most of the family members became adapted to insectivory. The type of insectivory used by most timaliids is not a simple collecting of abundant and easily-spotted insects, as in several Muscicapidae, Sylviidae, and some Turdidae. Timaliid insectivory involves intensive searching and excavating of slow-moving invertebrates or immobile arthropods hidden in the foraging substrate or ephemeral shelters. Field observations show that clusters of dry leaves, cocoons and pupae of insects hiding in rotten branches and bamboo stems are among the most attractive items for timaliids. This sort of basic adaptation is in good agreement with one idea of the origin of this group in high-elevation, montane regions with relatively long cold periods, when most arthropods are inactive (Kalyakin 2006b, 2007a). Proceeding from the modern biogeography of Timaliidae, they could have evolved in the Himalayas (Collar & Robson 2007).

Our conclusions regarding the origins of the morphological features of the timaliid jaw apparatus are well supported by field observations. Timaliids are indeed specialists in terms of intensive scrutiny of various kinds of substrates, and in the capture of immobile or slow-moving arthropods. No timaliid is specialized in the catching of flying insects, despite their great abundance in lowland tropical forests. They do not even capture flying termites, a very attractive food in tropical forest for a variety of other birds from swifts to hornbills (Stepanyan 1996; our observations).

CONCLUSIONS

Most of the timaliid species from the lowland forests of southern Vietnam, including species of the genera *Malacopteron, Macronous, Pellorneum,* and *Erpornis zantholeuca*, form a guild of insectivorous birds, which likely has never used small fruits as a principal dietary item, like (e.g.) the Striped Tit Babbler. Birds of this guild, together with several other groups of Timaliidae, probably represent an early stage in the colonization by the family of lowland ecosystems. They have lost or never possessed frugivory as a foraging focus, and occupy niches as hunters of slow-moving or immobile arthropods that depend upon crypsis or hiding to avoid predators. Some of these timaliids, such as the Scaly-crowned Babbler, show initial trends to hunting active insects, including flying ones. Slowly moving timaliids in the process of scrutinizing the substrate in search of arthropods are good companions for flycatching birds, such as the Racket-tail Drongo *Dicrurus paradisaeus* (King & Rappole 2001). Insects, flushed by timaliids, become the prey of a number of other avian species, perhaps resulting in the formation of mixed-species flocks in which some members capitalize on the foraging activities of others.

Several timaliid species, occupying various strata of the forest and its borders, are good runners and climbers, but not flycatchers. They have long powerful legs, well adapted for acrobatic types of movement in branches in a search of food, using visual control at a short distance. Two lineages of timaliids have species that appear partially adapted to frugivory, e.g., the Black-browed Fulvetta, a member of the genera or subgenera of mountain grey-headed fulvettas, and the Large Scimitar Babbler, adapted to searching in different substrates. Larger species, such as laughingthrushes, are also historically connected to montane habitats. Species of *Garrulax* that later occupied lowland forests retained the prerequisites for frugivory and, due to their larger size and powerful jaw apparatus, also for carnivory.

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