Cryptic Species of a Cascade Frog from Southeast Asia: Taxonomic Revisions and Descriptions of Six New Species

Authors: BAIN, RAOUL H., LATHROP, AMY, MURPHY, ROBERT W., ORLOV, NIKOLAI L., and CUC, HO THU

Source: American Museum Novitates, 2003(3417) : 1-60

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2003)417<0001:CSOACF>2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3417, 60 pp., 14 figures, 15 tables October 29, 2003

Cryptic Species of a Cascade Frog from Southeast Asia: Taxonomic Revisions and Descriptions of Six New Species

RAOUL H. BAIN,[1] AMY LATHROP,[2] ROBERT W. MURPHY,[3]
NIKOLAI L. ORLOV,[4] AND HO THU CUC[5]

ABSTRACT

The Southeast Asian cascade frog, *Rana livida* (Blyth, 1856), has long been suspected to be a complex of species. Several different forms are described from across its vast range. The loss of type material and disparate sampling efforts are challenges. Is variability in this species due to geographic variation or to the presence of multiple species? We use concordant evidence from morphology, morphometrics, cellular DNA content, and allozyme electrophoresis to investigate diversity in *R. livida* from Vietnam. Three distinct species are recognized on the basis of morphology, as are four other suspect groups (morphotypes). Discriminant function analyses of morphometric data detect patterns of morphological variation among all seven groups. Pairwise comparison of cellular DNA content using *t*-tests shows significant differences among sympatric morphotypes, suggesting they represent distinct species. This hypothesis is supported by an analysis of 14 allozymic loci, in which fixed allelic differences are found among specimens in sympatry and allopatry. Examination of available type material of four junior synonyms of *R. livida* results in their recognition as species. One of these species,

[1] Biodiversity Specialist, Center for Biodiversity and Conservation, and Division of Zoology (Herpetology), American Museum of Natural History. e-mail: bain@amnh.org
[2] Herpetology Technician, Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada. e-mail: amyl@rom.on.ca
[3] Senior Curator, Herpetology, Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada. e-mail: drbob@rom.on.ca
[4] Research Scientist, Department of Herpetology, Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034, Russia. e-mail: azemiops@zin.ru
[5] Senior Herpetologist, Institute of Ecology and Biological Resources, Vietnam National Center for Natural Sciences and Technology, Nghia Do, Tu Liem, Hanoi, Socialist Republic of Vietnam.

 ISSN 0003-0082

R. chloronota, is a wide-ranging species erroneously referred to as *R. livida*. Seven species occur in Vietnam.

We describe six new cryptic species belonging to the *Rana chloronota* complex, redescribe *R. chloronota*, *R. livida*, *R. sinica*, and *R. graminea*, and give comments on *R. leporipes*. Three of these new species (*R. bacboensis*, new species, *R. hmongorum*, new species, and *R. daorum*, new species) occur in montane forests in northern Vietnam, and two (*R. banaorum*, new species and *R. morafkai*, new species) are known only from the Tay Nguyen Plateau of Vietnam's Central Highlands. One species, *R. megatympanum*, new species, occurs in portions of both northern Vietnam and the Central Highlands. An identification key for the *Rana chloronota* complex from Vietnam is provided. The finding of six cryptic species within a small portion of the geographic region of *R. chloronota* suggests that many more cascade ranids await discovery. This documentation has serious implications for conservation; each of the new species occurs in sympatry with at least one other member of the complex. Consequently, far more species are being affected by habitat loss than was previously thought.

INTRODUCTION

Recent herpetological surveys in Vietnam have resulted in the discovery of several previously undescribed species of frogs (e.g., Lathrop et al., 1998a, 1998b; Inger et al., 1999; Ohler et al., 2000; Orlov et al., 2001; Ziegler and Kohler, 2001). Similarly, several Southeast Asian species with vast ranges have been found to be complexes of cryptic species—multiple species currently referred to as a single taxon (Emerson, 1998; Inger, 1999; Fei et al., 2001). Disparate sampling efforts contribute to this problem of unidentified cryptic species. One complex of cryptic species likely involves an odoriferous, green cascade frog *Rana livida* (Werner, 1930; Taylor, 1962; Murphy et al., 1997; Inger, 1999).

Rana livida (Blyth, 1856) occurs near fast-moving montane rivers and streams of the Southeast Asian mainland, from southern China, across Indochina, to the eastern Himalayas in India (Boulenger, 1920; Smith, 1921; Pope, 1931; Smith, 1931; Bourret, 1942; Liu and Hu, 1961; Taylor, 1962; Frost, 1985; Zhao and Adler, 1993; Fellows and Hau, 1997; Fei, 1999; Stuart, 1999; Frost, 2002). Like all Southeast Asian cascade ranids, it is dorsoventrally compressed and has long, powerful legs and fully webbed feet. These attributes facilitate swimming in fast-moving water. It has greatly expanded toe pads that allow it to cling to rocks in the torrents and vegetation in the surrounding forest. The snout–vent length of female *R. livida* is nearly twice that of males. Females have white eggs, but the larvae are unknown (Inger, 1996). *Rana livida* has odoriferous, highly toxic skin secretions (Pope, 1931; Karsen et al., 1998).

The taxonomy of *R. livida* is confusing and unstable. Variation within *R. livida* is documented. Taylor (1962) reported that male *R. livida* from Thailand are significantly larger than other conspecific males (Boulenger, 1882, 1920; Bourret, 1942). Inger and Chanard (1997) also reported that male *R. livida* from northern Thailand differ in having larger snout–vent lengths and colorless spinules along the chin, throat, chest, and upper lip. Despite these observations, *R. livida* has not been studied across its range. Major systematic works on Southeast Asian amphibians continue to treat *R. livida* as a single taxon (e.g., Liu and Hu, 1961; Taylor, 1962; Frost, 1985; Fei et al., 1990; Yang, 1991a; Zhao and Adler, 1993; Inger et al., 1999; Frost, 2002). Comparative study has been complicated by two factors. First, the type series of *R. livida*, and those of some of its currently recognized junior synonyms, cannot be located because either the original descriptions do not include specimen accession numbers or the types are lost. Second, the type specimens are from disparate parts of the extensive distribution of *R. livida*. Thus, it has been unclear whether the morphological variability of this species owes to geographic variation or the presence of multiple species.

Is *R. livida* a single species or a set of cryptic species? We used concordant evidence from morphology, morphometrics, cellular DNA content, and allozymic loci to investigate this question in a series of frogs

from Vietnam. Because Vietnam represents only a small portion of the proposed range of *R. livida*, this study asseses the potential variability that may be found across its large distribution. We also review the junior synonyms and briefly discuss the specific, generic, and subgeneric taxonomic history in order to establish a stable taxonomy.

SYSTEMATIC REVIEW OF *RANA LIVIDA* (BLYTH, 1856)

***Rana livida* (Blyth, 1856)**
?*Polypedates smaragdinus* Blyth, 1852
Polypedates lividus Blyth, 1856
?*Rana nebulosa* Hallowell, 1861
Polypedates chloronotus Günther, 1875
Rana chloronota Boulenger, 1882
Rana livida Boulenger, 1887
Rana graminea Boulenger, 1899
Rana (*Hylorana*) *livida* Boulenger, 1920
Rana (*Hylorana*) *sinica* Ahl, 1925
Rana leporipes Werner, 1930
Odorrana livida Fei, Ye, and Huang, 1990
Rana (*Eburana*) *livida* Dubois, 1992

Polypedates smaragdinus: Blyth (1852) ambiguously described *Polypedates smaragdinus* in a three sentence description: ''A tree frog from the Naga hills, Assam (*P. smaragdinus*, nobis). Length of the body 3¼ inches, hind limb 5¼ inches. Wholly green above, changing in spirit to livid blue; underparts white.'' No illustrations are associated with the description and type specimens are not designated. *Polypedates smaragdinus* is not mentioned in the Indian Museum Reptile Registry, in any catalog, or in other early reports in the Indian Museum (Chanda et al., 2000). There are no vouchers in the collections of the Zoological Survey of India collections (Chanda et al., 2000). The type material is not in the British Museum (Clarke, personal commun.). Presumably, the types are lost. Chanda et al. (2000) erroneously reported that Anderson (1871) redescribed the ''now lost syntypes'' of *P. smaragdinus*; in contrast, Anderson's redescription was based on specimens already described by Jerdon (1870) from the Khasi Hills, India. Günther (1875) and Boulenger (1887) correctly stated that Blyth's original description was so vague that it could be referred to a number of cascade ranids. This, coupled with the absence of an illustration and type material, leads us to conclude that *Polypedates smaragdinus* fails to conform to Article 12 of the International Zoological Code of Nomenclature (1999).

Polypedates lividus: Blyth (1856) described *P. lividus* in a report on specimens procured by Capt. Berdmore and W. Theobold from Burma (now Myanmar). However, the type locality is uncertain. Although Blyth (1856) reported that the specimens given to him by Theobold were from the Tenasserim River Valley, Burma, Theobold (1860: 325) reported that ''Mr. Blyth described a new species of tree frog received from Major Berdmore at Mergui.'' Mergui (today Myeik) is a coastal seaport, far from inland Tenasserim Valley.

The type series of *P. lividus* is not present in the Indian Museum Reptile Registry, any catalog or other early reports in the Indian Museum, and it cannot be found in the Zoological Survey of India collections (Chanda et al., 2000). The type specimens of *P. lividus* are neither in the British Museum (Natural History) (Clarke, personal commun.), nor are they referred to in any other publication other than the original description. No illustrations accompanied the description. Presumably, the type series is lost.

Polypedates chloronotus: Günther (1875) described another series of frogs collected by Jerdon from Darjeeling, India as *Polypedates chloronotus*, noting that it resembles a ''*Hylorana*''. He included specimens from the Khasi Hills, India, that Jerdon (1870) and Anderson (1871) referred to as *P. smaragdinus*. Boulenger (1882) reevaluated the syntypes and assigned *P. chloronotus* to the genus *Rana* based on extensive webbing and T-shaped distal phalanges. Reporting on the ''Fea series'' from northern Tenasserim Burma, Boulenger (1887) noted that some specimens are ''beyond doubt to belong to the species named *Polypedates lividus* by Blyth, and also to be inseparable from Günther's *P. chloronotus*''; he made *Rana chloronota* a junior synonym of *P. lividus*, as *R. livida*.

Rana livida and *R. chloronota* differ significantly: *R. livida* is ''uniformly dusky-plumbeous above'', but *R. chloronota* has a green dorsum with dark sides that are ''sharply defined'' and have ''dark cross bars'' on the limbs. This diagnosis of *P.*

chloronotus agrees with the color plate that accompanies the original description. Moreover, whereas *R. livida* has smooth skin and is ''only slightly granulose on the hind surface of the thighs'', *R. chloronota* has a smooth dorsum and granular flanks. These characteristics, as well as the differences in color patterns on the thighs and flanks, remain visible on the syntypes of *R. chloronota* and Fea's series of *R. livida*. Boulenger's (1890) description of *R. livida* in the *Fauna of British India* is actually *R. chloronota*. All subsequent works have used Boulenger's (1890) taxonomy (e.g., Boulenger, 1920; Smith, 1921; Pope, 1931; Smith, 1931; Bourret, 1942; Liu and Hu, 1961; Taylor, 1962; Fei et al., 1990; Yang, 1991a; Zhao and Adler, 1993; Inger and Chanard, 1997; Fellows and Hau, 1997; Karsen et al., 1998; Fei, 1999; Inger, 1999; Inger et al., 1999; Stuart, 1999; Ziegler, 2002; Orlov et al, 2002).

Rana nebulosa: Hallowell (1861) described this species from Hong Kong based on a juvenile specimen. The ambiguous description did not designate a type specimen. The type is not included in the list of herpetological type specimens of the National Academy of Sciences, Philadelphia (Malnate, 1971), and it is not present in the collection (Gilmore, personal commun.). It is lost. Because the validity of the species can neither be confirmed nor denied, Boulenger (1882) considered *R. nebulosa* to be an uncertain species. Dubois and Ohler (2000) suggested that *R. nebulosa* is a possible junior synonym of *R. chloronota* (as *R. livida*) because its description does not contradict that of *R. chloronota*. They advocated designation of a lectotype from Hong Kong. We agree with Boulenger's assessment and conclude that *R. nebulosa* fails to conform to Article 12 of the International Zoological Code of Nomenclature (1999).

Rana graminea: Boulenger (1899) described *Rana graminea* from the Five Finger Mountains on Hainan Island, China. Although it closely resembles *R. chloronota* (Boulenger, 1899, 1920), the two male syntypes have a larger tympanum, oblique, nearly vertical (versus concave) loreal region, smaller hands, smaller digital disks, smooth flanks (versus granulate), and weak dorsolateral folds (versus absent). Smith (1930) synonymized *R. graminea* with *R. chloronota* (as *R. livida*) based on two male specimens from the Nakon Sritamarat Mountains of the Malay Peninsula. Nevertheless, some subsequent works recognized *R. graminea* (e.g., Pope, 1931; Boring, 1932; Bourret, 1942). Bourret (1942) considered *R. graminea* to be a ''northern variety'' of Indochinese *R. chloronota* (as *R. livida*) because of its weak dorsolateral fold. Inger et al. (1999) did not find evidence of *R. graminea* in their series of frogs from central Vietnam. Currently, *R. graminea* is a junior synonym of *R. chloronota* (as *R. livida*) (Zhao and Adler, 1993; Frost, 2002), although this is unjustified.

Rana sinica: Ahl (1925) described *Hylorana sinica*, and Bourret (1942: 371) listed it as a possible synonym of *R. chloronota* (as *R. livida*): ''?*Rana* (*Hylarana*) *sinica*''. However, many differences separate the two species: in *R. sinica*, finger I is shorter than finger II, and finger III is shorter than the snout; in *R. chloronota*, II $<$ I $<$ IV $<$ III, and finger III is longer than snout. *Rana sinica* has large, round black spots on its flanks but *R. chloronota* does not. *Rana sinica* lacks the white lip-stripe that is present in *R. chloronota*. The tympanum of *R. sinica* is covered by a layer of skin, but in *R. chloronota* the distinct tympanum does not have a superficial layer of skin. It is still recognized as a junior synonym (Frost, 2002).

Rana leporipes: Werner (1930) described this species as a southern Chinese member of the ''*Rana livida* group''. It differs from *R. chloronota* in having slender legs that lack transverse bands, smaller disks, a white supratympanic fold, a weak dorsolateral fold, and webbing that only reaches the base of the distal phalanx. Bourret (1942) synonymized *R. leporipes* with *R. livida* var. *graminea*, and Liu and Hu (1961) agreed with this synonymy. The type series of *R. leporipes* is not in the Museum für Naturkunde der Humboldt-Universität, Berlin, Germany, and is considered lost; all of Werner's collections are deposited there. It is likely that the specimens were lost during World War II (Guenther, personal commun.). Despite its current recognition as a junior synonym (Frost, 2002), the diagnostic characters indicate that *R. leporipes* is a valid species.

Generic and Subgeneric Placements of *Rana livida*

Rana chloronota (as *R. livida*) is variously placed in subgenera *Eburana* (Dubois, 1992; Duellman, 1993), *Hylarana* (Boulenger, 1920; Bourret, 1942), and *Odorrana* (Fei et al., 1990; Matsui, 1994; Zhao, 1994; Fei et al., 1999). To add confusion, the latter two taxa are occasionally considered to be genera. *Rana chloronota* has diagnostic characters that are unique to each of these taxa: fully webbed feet are typical of *Rana*, enlarged toe disks of *Hylarana*, odoriferous secretions of *Odorrana*, and white eggs of *Eburana*. We review the generic and subgeneric taxonomy that includes *R. chloronota* and discuss the validity of placement into each group.

Rana Linneaus, 1758: The content and diagnosis of the genus *Rana* has changed since its original description. Boulenger (1887) thought that *Polypedates chloronotus* belonged in *Rana* because of its extensive webbing and T-shaped terminal phalanges; *R. chloronota* remained in the genus *Rana* for almost a century.

Hylarana Tschudi, 1838: *Hylarana* has horseshoe-shaped circummarginal grooves on the ventral surface of very large digital disks. Boulenger (1882) originally thought that *Hylarana* should not be recognized. Later, he (Boulenger, 1920) revised its definition, making it a subgenus, but he erroneously used the name *Hylorana* instead of *Hylarana*.

Rana chloronota conforms to the diagnosis of *Hylarana* in having dilated disks with circummarginal grooves, T-shaped terminal phalanges, and an unforked omosternal style. Boulenger (1920) placed *R. chloronota* (as *R. livida*) in the subgenus *Hylorana* [=*Hylarana*], section *Ranae chalconotae,* allying it with *R. chalconota*, *R. hosii*, and *R. graminea*, among others. He recognized that the subgenus *Hylorana* [=*Hylarana*] as an ''unnatural assemblage'' because it is formed on the basis of specialized fingers and toes. For the next 70 years, *R. chloronota* was referred to as a member of the subgenus *Hylarana* (e.g., Bourret, 1942), or its subgeneric placement was ignored entirely (e.g., Pope, 1931; Taylor, 1962; Zhao and Adler, 1993; Nguyen and Ho, 1996; Karsen et al., 1998; Inger, 1999; Inger et al., 1999). The status of *Hylarana* remains controversial. Whereas *Hylarana* is usually considered to be a genus by those working on the African fauna, those working on the Asian fauna consider it to be a subgenus of *Rana* (Frost, 1985, 2002).

Odorrana Fei, Ye, and Huang, 1990: Fei et al. (1990) placed 12 species of Chinese odoriferous *Hylarana* in a new genus, *Odorrana*. The genus is diagnosed primarily by external morphology and sternal elements, including a very small and cartilaginous omosternum where the omosternal bone (= style) is not forked; mesosternum long and slender and proximally much thicker; and xiphisternal cartilage much larger than omosternum and deeply notched posteriorly (Fei et al., 1990). The odoriferous properties of the skin are not included as a diagnostic character, even though the generic name was derived from this trait. Although Boulenger (1920) placed *R. chloronota* (as *R. livida*) in section *Ranae* (*Hylorana* [= *Hylarana*] *chalconotae*), results from karyological studies suggest that it is a member of the *Rana* (*Hylarana*) *andersonii* group (Li and Wang, 1985; Wei et al., 1993). Consequently, Fei et al. (1990) placed the *Rana andersonii* group and *R. chloronota* (as *R. livida*) into *Odorrana*. Neither Yang (1991a) nor Zhao and Adler (1993) recognized *Odorrana*. Others have suggested that *Odorrana* be considered a subgenus because many species of *Rana* share some of its ''diagnostic'' characters (Dubois, 1992; Inger, 1996; Matsui, 1994; Zhao, 1994).

Eburana Dubois, 1992: Dubois (1992) established Subsection *Hylarana* with 10 subgenera, including revisions of *Hylarana* and *Odorrana*, and the description of a new subgenus *Eburana*. *Eburana* is diagnosed by larval denticular formula (4–5/4), the absence of nuptial spines on the chest of the males, and the absence of pigmented eggs. Subsection *Hylarana* is defined by the lack of humeral glands in the males. Dubois removed *R. chloronota* (as *R. livida*) from *Odorrana* and placed it into *Eburana* (along with *R. swinhoana* and *R. narina*).

Dubois' (1992) provisional classification of the family Ranidae has received spirited criticism due to philosophical and empirical

issues. Criticisms focus on the phenetic basis of the classification, a selective treatment of characters inferred from the literature, and an inadequate analysis of variation of the defining characters (Emerson and Berrigan, 1993; Matsui et al., 1995; Inger, 1996, 1999). Data from karyological studies suggest that *R. chloronota* shares a closer affinity with *Odorrana* (sensu Fei et al., 1990) than with other *Eburana* (Wei et al., 1993; Matsui, 1994; Matsui et al., 1995). *Rana chloronota* is the only member of *Eburana* to have odoriferous skin secretions. Furthermore, the larvae of *R. chloronota* are unknown, making it impossible to evaluate this as a diagnostic character (Inger, 1996).

Taxonomic Conclusions

We adopt the collective recommendation of Inger (1996), Matsui (1994), and Zhao (1994) in recognizing *Odorrana* as a subgenus of *Rana*. The monophyly of *Odorrana* is supported by a phylogenetic analysis of more than 2000 base pairs of mitochondrial DNA sequence data (Chen and Murphy, unpubl.). We recognize *P. smaragdinus* and *R. nebulosa* as nomen dubium, since they fail to conform to Article 12 of the Code (1999). We also remove *R. leporipes*, *R. sinica*, *R. graminea*, and *R. chloronota* from synonymy because each is defined by distinct, diagnostic characters. Below we redescribe *R. sinica*, *R. graminea*, *R. chloronota*, and *R. livida*, and comment on *R. leporipes*. We designate a neotype of *R. livida*, since no name-bearing type exists and its designation qualifies under the conditions of Article 75.3 of the Code (1999). Because the voucher type specimens of *R. leporipes* have been lost, the type specimen of *R. leporipes* is now the photograph of the holotype (an iconotype), which is published as figures 1 and 2 in the original description (Werner, 1930: 49, pl. IV).

MATERIALS AND METHODS

Collection Abbreviations

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
IEBR	Institute of Ecology and Biological Resources, Hanoi
ROM	Royal Ontario Museum, Toronto
ZMB	Museum für Naturkunde der Humboldt-Universität, Berlin

Methodological Outline

Specimens of *R. chloronota* were segregated a priori into morphotypes. Consistently detected morphological and molecular groups were considered to be distinct species. We analyzed morphometric data with discriminant function analyses to distinguish among forms and shapes. We also used *t*-test evaluations of cellular DNA content data to differentiate among sympatric species, assuming that conspecific individuals have equal amounts of DNA. We further evaluated species boundaries with allozyme electrophoresis. Fixed allelic differences provided diagnostic characters for species.

General Collecting Procedures

Specimens of *Rana chloronota* from Hong Kong, and eight localities in Vietnam were collected at various times of the year from 1994 to 1999. Localities in Vietnam included: Hoang Lien Mountains near Sa Pa (Lao Cai Province); Ba Be National Park (Bac Kan Province); Tam Dao Mountain, Tam Dao National Park (Vinh Phu Province); Na Hang Nature Reserve (Tuyen Quang Province); Con Cuong region (Nghe An Province); and Tay Nguyen Plateau, An Khe District (Gia Lai Province) (fig. 1). Coordinates were recorded in geographic projection using handheld GPS units (see table 1). Although error and precision were carefully monitored, position coordinates collected before 1 May 2000 were subject to the effects of selective availability (White House Press Secretary, 2000). Because real-time and postdifferential corrections were not feasible or available in this region, positional accuracy should be judged accordingly.

Most frogs were collected at night and all were euthanised using MS-222 or chlorobutanol within 24 hours of collection. Samples of liver, leg muscle, and heart were taken from representative specimens. Frozen tissues deposited in the ROM were flash frozen in liquid nitrogen. All tissue samples in the

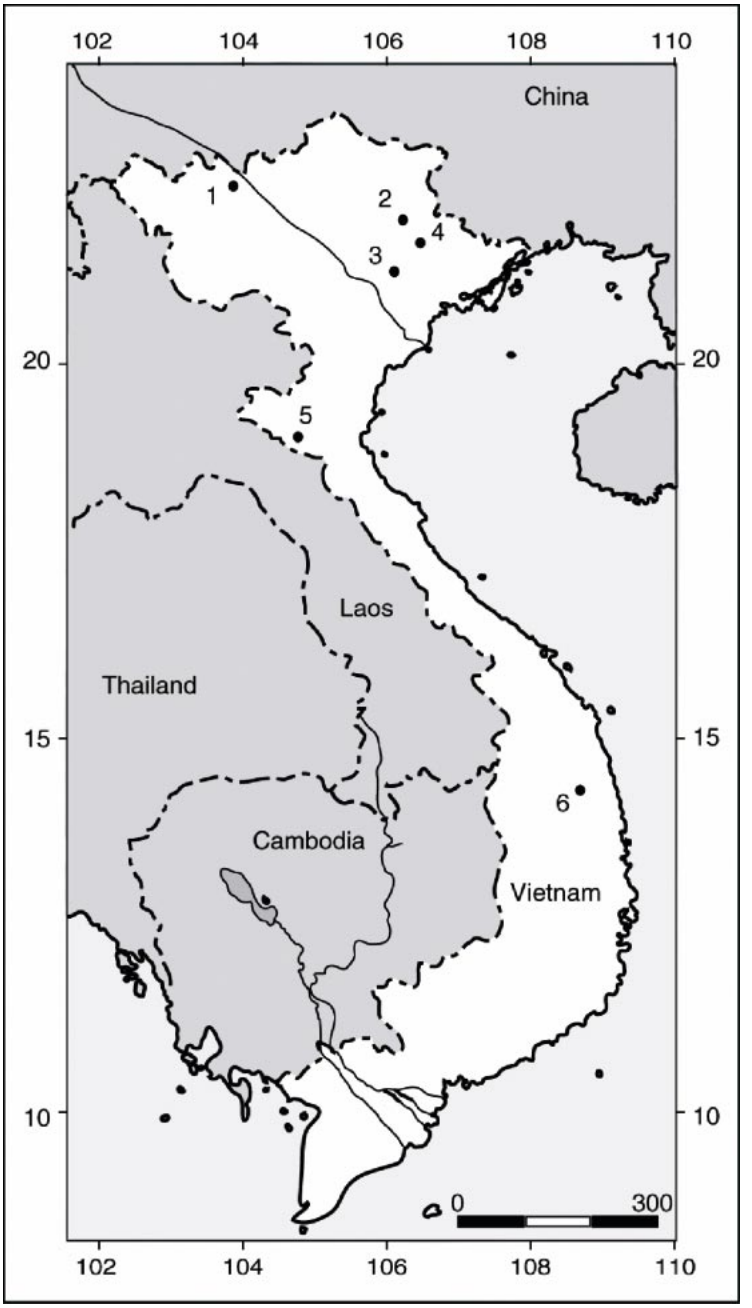

Fig. 1. Map of Vietnam. Collecting localities of odoriferous frogs of the genus *Rana* are indicated by numbers, referable to table 1.

AMNH were preserved in 95% ethanol. Blood samples obtained for flow cytometry were suspended in a freezing solution (Vindelov et al., 1982; Murphy et al., 1997), initially frozen in liquid nitrogen and subsequently stored at −80°C in the ROM. Frogs were fixed in either 90% ethanol for 24 hours or in 10% formalin for several hours and subsequently rinsed in water. All tissue collections are stored in the ROM and AMNH,

TABLE 1
Locality and Seasonal data for Collections of *Rana chloronota*
When known, exact coordinates and months are provided. Missing data suggest that the information was not available. Number refers to locations indicated on map in figure 1.

Number	Locality	Coordinates	Elevation (m)	Season
1	Sa Pa and vicinity, Lao Cai Province, Vietnam	22°20′09″N, 103°50′14″E 22°20′58″N, 103°46′14″E	1400 1900	October 1994, May 1995 August 1997 April-May 1999
2	Ba Be National Park, Bac Kan Province (formerly Cao Bang Province),Vietnam	22°25′05″N, 105°38′05″E		May 1996
3	Tam Dao, Vinh Phu Province, Vietnam	21°27′N, 105°39′E		October 1994 May-June 1995–1997
4	Na Hang Nature Reserve, Tuyen Quang Province,Vietnam	22°21′54″N, 105°25′40″E		May 1997
5	Con Cuong District, Nghe An Province, Vietnam	18°56′30″N, 104°48′35″E 19°02′17″N, 104°42′06″E 18°56′N, 104°45′E	200 300	October 1994, June 1995 April 1998 September 1998
6	An Khe District, Tay Nguyen Plateau,Gia Lai Province, Vietnam	Tram Lap, 14°26′N, 108°33′E		July 1996
		Buon Loi	700–750	November 1993
		Krong Pa	900	July 1996
—	Hong Kong, People's Republic of China	22°15′N, 114°10′E		April 1996
—	Ch'ungan Hsien and Yenping Fujien Province, People's Republic of China			April-September 1931
—	India			1882
—	Lao PDR, Khammouane Province, Nakai District			November 1998
—	Myanmar			Early 1887

and all vouchers are maintained in 65% ethanol in the AMNH, ROM, or IEBR.

Laboratory Procedures

A total of 343 adult *R. chloronota* including recognized synonyms were examined (appendix 1, fig. 1, table 1). We compared all recently collected samples to specimens of *R. livida* from Fea's collection of *R. livida* from Myanmar (see above), to currently recognized junior synonyms of *R. chloronota*, as well as to series of *R. chloronota* from Fujian Province, China, Lao PDR, and India. Frogs not identified as *R. chloronota* or any of its synonyms were treated as separate OTUs in subsequent analyses.

Morphology: The sex of each frog was recorded and all measurements made with digital calipers to the nearest 0.01 mm and rounded to the nearest 0.1 mm. External measurements included snout–vent length (SVL), head length (HDL) from tip of snout to the articulation of the jaw, head width (HDW) between left and right articulations of the quadratojugal and maxilla, snout length (SNT), eye diameter (EYE), interorbital distance (IOD), tympanum diameter (TMP), tympanum–eye distance (TEY), fin-

ger disk length (FPL) from the base of the pad of III to its tip, finger disk width (FPW) at the widest part of the pad of III, toe disk length (TPL), and toe disk width (TPL). Osteological measurements taken from radiographs included the following: finger length (FGR) from tip of the distal phalanx to the base of the proximal phalanx of finger II, hand length (HND) from distal end of radioulna to tip of distal phalanx of II, foot length (FTL) from distal end of tibia to tip of distal phalanx of III, and tibial length (TIB). Pectoral girdle terminology follows Duellman and Trueb (1986) and gular pouches are defined using Inger (1956).

MORPHOMETRICS: Morphometric analyses were performed on 150 recently collected specimens from Vietnam, following the recommendations of Tabachnick and Fidell (1989) and Hair et al. (1995). For this analysis, HDL (from posterior edge of otoccipital to tip of premaxilla) and HDW (distance between left and right quadratojugal-maxillary suture) were measured from radiographs; other measurements were taken as described above. Raw morphometric data were log-transformed and tested for normality using categorized probability plots. Serial correlation plots were used to test for heterogeneity and detect redundancies among the variables. A pooled within-group correlation-variance matrix was used in a principal components analysis (PCA). The first principal component (PC1) was used as a size component and regressed against each log-transformed variable. Resulting residuals were used in a pooled-within group correlation-variance matrix for a discriminant functions analysis (DFA). The effect of size on the measurements was factored out. All a priori classification error rates were made proportional to group size. Robustness of the morphotype groupings was tested by reclassification methods. When possible (i.e., where $n > 15$), morphotypes were divided into subgroups, with part of the group being used in the initial DFA, and part being used in a reclassification. Sexes were treated both separately and together in the DFA. All analyses were performed on STATISTICA ver. 5.1 (StatSoft, 1995).

CELLULAR DNA CONTENT: Cellular DNA content data were gathered for 73 specimens from six localities within Vietnam and Hong Kong using flow cytometry (Murphy et al., 1997). DNA content analysis was carried out with a Becton Dickinson FACScan or a Becton Dickson FACScalibur flow cytometer in the Faculty of Medicine, Department of Immunology, University of Toronto, between 1995 and 1997. Both systems used an argon laser at a wavelength of 488 nm at 15 mW. Fluorescence at wavelengths between 560 and 640 nm was collected and digitally transferred to a histogram of mean DNA content concentration. Each sample was measured simultaneously with a known standard, either *Nerodia sipedon* or *Bufo woodhousi fowleri*. No sample was tested on both flow cytometers. Only samples measured on the same machine at the same time were compared with each other to ensure accuracy; these included samples taken from a single locality. Cellular DNA content data of specific morphotypes were compared using *t*-tests to determine whether they exhibited statistically different levels of DNA.

PROTEIN ELECTROPHORESIS: Allozyme variation was surveyed among 64 specimens of *R. chloronota* from six localities within Vietnam and six specimens from Hong Kong. All morphotypes were used as a priori groupings of prospective species. A population of *Huia nasica* from Vietnam was included for comparison. All procedures follow protocols of Murphy et al. (1996). Electrophoretic conditions were optimized for 53 histochemical stains on 11 buffer systems using a subset of the samples (appendix 2). Locus nomenclature followed Murphy and Crabtree (1985) and Murphy et al. (1996). After optimal buffer systems were identified, electrophoresis was performed using the same lot of 11.5% hydrolyzed potato starch (Connaught, lot no. 514–3). Species boundaries were examined via population aggregation analysis modified from Davis and Nixon (1992). Genotypes of individuals within the same population (sympatric morphotypes) were summarized in a population profile, and groups of populations were subsequently examined for fixed allelic differences. Populations with a sample size of one or two specimens were included with allopatric populations of their own morphotypes, regardless of their allelic profiles. All specimens were also evaluated using an un-

biased minimum distance (Nei, 1978), and genetic similarity (Rogers, 1972) using BIOSYS ver. 1.7 (Swofford and Selander, 1989).

RESULTS

Morphology

Seven morphotypes occurred among specimens from Vietnam and Hong Kong. Morphotype 1, ''Typical'', conformed to the diagnosis of *R. chloronota* and was assigned to this species. None of the remaining six morphotypes was assignable to any synonym of *R. chloronota*. Specimens from Fujian Province, China, were identified as *Rana graminea*.

Morphotypes 2, 3, and 4 are distinct species based on morphological differences. Morphotype 2, or ''Black Egg'', differs from all others in not having a white lip line, possessing a shagreened (not smooth) completely brown (green entirely absent) dorsum, and in bearing black eggs. Morphotype 3, or ''Speckled'', was unique in having large granules laterally and in males lacking gular pouches. Morphotype 4, or ''Small'', is distibguished by its small size, white dorsolateral glandules, white flank spot, webbing to the distal subarticular tubercle but not to the toe pad, a forked xiphisternum, and absence of vomerine teeth. Differences among the three remaining morphotypes were equivocal at the species level. Morphotype 5, or ''Mottled'', includes males that are relatively smaller than *R. chloronota* (SVL of 39–46 mm, vs. 41–53 mm) with a much larger tympanum (96% diameter of the eye) and webbing that reached the distal tubercles. The dorsal skin of both males and females may be either shagreened or smooth and their color varied from brown to green. Morphotype 6, or ''Southern Big-Eye'', is very similar to ''Mottled''. The males are larger (42–55 mm) with large tympani (89% diameter of the eye) and webbing to the proximal parts of the toe pads. The dorsal skin of males and females is variable, being either shagreened or smooth, spotted and/or uniform in color, partially or wholly brown or green, with slight dorsolateral folds. Morphotype 7, or ''Large'', has an SVL larger than that of *R. chloronota* (48–55 mm for males, 93–105 mm for females), a lip line, when present, that is yellow (not white), the tympanum in males is enormous (120% of the eye diameter), the dorsal skin is shagreened with slight dorsolateral folds present in males, and the dorsum is spotted brown-olive.

Morphometrics

Morphometric analyses were performed on female *R. chloronota* (no.1, ''Typical''), ''Speckled'' (no. 3), ''Mottled'' (no. 5), and ''Large'' (no. 7), as well as on male *R. chloronota*, ''Small'' (no. 4), ''Mottled'' (no. 5) and ''Southern Big Eye'' (no. 6). Small sample sizes ($n < 5$) precluded the analysis of the remaining morphotypes. Only *R. chloronota* included enough specimens to be divided into two subsets for reclassification. All other OTUs were included both in the classification and reclassification using discriminant functions analysis (DFA).

Categorical probability plots showed normal frequency distribution in the log-transformed data. A high correlation between finger length and hand length, and between toe length and foot length was detected in serial correlation plots. Consequently, the finger and toe length data were considered to be redundant variables and were omitted from the analysis. The loadings of PC1 show that it represented a size factor (table 2).

A DFA of females indicated strong, detectable patterns of morphological variation (F-statistic = 6.86; $p < 0.0001$). Reclassification of all four OTUs was performed at a rate of 90% or higher (table 3). The discriminant loadings indicated that TMP had the greatest effect on factor 1, while FPW had the greatest effect on factor 2, and HDW and EYE each had the greatest load on factor 3 (table 4). A plot of factor 1 vs. factor 2 showed clear differentiation among three OTUs: *R. chloronota* (''Typical'', no. 1), ''Large'' (no.7), and ''Speckled'' (no. 3) (fig. 2). ''Southern Big Eye'' had a centroid within the 95% confidence limit of both ''Large'' and *R. chloronota*. A plot of factor 3 vs. factor 1 also showed separation of ''Speckled'' from the other three groups (fig. 3).

A DFA of the four male OTUs resulted in an associated F-statistic of 9.64 ($p < 0.0001$). *Rana chloronota* was very distinct

TABLE 2
Coefficients of the First Principal Component (PC1) for a Principal Components Analysis (PCA) of 17 Variables
Refer to text for variable abbreviations.

Variable	PC1
SVL	0.982
HDL	0.963
HDW	0.970
FGR	0.962
HND	0.968
TL	0.845
FT	0.812
TIB	0.983
IOD	0.782
EYE	0.772
TEYE	0.932
TMP	0.697
SNT	0.897
FPL	0.917
FPW	0.896
TPL	0.931
TPW	0.923
Explained variation	13.765
Proportion of total variation	0.810

TABLE 4
Factor Loadings of Female Morphogroups of the *Rana chloronota* Complex from a DFA
Refer to text for variable abbreviations.

Variable	Factor 1	Factor 2	Factor 3
HDL	−0.06	−0.17	0.04
HDW	0.27	−0.45	0.49
HND	0.33	−0.24	−0.11
FT	−0.18	0.03	0.10
TIB	−0.09	−0.29	0.33
IOD	0.03	0.06	−0.04
EYE	0.18	−0.29	−0.48
TEYE	−0.05	−0.01	0.26
TMP	−0.53	−0.02	−0.23
SNT	−0.07	−0.17	0.20
FPL	0.11	0.27	−0.03
FPW	0.10	0.59	−0.22
TPL	0.12	0.43	−0.05
TPW	0.10	0.24	0.06

from ''Small'' (no. 4); the correct reclassification scores were 97% for the former and 100% for the latter (table 5). The two Indian specimens were reclassified correctly as *R. chloronota*. The reclassification score of ''Mottled'' (no. 5) was also robust at 84%, well above the a priori error rate. All incorrectly classified ''Mottled'' were classified as ''Southern Big Eye'' (no. 6). The 36% reclassification of ''Southern Big Eye'' was well above the a priori expected error rate of 14%, but was still equivocal with ''Mottled''. The similarity between the two sympatric morphotypes from the south was reflected in the factor plot of the groups (fig. 4). Factor loadings indicated that the first factor was most indicative of TMP, the second EYE, and the third FPW and HDL (table 6).

A DFA of the combined male and female datasets resulted in an *F*-statistic of 6.78 ($p < 0.0001$). All groupings were morphologically distinct, with the exception of male ''Southern Big Eye'' (no. 6), which was reclassified as ''Mottled'' (no. 5) 54% of the time (table 7). In the discriminant loadings, TMP had the greatest effect on factor 1, FPW and EYE on factor 2, HDW and TIB on factor 3 (table 8).

Cellular DNA Content

t-tests indicated that cellular DNA content for each pair of sympatric morphotypes was

TABLE 3
Reclassification Matrix for Available Female Morphogroups of the *Rana chloronota* Complex from a Discriminant Function Analysis (DFA)

	Percentage	Typical	Southern Big Eye	Speckled	Large
no. 1, Typical	97.83	45	1	0	0
no. 2, Southern Big Eye	100.00	0	10	0	0
no. 5, Speckled	100.00	0	0	6	0
no. 7, Large	90.00	1	0	0	9
Total	97.22	46	11	6	9

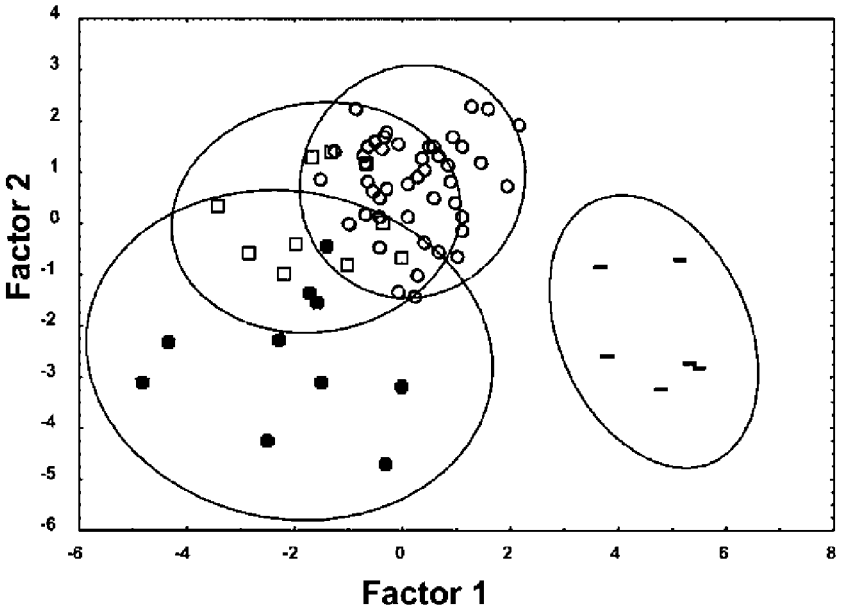

Fig. 2. Results of a DFA using morphometric data from females referable to *R. chloronota* from Vietnam (factor 1 vs. factor 2). Morphotypes are represented by the following symbols: ○, no. 1 (Typical); □, no. 6 (Southern Big Eye); —, no. 3 (Speckled); ●, no. 7 (Large).

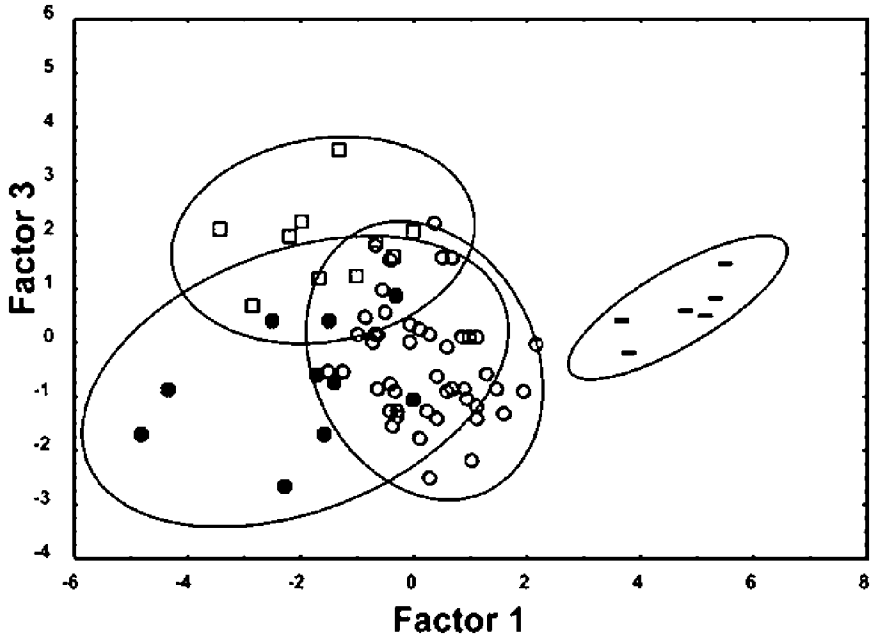

Fig. 3. Results of a DFA using morphometric data from females referable to *R. chloronota* from Vietnam (factor 3 vs. factor 1). Morphotypes are represented by the following symbols: ○, no. 1 (Typical); □, no. 6 (Southern Big Eye); —, no. 3 (Speckled); ●, no. 7 (Large).

TABLE 5
Reclassification Matrix for Male Morphogroups of the *Rana chloronota* Complex from a DFA

	Percentage	Typical	Southern Big Eye	Mottled	Small
no. 1 Typical	97.22	35	1	0	0
no. 6 Southern Big Eye	36.36	1	4	6	0
no. 5 Mottled	84.21	0	3	16	0
no. 4 Small	100.00	0	0	0	12
Total	85.90	36	8	22	12

significantly different (table 9). In Sa Pa, ''Speckled'' (no. 3) had a mean DNA content level of 14.86 pg (±1.50), whereas ''Small'' (no. 4) had 13.26 pg (±0.42) ($t = 8.40$, $p < 0.0001$). In Na Hang, *R. chloronota* had 13.05 pg (±0.54) of DNA/cell and ''Large'' (no. 7) 14.43 pg (±0.06) ($t = 3.59$, $p < 0.007$). In Con Cuong, *R. chloronota* had 12.45 pg (±0.33) of DNA per cell, whereas sympatric ''Large'' (no. 7) had 13.98 pg (±0.14) ($t = 13.00$, $p < 0.0001$). The two morphotypes from the Central Highlands also had distinct levels of cellular DNA from each other, with ''Mottled'' (no. 5) exhibiting 12.10 pg of DNA/cell (±0.11), and ''Southern Big-Eye'' (no. 6) 13.02 pg/cell (±0.10) ($t = 7.02$, $p < 0.0007$). The congruence of DNA content with the proposed morphotypes is indicative of their strength as a priori groups used for electrophoretic studies.

Protein Electrophoresis

Fourteen presumptive enzyme loci were satisfactorily resolved on six buffer systems (table 10). Two of these, AK-A and MDHP-A, were monoallelic among all samples and populations. The 12 remaining loci were po-

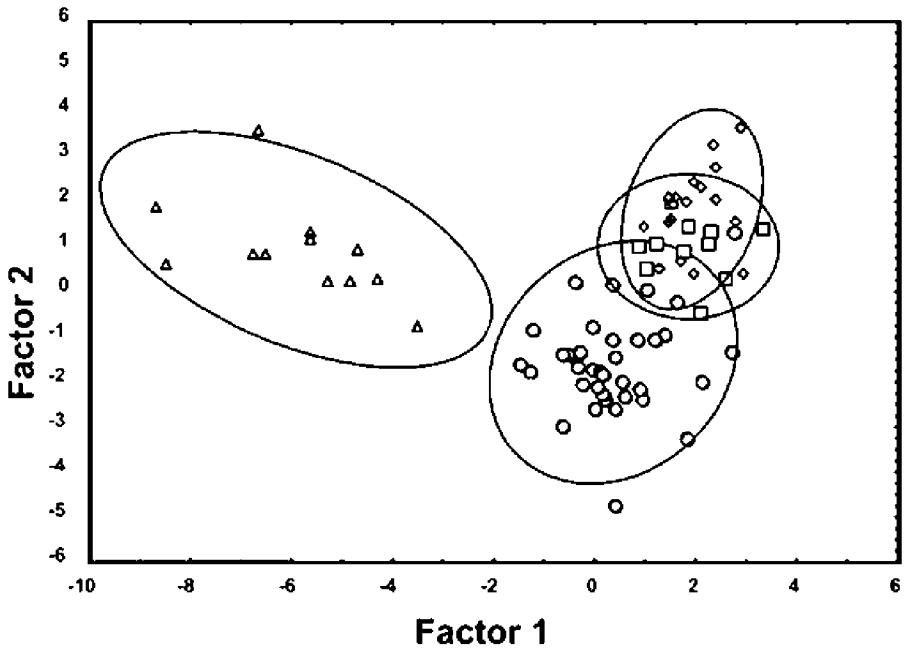

Fig. 4. Results of a DFA using morphometric data from males referable to *R. chloronota* from Vietnam (factor 1 vs. factor 2). Morphotypes are represented by the following symbols: ○, no. 1 (Typical); □, no. 6 (Southern Big Eye); ◊, no. 5 (Mottled); △, no. 4 (Small).

TABLE 6
Factor Loadings of Male Morphogroups of the *Rana chloronota* Complex from a DFA
Refer to text for variable abbreviations.

Variables	Factor 1	Factor 2	Factor 3
HDL	0.142	0.169	0.646
HDW	0.025	0.165	0.174
HND	0.049	−0.036	0.343
FT	−0.169	−0.297	0.145
TIB	−0.025	0.265	0.338
IOD	0.054	−0.021	0.166
EYE	−0.181	−0.427	−0.242
TEYE	0.251	−0.128	0.050
TMP	0.681	−0.193	−0.413
SNT	0.227	0.201	−0.372
FPL	−0.095	0.115	−0.144
FPW	−0.373	0.200	−0.654
TPL	−0.079	0.100	−0.138
TPW	−0.213	0.278	0.135

TABLE 8
Factor Loadings of Female and Male Morphogroups of the *Rana chloronota* Complex from a DFA
Refer to text for variable abbreviations.

Variables	Factor 1	Factor 2	Factor 3
HDL	0.10	−0.07	−0.30
HDW	−0.01	−0.14	−0.53
HND	0.00	−0.31	−0.16
FT	−0.05	−0.02	0.27
TIB	−0.02	−0.01	−0.52
IOD	0.05	0.00	0.04
EYE	−0.15	−0.57	0.38
TEYE	0.25	−0.10	0.03
TMP	0.71	−0.12	0.25
SNT	0.16	−0.02	−0.35
FPL	−0.09	0.27	0.04
FPW	−0.35	0.57	0.21
TPL	−0.08	0.37	0.13
TPW	−0.21	0.35	−0.19

lyallelic and they provided evidence of differentiation at the species level for all seven morphotypes (table 10).

WITHIN-GROUP GENOTYPES: Three of the OTUs were sampled from multiple populations: *R. chloronota* was represented by five populations, ''Black Egg'' (no. 2) by four, and ''Large'' (no. 7) by two. Neither *R. chloronota* nor ''Black Egg'' exhibited fixed differences among their populations. Sample sizes of the ''Black Egg'' populations from Na Hang and Tam Dao were too small (n = 1) to be used in the population aggregate analysis. They were combined with allopatric populations of their own morphotypes because they did not exhibit any unique alleles that could have been interpreted as being fixed character differences. The all-male ''Large'' series from Na Hang was distinguishable from the all-female sample at Con Cuong by one fixed allele at FUMH-A.

AMONG-GROUP GENOTYPES IN SYMPATRY: Fixed allelic differences in eight loci (mAAT-A, CK-C, GTDH-A, LDH-B, mMDH-A, sMDH-A, PGM-A, FUMH-A) diagnosed five of the a priori OTUs (table 10). ''Small'' (no. 4) had unique fixed allelic differences at three loci, mAAt-A, mMDH-

TABLE 7
Reclassification Matrix for Female and Male Morphogroups of the *Rana chloronota* Complex from a Combined DFA

	Percentage	Typical (M)	Typical (F)	S. Big Eye (M)	S. Big Eye (F)	Mottled (M)	Speckled (F)	Large (F)	Small (M)
no. 1 Typical (M)	61.11	22	9	1	0	3	0	1	0
no. 1 Typical (F)	82.61	5	38	0	2	1	0	0	0
no. 6 Southern Big Eye (M)	36.36	2	0	4	0	5	0	0	0
no. 6 Southern Big Eye (F)	60.00	0	3	0	6	1	0	0	0
no. 5 Mottled (M)	84.21	0	0	1	2	16	0	0	0
no. 3 Speckled (F)	100.00	0	0	0	0	0	6	0	0
no. 7 Large (F)	80.00	2	0	0	0	0	0	8	0
no. 4 Small (M)	91.67	0	1	0	0	0	0	0	11
Total	74.00	31	51	6	10	26	6	9	11

TABLE 9
***t*-test of Cellular DNA Contents of Sympatric Morphotypes**
Refer to table 1 for exact locality references.

Locale	Morphotype	Sample size (n)	Mean DNA content (pg)	*t*-statistic	p (0.995)
Sa Pa	Speckled (no. 3)	7	14.86		
	Small (no. 4)	8	13.26	8.40	0.0001
Na Hang	Typical (no. 1)	6	13.05		
	Large (no. 7)	3	14.43	3.59	0.007
Con Cuong	Typical (no. 1)	7	12.45		
	Large (no. 7)	5	13.98	13.00	0.0001
An Khe	Mottled (no. 5)	14	12.1		
	Southern Big Eye (no. 6)	21	13.02	7.02	0.0006

A, and sMDH-A. ''Southern Big Eye'' (no. 6) had unique fixed alleles at CK-C and Pgm-A. ''Speckled'' (no. 3) had one fixed unique allele at GTDH-A, as did ''Large'' (no. 7) from Con Cuong at Fumh-A. ''Black Egg'' (no. 2) had a unique fixed allele at LDH-B.

Many fixed differences were congruent with hypothesized species boundaries. The two species found in Sa Pa, ''Small'' (no. 4) and ''Speckled'' (no. 3), exhibited fixed allelic differences from each other at 10 loci: mAAT-A, CK-C, GPI-A, GTDH-A, mIHD-A, LDH-A, LDH-B, mMDH-A, sMDH-A, and FUMH-A. ''Southern Big Eye'' and ''Mottled'', both from the Central Highlands, were also distinct from each other at seven loci with fixed differences: CK-C, LDH-B, sMDH-A, PEP-A, PGM-A, sSOD-A and FUMH-A. *Huia nasica* and *R. chloronota* from Tam Dao were separated by six fixed differences: mAAT-A, CK-C, mIDH-A, LDH-A, sSOD-A, and FUMH-A. ''Large'' (no. 7) and sympatric *R. chloronota* at Na Hang exhibited fixed differences at five loci: mAAT-A, CK-C, LDH-B, sSOD-A, and FUMH-A.

Three sympatric OTUs occurred in Con Cuong: *R. chloronota* (no. 1), ''Large'' (no. 7), and ''Black Egg'' (no. 2). All three could be distinguished from each other with alternate fixed alleles at FUMH-A. ''Large'' was also discernible with a fixed difference at sSOD-A, while ''Black Egg'' was distinct at three loci: LDH-B, CK-C, and mAATt-A.

AMONG-GROUP GENOTYPES IN ALLOPATRY: All allopatric groups exhibited at least one fixed allelic difference from each other (table 10). Although the allozyme data provided substantial evidence for the recognition of new species, the sample sizes were too low to make inferences about population substructure.

PHENETIC ANALYSES

A phenetic analysis of the allozyme data summarized overall similarity for 14 loci. Because all loci were not resolved in ''Small'' (no. 4), it was deleted from this analysis. Similarly, ''Black Egg'' (no. 2) from Ba Be, Tam Dao, and Na Hang were also omitted in order to maximize the number of loci. A matrix of the two measures of genetic distance, the unbiased minimum distance (Nei, 1978) and Roger's genetic distance (table 11), generally reflect the numbers of fixed allelic differences among groups. The largest genetic distance was found between the ''Black Egg'' and ''Mottled'' morphotypes (Nei's D = 0.595, Roger's D = 0.631). Allopatric populations of *R. chloronota* exhibited the smallest genetic distance. The smallest distance was found between populations of *R. chloronota* from Tam Dao and Na Hang (Nei's D = 0.000, Roger's D = 0.003).

PHYLOGENETIC ANALYSES OF MORPHOLOGICAL AND MOLECULAR DATA

These morphological and allozyme data were potentially amenable to phylogenetic

TABLE 10

Allozyme Frequencies at all Resolved Presumptive Loci of the *Rana chloronota* Complex

Locality data appear below species name/morphogroup number [refer to text] with sample sizes in parentheses. Alleles are indicated with lowercase letters. Missing data are indicated by "nr". Locality abbreviations: B, Ba Be: HK, Hong Kong; NH, Na Hang; TD, Tam Dao; CC, Con Cuong; AK, An Khe; S, Sa Pa. Refer to table 1 for locality references. Refer to appendix 2 for enzyme system abbreviations.

	no. 1					no. 5	no. 4	no. 7		no. 6	no. 3	*H. nasica*	no. 2			
	B (5)	HK(6)	NH (4)	TD (5)	CC (5)	AK (5)	S (3)	CC (5)	NH (3)	AK (5)	S (3)	TD (5)	NH (4)	TD (1)	B (1)	CC(5)
AK-A	aa (5)	aa (6)	Aa (4)	aa (5)	aa (5)	aa (9)	aa (3)	aa (5)	aa (3)	aa (10)	aa (3)	aa (5)	nr	nr	nr	aa (5)
mAAT-A	aa (5)	aa (6)	Aa (4)	aa (5)	aa (5)	aa (9)	bb (3)	aa (5)	aa (3)	aa (10)	aa (3)	cc (5)	aa (1) dd (3)	dd (1)	dd (1)	dd (5)
CK-C	aa (4) ab (1)	aa (6)	Aa (4)	aa (5)	aa (4) dd (1)	aa (9)	cc (3)	aa (1) dd (2)	dd (3)	bb (10)	aa (3)	cc (5)	cc (4)	cc (1)	cc (1)	cc (2)
GPI-A	aa (5)	aa (6)	Aa (3) bb (1)	aa (4) bb (1)	aa (3) bb (2)	dc (2) dd (7)	bb (1) ff (1) gg (1)	aa (5)	aa (3)	dd (8) db (2)	aa (3)	aa (1) dd(2) ff(1) gg(1)	aa(1) de(1) ee(1) hh(1)	ii (1)	ee (1)	aa (2) ai(1) ff(1)
GTDH-A	aa (5)	aa (6)	Aa (4)	aa (5)	aa (5)	aa (9)	aa (3)	aa (5)	aa (3)	aa (10)	bb (2)	aa (5)	aa (4)	aa (1)	aa (1)	aa (5)
IDH-A	aa (4)	aa (6)	Aa (4)	aa (5)	aa (2) bb (1)		aa (9)	aa (3)	aa (5)	aa (3)	aa (10)	cc (3) cc(1)	bb (3)			
LDH-A	aa (5)	aa (6)	Aa (4)	aa (5)	aa (5)	aa (9)	bb (3)	aa (5)	aa (3)	aa (10)	aa (3)	bb (1) cc (4)	aa (4)	aa (1)	aa (1)	aa (4)
LDH-B	aa (5)	aa (6)	Aa (4)	aa (5)	aa (1) ac (1) dd (2)	bb (9)	aa (3)	dd (3) ee (2)	aa(3)	bb (3) dd (2) ff (1) af (4)	af(1)gg (4)	gg (1) bb (1) cc (1) ff(1)	gg (1)	gg (5)		
mMDH-A	aa (1) ab (1)	aa (6)	Aa (4)	aa (5)	aa (5)	aa (9)	bb (3)	aa (5)	aa (3)	aa (6) ab (1)	aa (3)	aa (5)	cc (4)	cc (1)	cc (1)	aa (1) cc (4)
SMDH-A	aa (5)	aa (6)	Aa (4)	aa (5)	aa (2) bb (3)	bb (9)	cc (3)	aa (3) bb (1)	aa (3)	aa (10)	aa (2)	aa (5)	nr	nr	nr	aa (5)
PEP-A	aa (4) ab (1)	aa (6)	Aa (4)	aa (5)	aa (4) bb (1)	bb (9)	aa (1)	aa (5)	aa (3)	aa (10)	aa (3) bb (1)	aa (5)	aa (3)	aa (1)	aa (1)	aa (2) cc (2)
PGM-A	aa (4) ab (1)	aa (6)	Aa (4)	aa (5)	aa (5)	aa (9)	aa (3)	aa (5)	aa (3)	cc (10)	aa (3)	aa (5)	aa (4)	aa (1)	aa (1)	aa (5)
sSOD-A	aa (5)	aa (6)	Aa (4)	aa (5)	aa (5)	bb (9)	nr	cc (5)	cc (3)	aa (10)	cc (3)	bb (5)	aa (4)	aa (1)	aa (1)	aa (5)
FUMH-A	aa (5)	aa (6)	Aa (4)	aa (5)	aa (5)	aa (9)	aa (3)	bb (5)	cc (3)	cc (10)	cc (3)	cc (5)	cc (4)	cc (1)	cc (1)	cc (5)

TABLE 11

Genetic Distance Measures for Members of the *Rana chloronota* Complex

Unbiased minimum genetic distance measures [Nei, 1978] are shown above the diagonal, and Rogers' [1972] genetic distance is shown below the diagonal. Refer to text for morphogroup number. Locality abbreviations: B, Ba Be; HK, Hong Kong; NH, Na Hang; TD, Tam Dao; CC, Con Cuong; AK, An Khe; S, Sa Pa. Refer to table 1 for locality references.

Population	no. 1 B	no. 1 K	no. 1 NH	no. 1 TD	no. 1 CC	no. 5 AK	no. 3 S	no. 2 CC	no. 7 CC	no. 7 NH	no. 6 AK	H nas TD
no. 1 B	–	0.001	0.003	0.002	0.054	0.314	0.334	0.371	0.208	0.258	0.242	0.423
no. 1 HK	0.048	–	0.002	0.001	0.058	0.326	0.333	0.394	0.211	0.269	0.269	0.433
no. 1 NH	0.065	0.017	–	0.000	0.047	0.312	0.336	0.390	0.214	0.271	0.253	0.422
no. 1 TD	0.062	0.013	0.003	–	0.048	0.315	0.335	0.39	0.213	0.271	0.256	0.424
no. 1 CC	0.180	0.154	0.137	0.140	–	0.209	0.327	0.335	0.169	0.225	0.256	0.378
no. 5 TL	0.365	0.330	0.323	0.324	0.292	–	0.460	0.595	0.371	0.462	0.442	0.474
no. 3 S	0.382	0.333	0.350	0.347	0.408	0.463	–	0.461	0.278	0.269	0.436	0.408
no. 2 CC	0.448	0.442	0.439	0.438	0.440	0.631	0.509	–	0.427	0.396	0.401	0.295
no. 7 CC	0.291	0.253	0.269	0.266	0.277	0.416	0.319	0.509	–	0.085	0.327	0.408
no. 7 NH	0.302	0.283	0.300	0.297	0.336	0.480	0.283	0.459	0.149	–	0.282	0.374
no. 6 AK	0.308	0.312	0.304	0.305	0.363	0.482	0.472	0.475	0.396	0.317	–	0.385
H. nasica TD	0.514	0.493	0.486	0.487	0.497	0.538	0.477	0.394	0.496	0.434	0.460	–

analyses. Unfortunately, the morphological data gave a matrix of only plesiomorphies or autapomorphies (i.e., all phylogenetically uninformative characters). The allozymic data had six potentially informative characters using mutation coding (Murphy, 1993; Murphy and Doyle, 1998). However, the putative synapomorphies exhibited no significant character covariation (Faith and Cranston, 1991; Fu and Murphy, 1999). Although all of our data proved to be extremely valuable in diagnosing species, they did not provide information on the phylogenetic relationships of these species.

Taxonomic Conclusions

We recognize each of the seven morphotypes as distinct species, based on concordant evidence of diagnostically fixed character differences among sympatric samples. Morphotype 1, ''Typical'', conforms to the diagnosis of *R. chloronota*, and we assign it to this species. None of the remaining six species from Vietnam can be assigned to currently recognized synonyms of *R. chloronota*, and below all are described as new species. We include all of these species in a species complex as a matter of taxonomic convenience, while acknowledging the need for additional systematic work.

SPECIES ACCOUNTS

Rana chloronota (Günther, 1875)

Figures 5, 6A, B, 7A, B, 11A, B, 12A–D, 13A

Polypedates chloronotus Günther, 1875
Rana chloronota: Boulenger, 1882
Rana livida: Boulenger, 1887
Rana (*Hylorana*) *livida*: Boulenger, 1920
Odorrana livida: Fei, Ye, and Huang, 1990
Rana (*Eburana*) *livida*: Dubois, 1992

Syntypes Studied: BMNH 1947.2.28.4, 1947.2.28.6, and 1947.2.28.12 from Darjeeling, India, on the hills collected by T.C. Jerdon. BMNH 1947.2.28.4 is an adult female; the other two specimens are adult males. The female has two incisions on its right side, one laterally, one ventrolaterally. The female also has had the shape of its head distorted during preservation.

Diagnosis: *Rana chloronota*, a member of the subgenus *Odorrana* (sensu Fei et al.,

Fig. 5. Syntypes of *Rana chloronota*: dorsal view of adult male (BMNH 1947.2.28.12) (**left**); adult female (BMNH 1947.2.28.4) (**right**). Not to scale.

1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL means of males 46 mm (41–53 mm), females 92 mm (80–100 mm); (3) vomerine teeth in rows oblique to choanae; (4) lip-stripe white, extending across upper lip, terminating in glandule above insertion of arm; (5) head broad, snout rounded in dorsal view, bluntly rounded in profile; (6) tympanum round, distinct, TMP:EYE of males (0.57) greater than females (0.48); (7) supratympanic fold weak; (8) dorsal skin smooth, flanks weakly granular, dorsolateral folds absent, venter smooth; (9) dorsum green, sometimes with black spots; forelimbs and hindlimbs brown, with transverse bars; (10) median callous pad on finger III to proximal tubercle; (11) disks on fingers and toes greatly enlarged (>2× base of phalanges); (12) feet fully webbed to disks, weak lateral fringes on I and V to terminal phalanges, webbing brown; (13) subarticular tuber-

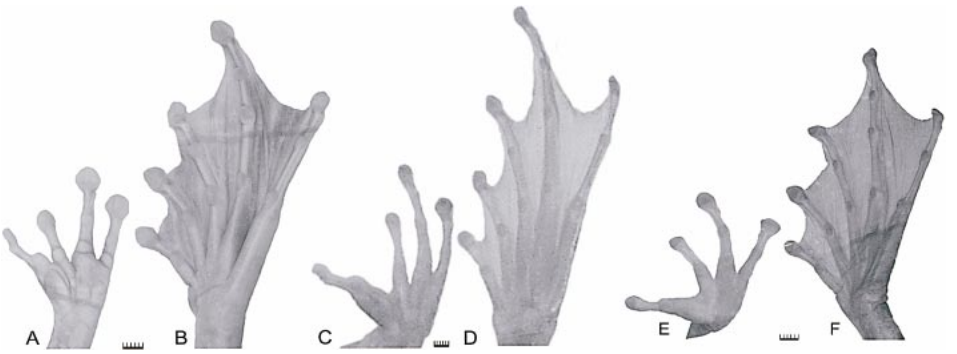

Fig. 6. Hands and feet of (**A, B**) *Rana chloronota*, female syntype (BMNH 1947.2.28.4); (**C, D**) *Rana graminea*, male syntype (BMNH 1947.2.27.97); (**E, F**) *Rana livida* neotype (BMNH 1889.3.25.48). Scale equals 5 mm.

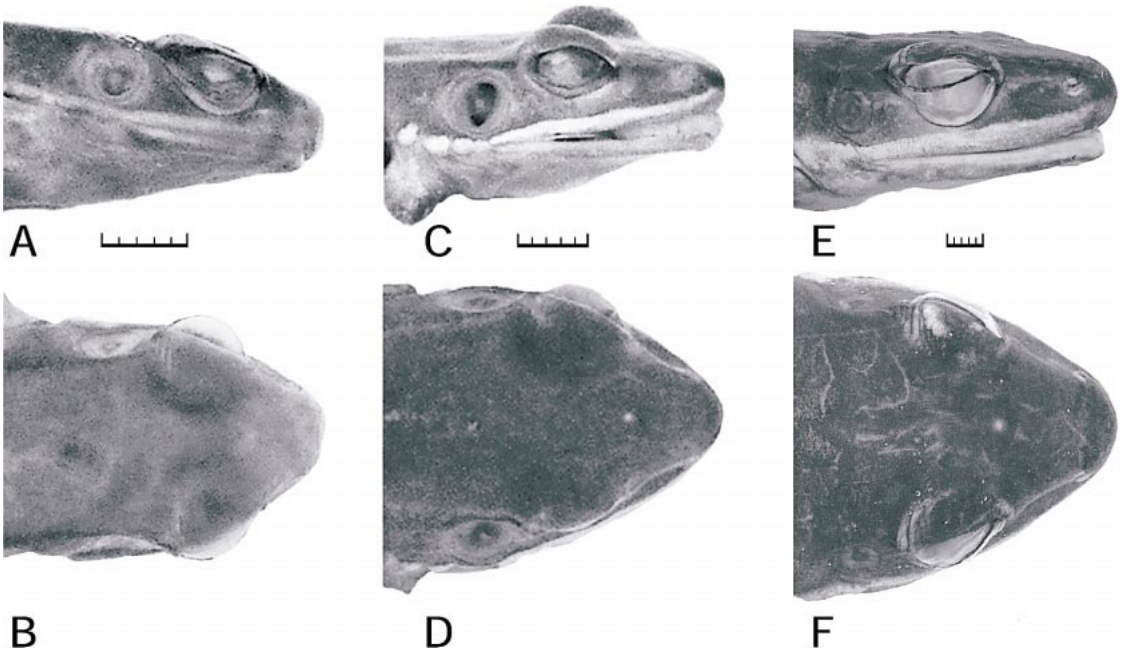

Fig. 7. Heads in lateral and dorsal views: (**A, B**) *Rana chloronota*, female syntype (BMNH 1947.2.28.4); (**C, D**) *Rana graminea*, male syntype (BMNH 1947.2.27.97); (**E, F**) *Rana livida*, neotype female (BMNH 1889.3.25.48). Scale equals 5 mm.

cles and inner metatarsal tubercle distinct, conical; (14) terminal phalanges T-shaped; (15) xiphisternum large, deeply notched posteriorly; (16) male with velvety nuptial pads on thumb, paired gular pouches, pectoral spines absent; (17) eggs white.

COMPARISONS: *Rana chloronota* superficially resembles other Asian cascade ranids, including: *Huia nasica*, *Rana andersonii*, *R. archotaphus*, *R. chalconota*, *R. grahami*, *R. graminea*, *R. hainanensis*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica*, and *R. tiannensis* (table 12). Eggs of *H. nasica*, *R. andersonii*, *R. chalconota*, *R. grahami*, *R. junlianensis*, *R. margaretae* and *R. schmackeri* are white with melanic poles, while those of *R. chloronota* are entirely white. The smooth green dorsum further distinguishes *R. chloronota* from *H. nasica*, *R. chalconota*, *R. graminea*, *R. hosii*, *R. jingdongensis*, *R. andersonii*, *R. grahami*, and *R. tiannensis*. *Huia nasica* differs from *R. chloronota* with its olive-brown dorsum (*R. chloronota* green or green with brown), longer and more pointed snout, and smaller females (SVL 67 mm, mean of 92 mm in *R. chloronota*). *Rana hainanensis* further differs from *R. chloronota* in its size (mean female SVL of *R. hainanensis* 102.6 mm), relative lengths of fingers (II < IV < I < III for *R. hainanensis*, II < I < IV < III for *R. chloronota*), and absence of gular pouches in males. *Rana heijiangensis* differs from *R. chloronota* in finger size (II < I < III < IV) and smaller digital disks. Adult male *R. jingdongensis* (mean SVL of 75 mm) are larger than those of *R. chloronota* (46 mm), lack subgular pouches, and possess pectoral spines (absent in *R. chloronota*). *Rana junlianensis* has brown lip bands (absent in *R. chlronota*), and its larger males (SVL 68–80 mm) possess pectoral spines (absent in *R. chlornota*) and lack gular pouches. Unlike *Rana chloronota*, *R. kwangwuensis* has small digital disks and males lack gular pouches. *Rana andersonii* has a rough, olive-brown dorsum, small disks on fingers, and males possess pectoral spines and lack gular pouches. *Rana grahami* males are larger (SVL 66–84 mm), have pustules on the dorsum and flanks that can form dor-

TABLE 12

Adult Frogs of the *Rana chloronota* Complex Compared with Other Southeast Asian Cascade Ranids

	SVL (mm)		Vomerine	Lip	Lip			TMP:EYE		Dorsum	
	(♂)	(♀)	teeth	stripe	bands	Head	Snout	(♂)	(♀)	skin	DL
A. chunganensis	33–40	53.5	+	White	−	1	1	0.6	?	S	Feeble
H. nasica	41–49	67	+	White	−	2	2	0.5	?	S	− or weak
R. andersonii	53–78	88–107	+	−	+	2	2	0.5	0.45	Sh	−
R. archotaphus	38–42	59–62	Usually +	White	−	2	1	= ♀	= ♂	S or Sh	− or weak
R. bacboensis	55	82–105	+	−	+	1	1	0.66	0.43	Sh	−
R. banaorum	42–55	83–99	+	White	−	1	1	0.89	0.75	Sh	slight
R. chalconota	32–44	45–60	+	Yellow-White	−	3	2	> ♀	< ♂	Coarsely Sh	glandular
R. chloronota	41–53	80–100	+	White	−	1	1	0.57	0.48	S	−
R. daorum	32–38	55–58	−	White	−	1	1	0.29	0.45	S	White, glandular
R. grahami	66–84	80–107	+	Gold-Green network	−	1	1/2	0.53	0.48	S or Sh, ±warts	− or broad, glandular
R. graminea	42–54	78–100	+	White	−	1	1	0.77	0.56	S, flank tubercles	Slight to hip
R. hainanensis	49–62	75–122	+	−	+	2	1	0.66	0.55	S, tubercles	−
R. hmongorum	54–65	74–87	+	Yellow	−	1	1	0.43	0.31	S, pustules, flank tubercles	− or pustular
R. hejiangensis	47	87	+	+	−	1	1	0.5	0.5	S; flank, posterior tubercles	−
R. hosii	50–60	85–100	+	White	−	2	1	0.75	0.4	Sh	+
R. jingdongensis	62–81	65–108	+	−, lips Green or Yellow	+	1	1/2	0.5	0.5	Tubercles, warts	−
R. junlianensis	68–80	87–102	?	+	Y	1	1	?	0.50	S; flank, posterior tubercles	−
R. kwangwuensis	57	69	+	+	−	1	1	?	0.5	S, posterior tubercles	−
R. leporipes	93?[a]	52–102[a]	+	White	−	?	?	?[a]	0.5[a]	S	Slight
R. livida	?	89, 97	+	White	−	1	1	?	0.41	S	−
R. margaretae	78–88	93–113	+	−	+	1	1	> ♀	<♂	S or Sh, posterolateral tubercles	−
R. megatympanum	48–55	93–105	+	♂ Yellow, ♀ weak or −	−	1	1	1.2	0.51	Sh	+ in ♂
R. morafkai	39–46	80–100	+	Yellow-White	−	1	1	0.96	0.71	S or partly Sh	−
R. schmackeri	42–44	80	+	−	+	1	2	> ♀	< ♂	S or finely Sh	−
R. sinica	66.6	?	+	−	−	1	1	?	0.52	S, flanks weakly granular	−
R. tiannensis	54	91–108	+	−	+	1	1	?	?	R, flanks granular	−

Codes and abbreviations for characters: **SVL**, snout-vent length; **Head**, head shape in dorsal view: (1) rounded, (2) obtusely pointed, (3) triangularly pointed; **Snout**, snout profile: (all species have protruding snouts): (1) broadly round, (2) obtusely pointed; **TMP:EYE**, tympanum diameter:eye diameter; **Dorsum skin**: (S) smooth, (Sh) shagreened, (R) rough; **DL**, dorsolateral folds; **Day**, different day and night color; **Limbs**, arm and leg banding: (1) present, (2) present or absent, (3) leg bands absent; **Disk**, finger disk: (0) no disk, (1) disk <2× base of phalanges, (2) disk >2× base of phalanges; **OT**, outer metatarsal tubercles; **PHAL**, shape of distal phalanges: (1) T-shaped, (2) oblong, somewhat pointed, (3) rounded; **Web**, (1) complete to disk; all others

TABLE 12
(*Continued*)

	Dorsum color (in life)	Flank color (in life)	Day	Limbs	Finger length	Disk	OT	PHAL	Web	Egg	Gular pouches	Spines
A. chunganensis	Red-Brown, speckles	Black, snout to thigh	−	1	I < II < IV < III	1	−	1	3	1	+	−
H. nasica	Olive-Gray to Brown	Yellow	−	1	II < I < IV < III	1	−	1	1	2	+	−
R. andersonii	Olive, Brown spots	Black	−	1	II ≤ I < IV < III	1	−	1	1	2	−	+
R. archotaphus	Olive-Green, Brown spots	Brown, ± Green	−	1	I < II	1/2	+	1	2	1	+	−
R. bacboensis	Brown, Black blotches	Brown, Black blotches	−	1	II < I < IV < III	1	−	1	4	3	+	−
R. banaorum	Green or Brown, spots	Gray	−	1	II < I < IV < III	2	−	1	5	1	+	−
R. chalconota	Pale Yellow to Yellow-Green	Pale Green	+	2	I ≤ II < IV < III	2	+	1	4	2	−	−
R. chloronota	Green, ± Black spots	Brown	−	1	II < I < IV < III	2	−	1	1	1	+	−
R. daorum	Green, Black spots	Brown, large White spot	−	1	I < II < IV < III	2	−	1	2	1	+	−
R. grahami	Olive, Black spots	Yellow, Black spots	−	1	II = I < IV < III	0	−	1	3	2	−	+
R. graminea	Bright Green, ± Black spots	Brown	−	1	II ≤I < IV < III	2	−	1	5	1	+	−
R. hainanensis	Olive, Dark Green, or Brown	Light Green, Brown; Green tubercles	−	1	II < III < I < IV	2	−	1	1	1	−	−
R. hmongorum	Green, Black spots	Red-Brown; Yellow tubercles	−	1	II < I < I V < III	1	−	1	4	1	−	−
R. hejiangensis	Green,Brown-Green or Dark Green spots	Green, Tan below, Brown spots	−	1	II < I < III < IV	1	−	?	4	?	+	−
R. hosii	Dark Green	Brown	−	2	II ≤ I < IV < III	2	−	1	1	1	−	−
R. jingdongensis	Green, Black-Brown marks	Uniform Brown	−	1	II < I < IV < III	1	−	1	1	1	−	+
R. junlianensis	Olive-Green, Brown spots	Tan, light or dark Brown spots	−	1	II < I < IV < III	1	−	?	4	2	−	+
R. kwangwuensis	Dark Green, Black spots	Gray-Yellow, dark Brown-Black spots	−	1	II < I < IV < III	1	−	?	4	1	−	−
R. leporipes	Dark Green	Stony gray	?	3	I = II	1	−	2	3	?	?[a]	?[a]
R. livida	Olive?[b]	Same as dorsum	?	3	II < I < IV < III	2	−	1	1	1	?	?
R. margaretae	Uniform Dark Green	Brown, Black marbling; arms with Green	−	1	II < I < IV < III	1	−	1	7	2	−	+
R. megatympanum	Olive-Brown, Black spots	Marbled Brown -Gray, Yellow	−	1	II < I < IV < III	2	−	1	1	1	+	−
R. morafkai	Green and/ or Brown, Black spots	Green to Brown	+	1	II < I < IV < III	2	−	1	6	1	+	−
R. schmackeri	Green, Brown spots	Brown	−	1	II < I < IV < III	2	−	1	8	2	+	+
R. sinica	Bronze-Green	Blue-gray	?	1	I < II < IV	1	−	3	9	1	?	?
R. tiannensis	Brown-Yellow	Black spots	−	1	II < I < IV < III	2	−	1	1	1	+	−

complete to disk with the following exceptions: (2) to distal subarticular tubercle on IV, (3) beyond distal subarticular tubercle on IV, (4) to disk as fringe on IV, (5) sometimes as fringe on IV, (6) sometimes as fringe on IV for females, only to distal tubercles for males, (7) not to disk on inner III, and IV, as narrow fringe to disk on I, (8) to either distal 2 phalanges of IV, (9) not to disk for inner I, and V; **Egg**, egg color: (1) wholly unpigmented, (2) pigmented pole, (3) black; **Spines,** ventral spines on male.

[a] It is unclear whether any of the paratypes of *R. leporipes* Werner, 1930 are male, so all male characters are treated as questionable.

[b] Character states from original description (Blyth, 1856).

solateral folds, and have no digital disks. *Rana schmackeri* has a smooth, heavily spotted dorsum, and males possess pectoral spines. *Rana tiannensis* has a brown dorsum that is rough with large, prominent lateral granulations. *Rana chalconota* differs from *R. chloronota* by having distinct dorsolateral folds, a pointed snout (vs. rounded) and smaller SVL (males 32–44 mm, females 46–59 mm), an outer metatarsal tubercle, and no gular pouches in males. In *R. archotaphus*, webbing on toe IV reaches base of distal subarticular tubercle (*R. chloronota*, webbing to base of disk), females are smaller (SVL 59–62 mm), TMP:EYE is more or less equal in males and females (sexually dimorphic in *R. chloronota*), and the outer metatarsal tubercle is present (absent in *R. chloronota*). *Rana sinica* can be distinguished from *R. chloronota* in lacking a lip-stripe, and in having smaller mature females (*R. sinica* holotype of 66.6 mm), an indistinct tympanum covered by a thin layer of skin (distinct, not obscured in *R. chloronota*), nares halfway between the eye and tip of the snout (nearer the snout in *R. chloronota*), and by relative finger lengths (I < II < IV for *R. sinica*, II < I < IV for *R. chloronota*). *Rana leporipes* can be distinguished from *R. chloronota* by a white supratympanic fold (not colored in *R. chloronota*), a weak dorsolateral fold (absent in *R. chloronota*), absence of transverse bands on the arms and legs (present in *R. chloronota*), webbing that extends only to the distal phalanges (to base of disks in *R. chloronota*), and smaller digital disks. *Rana graminea*, *R. hosii*, and *R. livida* bear the most striking resemblance to *R. chloronota*. *Rana graminea* and *R. hosii* can be distinguished by their dorsolateral folds. *Rana graminea* further differs from *R. chloronota* with its nearly vertical (versus concave) loreal region, depressed head, larger tympanum, smaller hands, and smooth sides (granulate in *R. chloronota*), whereas *R. hosii* can be further distinguished by its lack of gular pouches and feeble tarsal folds. *Rana livida* differs from *R. chloronota* in having a uniformly colored dorsum (green with dark sides in *R. chloronota*), absence of transverse bars on the limbs, smooth skin with pustules dorsal to the cloaca (smooth dorsum, laterally granular in *R. chloronota*), and white mottling on the flanks (absent in *R. chloronota*).

DESCRIPTION: Head length greater than head width (means are 132% for females, 144% for males), head width 33% of SVL, length 47% of SVL; snout short, protruding beyond margin of lower jaw, rounded in dorsal view, bluntly rounded in profile; eye large, prominent, 70% snout length in females, 84% in males; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold weak, reduced to a swollen rim of tissue dorsal to tympanum; tympanum round, distinctly visible, in females separated from eye by distance equal to TMP, less than length in males; tympanum 48% of EYE in females, 57% in males. Choanae ovoid; vomerine dentigerous processes prominent, oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately one-third its length.

Forearm robust; fingers moderately short, slender; hands 29% of SVL, relative lengths of fingers II < I < IV < III; ventromedial callous pad on III extends to proximal tubercle; disks greatly expanded (>2× base of phalanges), relative pad size II < I < IV III, pad width (III) 50% pad length; circummarginal grooves present ventrally; terminal phalanges T-shaped; subarticular tubercles conical. Hindlimbs moderately robust; tibia length 63% of SVL; FTL 68% of SVL in females, 80% in males; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet fully webbed to base of toe disk, lateral fringes on I and V to terminal phalanges; toes long, slender, with large, obliquely rounded disks, relative pad size I = II = III > IV ≫ V, pad width (IV) 82% of length in females, 90% in males; ventral circummarginal grooves present; subarticular tubercles prominent, conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum large, deeply notched posteriorly.

Skin on dorsum smooth, flanks with slight granulations; dorsolateral fold absent; small tubercles posteroventral to tympanum, sometimes absent in males; granules on thighs and

TABLE 13

Geographic Variation of Body Proportions in *Rana chloronota* Given as Means ± 1 SD and Ranges

See Materials and Methods for abbreviations.

Locality	N	SVL	HDL:HDW	TIB:SVL	IOD:HDL	TMP:EYE	EYE:HDL	SNT: HDL
FEMALES								
Tam Dao	56	95.1 ± 5.3 (80.4–101.7)	1.33 ± 0.08 (1.25–1.41)	0.62 ± 0.04 (0.51–0.67)	0.19 ± 0.02 (0.16–0.23)	0.49 ± 0.06 (0.40–0.59)	0.22 ± 0.02 (0.21–0.27)	0.34 ± 0.01 (0.33–0.35)
Buon Loi	10	92.5 ± 5.6 (81.5–98.7)	1.36 ± 0.06 (1.28–1.40)	0.63 ± 0.04 (0.57–0.67)	0.23 ± 0.05 (0.20–0.25)	0.44 ± 0.05 (0.37–0.52)	0.28 ± 0.01 (0.28–0.29)	0.27 ± 0.03 (0.24–0.34)
Hong Kong	1	74.0	1.43	0.66	0.20	0.50	0.24	0.32
Na Hang	9	89.2 ± 5.2 (79.5–95.0)	1.43 ± 0.06 (1.30–1.53)	0.64 ± 0.03 (0.61–0.71)	0.18 ± 0.01 (0.15–0.19)	0.43 ± 0.02 (0.41–0.44)	0.34 ± 0.03 (0.29–0.41)	0.35 ± 0.02 (0.34–0.44)
Con Cuong	13	90.6 ± 4.7 (79.2–98.4)	1.42 ± 0.02 (1.38–1.48)	0.63 ± 0.04 (0.56–0.70)	0.21 ± 0.02 (0.17–0.24)	0.48 ± 0.07 (0.40–0.61)	0.22 ± 0.01 (0.20–0.22)	0.29 ± 0.02 (0.20–0.32)
MALES								
Tam Dao	11	46.7 ± 1.8 (44.1–48.7)	1.47 ± 0.02 (1.44–1.49)	0.64 ± 0.03 (0.59–0.68)	0.16 ± 0.05 (0.12–0.21)	0.54 ± 0.06 (0.43–0.60)	0.25 ± 0.03 (0.21–0.30)	0.30 ± 0.03 (0.27–0.34)
Buon Loi	9	47.8 ± 2.4 (44.2–53.1)	1.48 ± 0.06 (1.41–1.59)	0.60 ± 0.02 (0.57–0.64)	0.25 ± 0.07 (0.18–0.44)	0.53 ± 0.07 (0.44–0.64)	0.32 ± 0.00 (0.32–0.32)	0.29 ±0.02 (0.26–0.30)
Na Hang	7	45.9 ± 2.1 (43.3–48.1)	1.61 ± 0.04 (1.58–1.65)	0.64 ± 0.03 (0.60–0.68)	0.18 ± 0.02 (0.16–0.2)	0.60 ± 0.07 (0.50–0.72)	0.24 ± 0.01 (0.22–0.25)	0.30 ± 0.01 (0.30–0.31)
India	2	46.7 ± 0.4 (46.5–47.0)	1.46 ± 0.04 (1.43–1.49)	0.65 ± 0.01 (0.65–0.66)	0.25 ± 0.01 (0.24–0.26)	0.54 ± 0.11 (0.46–0.62)	0.36 ± 0.02 (0.35–0.38)	0.35 ± 0.04 (0.33–0.38)
Con Cuong	8	45.6 ± 2.6 (41.7–48.4)	1.53 ± 0.06 (1.50–1.60)	0.67 ± 0.04 (0.59–0.71)	0.21 ± 0.05 (0.16–0.4)	0.54 ± 0.05 (0.46–0.61)	0.29 ± 0.03 (0.26–0.40)	0.34 ± 0.03 (0.30–0.59)
Hong Kong	4	44.6 ± 0.8 (43.6–45.5)	1.47 ± 0.02 (1.44–1.48)	0.65 ± 0.01 (0.64–0.66)	0.16 ± 0.02 (0.10–0.19)	0.76 ± 0.15 (0.62–0.85)	0.22 ± 0.01 (0.20–0.23)	0.28 ± 0.02 (0.36–0.31)

around cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

COLOR IN LIFE (in preservative): Dorsum green, sometimes with brown spots (brown to livid blue), flanks gray (light brown) with yellow (white) marbling; lip-stripe white, loreal region brown (dark blackish brown); tympanum beige with dark brown central ring; dorsal limbs and digits brown with dark brown transverse bands; posterior surface of thighs yellow (white) with brown marbling; venter creamy white; ventral side of limbs creamy yellow sometimes with dark mottling; webbing marbled white on dark brown (brown). Iris golden, pupil outlined in a distinct yellow border.

SECONDARY SEXUAL CHARACTERS: Gravid females with immaculate, white eggs, 2 mm in diameter (mature). Adult females have SVL approximately twice that of males. Males have relatively larger tympanum, distance between tympanum and eye less than that of females, velvety nuptial pads on thumb, and paired gular pouches below jaw articulations. Nuptial spines on chest and belly absent.

GEOGRAPHIC VARIATION: Measurements for the syntypes are given in Boulenger (1920) as specimens 1–10 (types of *P. chloronotus*). Measurements for other series of *R. chloronota* are given in table 13. Sexual size dimorphism is most pronounced in specimens from Tam Dao where mean SVL of males is 40% that of females.

DISTRIBUTION AND ECOLOGY: *Rana chloronota* occurs in forested, montane river systems throughout Southeast Asia. These rivers vary from shallow and slow moving to torrential and deep. Specimens can be found on boulders and logs, both in and around the water. Radiographs revealed that females feed on large invertebrates and small vertebrates, including a megophryid frog. *Rana chloronota* calls from the tops of boulders and overhanging branches in and around torrents and waterfalls (personal obs.). The audible part of the call is a very high squeak but the roar of the cascades obscures the remainder of the vocalization, as also observed by Pope (1931).

OTHER SPECIMENS EXAMINED FOR VARIATION (see appendix 1, tables 13, 15).

REMARKS: Like Inger et al. (1999), we cannot find the north-south partition of *R. chloronota* described by Bourret (1942). The large Thai form of *R. chloronota* (Inger and Chanard, 1997; Taylor, 1962) is not present in collections from Vietnam, India, Laos, and China. Male frogs from Khao Yai National Park and Loei Province, Thailand, are large (SVL 55–70 mm) and have white ventral spinules. None of our male specimens possess pectoral spines or attain an SVL beyond 55 mm, and all possess the finger formula II < I. The Thai form is an undescribed species. Although male *R. chloronota* from Hong Kong have a TMP:EYE (0.76) that is more similar to *R. graminea* (0.70) than it is to Vietnamese populations of *R. chloronota* (0.57), they agree with *R. chloronota* in every other aspect, including allozymes, and we consider them as such. *Rana chloronota* occurs in China, northern and southern Vietnam, India, and Lao PDR (FMNH 256493). This suggests that *R. chloronota* occupies a large portion of its currently recognized range of Assam, including Burma, Thailand, Indochina, and southern China.

Fig. 8. Syntype of *Rana graminea* (BMNH 1947.2.27.97), dorsal view. Tag equals 29 mm.

Rana graminea Boulenger, 1899

Figures 6C, D, 7C, D, 8, 11C

SYNTYPES: BMNH 1947.2.27.96, and 1947.2.27.97, adult males from Five Finger

Mountain, Hainan Island, China, collected by J. Whitehead.

DIAGNOSIS: *Rana graminea*, a member of the subgenus *Odorrana* (sensu Fei et al., 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL means of males 46 mm (42–53 mm), of females 94 mm (78–100 mm); (3) vomerine teeth in rows oblique to choanae; (4) lip-stripe white, extending across upper lip, terminating in glandule above insertion of arm; (5) head a little longer than broad, much depressed, snout bluntly rounded in profile; (6) tympanum round, distinct, transparent, TMP:EYE of males 0.77, females 0.56; (7) supratympanic fold weak; (8) dorsal skin smooth, flanks weakly granular, weak dorsolateral folds present, venter smooth; (9) dorsum green, sometimes with black spots; forelimbs and hindlimbs brown, with transverse bars; (10) median callous pad on finger III to proximal tubercle; (11) disks on fingers and toes enlarged ($>2\times$ base of phalanges); (12) feet fully webbed to disks, but as a fringe from distal subarticular tubercle of IV in some specimens, weak lateral fringes on I and V to terminal phalanges; (13) subarticular tubercles and inner metatarsal tubercle distinct; (14) terminal phalanges T-shaped; (16) male with strong forearms, slight hands, velvety nuptial pads, paired gular pouches, pectoral spines absent; (17) females bear white eggs.

COMPARISONS: *Rana graminea* superficially resembles other Asian cascade ranids, including: *Huia nasica*, *Rana andersonii*, *R. archotaphus*, *R. chalconota*, *R. chloronota*, *R. grahami*, *R. hainanensis*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica*, and *R. tiannensis* (table 12). The presence of dorsolateral folds distinguishes *R. graminea* from *R. andersonii*, *R. chloronota*, *R. hainanensis*, *R. hejiangensis*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica* and *R. tiannensis*. The presence of white eggs differentiates *R. graminea* from *H. nasica*, *R. andersonii*, *R. chalconota*, *R. grahami*, *R. margaretae* and *R. schmackeri* (white eggs with melanic poles). *Huia nasica* further differs from *R. graminea* with its olive-brown dorsum (*R. graminea* green or green with brown spots). *Rana hainanensis* further differs from *R. graminea* in its relative lengths of fingers (II $<$ IV $<$ I $<$ III for *R. hainanensis*, II $\leq$ I $<$ IV $<$ III for *R. graminea*), and absence of gular pouches in males. *Rana hejiangensis* further differs from *R. graminea* with its green flanks (brownish in *R. graminea*), relative finger length (II $<$ I $<$ III $<$ IV for *R. hejiangensis*), and small disk size. Adult males of *R. jingdongensis* are larger than those of *R. graminea* (*R. jingdongensis* SVL mean is 75 mm, *R. graminea* is 46 mm), lack subgular pouches, and possess pectoral spines (absent in *R. graminea*). *Rana junlianensis* has brown lip bands (absent in *R. graminea*), small disks, and larger males (SVL 68–80 mm) that possess pectoral spines (absent in *R. graminea*) and lack gular pouches. *Rana kwangwuensis*, unlike *Rana graminea*, has small disks, and males lack gular pouches. *Rana andersonii* has a rough, olive-brown dorsum, small disks on fingers, and males possess pectoral spines and lack gular pouches. Male *R. grahami* are larger (SVL 66–84 mm), have pustules on the dorsum, and have no digital disks. *Rana schmackeri* has a smooth, heavily spotted dorsum, and males possess pectoral spines. *Rana tiannensis* has a brown dorsum that is rough with large, prominent lateral granulations. *Rana chalconota* has a pointed snout (vs. rounded), smaller males (32–44 mm) that lack gular pouches, and an outer metatarsal tubercle. In *R. archotaphus*, the webbing (toe IV) reaches the base of distal subarticular tubercle (to base of disk in *R. graminea*), and the outer metatarsal tubercle is present (absent in *R. graminea*). *Rana sinica* lacks a lip-stripe (present in *R. graminea*), has an indistinct, skin-covered tympanum (distinct and uncovered in *R. graminea*), nares halfway between the eye and tip of the snout (nearer the snout in *R. graminea*), and a different finger formula (I $<$ II $<$ IV for *R. sinica*). *Rana leporipes* differs from *R. graminea* in having a white supratympanic fold, absence of transverse bands on the arms and legs (present in *R. graminea*), and webbing that only extends to the distal phalanges (to base of disks in *R. graminea*). *Rana chloronota*, *R. hosii*, and *R. livida* bear the most striking resemblance to *R. graminea*. *Rana*

chloronota and *R. livida* can be distinguished from *R. graminea* by the absence of dorsolateral folds. *Rana graminea* further differs from *R. chloronota* with its nearly vertical (versus concave) loreal region, depressed head, larger tympanum, transparent tympanum, and smooth sides (granulate in *R. chloronota*). Male *R. graminea* also possess smaller, more slender hands than *R. chloronota*. *Rana hosii* can be further distinguished from *R. graminea* by an obtusely pointed snout and the absence of gular pouches. *Rana livida* differs from *R. graminea* in having a uniformly colored dorsum (green with dark sides in *R. graminea*), white mottling on the flanks (absent in *R. graminea*), and absence of transverse bars on the limbs.

DESCRIPTION OF SYNTYPES: Head length greater than head width (112%), head width 35% SVL, length 39% of SVL; snout short, protruding beyond margin of lower jaw, bluntly rounded in dorsal view, much depressed, bluntly rounded in profile; eye large, prominent, 117% of snout length; eyelid broader than interorbital distance. Top of head flat; canthus rostralis prominent; loreal region feebly oblique or nearly vertical, weakly concave; nostril about three-fourths distance from eye to tip of snout; supratympanic fold weak; tympanum round, distinctly visible, transparent, 75% of EYE. Choanae ovoid; vomerine dentigerous processes prominent, oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately one-third its length.

Forearm robust; fingers very slender, relative lengths of fingers II $\leq$ I $<$ IV $<$ III; ventromedial callous pad on III to proximal tubercle; disks moderately expanded ($>2\times$ base of phalanges), relative pad size II $<$ I $<$ IV $<$ III; circummarginal grooves present ventrally; terminal phalanges T-shaped; subarticular tubercles rounded. Hindlimbs long, slender; tibia length 65% of SVL; FTL 58% of SVL; relative toe lengths I $<$ II $<$ III $<$ V $<$ IV; inner tarsal fold absent; feet fully webbed to base of toe disk, but as a fringe from distal subarticular tubercle of IV, lateral fringes on I and V to terminal phalanges; toes long, slender, with large, obliquely rounded disks, relative pad size I = II = III $>$ IV $\gg$ V; ventral circummarginal grooves present; subarticular tubercles moderately prominent, rounded; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Skin on dorsum smooth, flanks with slight granulations; weak dorsolateral fold present; white glandular tubercles posteroventral to tympanum; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

COLOR IN LIFE (in preservative): Dorsum green (brown to livid blue), flanks brown (light brown) with yellow (white) marbling; lip-stripe white, loreal region dark brown above (dark blackish brown), light brown below; tympanum transparent, perimeter white (light brown); dorsal limbs and digits brown with dark brown transverse bands; posterior surface of thighs yellow (white) with brown marbling; venter creamy white; ventral side of limbs creamy yellow, sometimes with dark mottling; webbing marbled white on dark brown (brown). Iris golden, margin of pupil outlined in a distinct yellow border.

VARIATION IN OTHER SPECIMENS EXAMINED (Fujian Province: AMNH A-28543–28545; A-28612; A-29973–29978; A-29980–29991) (table 14): Faint dorsolateral folds are present in some specimens of this series, although it is not clear whether their absence is an artifact of preservation. Some specimens have finger II $<$ I, whereas others have finger I = II. Male specimens from Fujian Province average 46.4 mm SVL (41.5–53.5), and females average 94 mm (78.3–100.2) (table 14).

SECONDARY SEXUAL CHARACTERS: Gravid females bear immaculate white eggs. Adult females have SVL approximately twice that of males and relatively larger digital disks than males. Males have strong arms, relatively larger tympanum, smaller distance between tympanum and eye, velvety nuptial pads on thumb, and paired gular pouches below jaw articulations. Males lack nuptial spines on chest and belly.

DISTRIBUTION AND ECOLOGY: The species is known from Hainan Island (syntypes), the Mao Son Mountains in Tonkin (northern Vietnam) (Boulenger, 1920), and Fujian Province, China (Pope, 1931).

REMARKS: Boulenger (1920) gave measurements of the syntypes, as well as the Mao Son specimen. Bourret (1942) consid-

TABLE 14
Geographic Variation in *Rana graminea* from Fujian Province, China, Given as Means ± 1 SD and Ranges
See Materials and Methods for abbreviations.

N	SVL	HDL:HDW	TIB:SVL	IOD:HDL	TMP:EYE	EYE:HDL	SNT: HDL
MALES							
16	46.4 ± 3.4	1.48 ± 0.08	0.66 ± 0.03	0.19 ± 0.01	0.77 ± 0.10	0.28 ± 0.02	0.32 ± 0.02
	(41.5–53.5)	(1.32–1.65)	(0.58–0.71)	(0.10–0.20)	(0.61–1.03)	(0.20–0.30)	(0.30–0.40)
FEMALES							
6	94.0 ± 8.0	1.28 ± 0.09	0.67 ± 0.04	0.20 ± 0.02	0.56 ± 0.03	0.24 ± 0.01	0.34 ± 0.04
	(78.3–100.2)	(1.14–1.38)	(0.63–0.74)	(0.14–0.23)	(0.52–0.60)	(0.22–0.24)	(0.31–0.42)

ered *R. graminea* to be a ''northern variety'' of Indochinese *R. chloronota* because of its weak dorsolateral fold. Like Inger et al. (1999), we did not find *R. graminea* in Vietnam. Our study of specimens treated as *R. graminea* by Pope (1935) agrees with the original description. We did not study the Mao Son specimen.

Rana leporipes Werner, 1930

HOLOTYPE: Two figures (Werner, 1930: 49, pl. IV) of Mell no. 15660, an adult female from Lung Tao Shan, North Kwangtung, China (700 m a.s.l.) collected on 4 July 1919 by R. Mell. The voucher specimens of the type series have been lost and the photographs of the holotype become the iconotype.

DIAGNOSIS (from text and plates of original description): *Rana leporipes* is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL reported for females between 52 and 102 mm; (3) vomerine teeth in rows oblique to choanae; (4) lip-stripe white; (6) tympanum very distinct, TMP:EYE is 0.5; (7) supratympanic fold milky white; (8) dorsal skin smooth, flanks weakly granular, dorsolateral folds slightly distinguishable, venter smooth; (9) dorsum dark green, flanks stony gray with white marbling, legs not banded; (11) disks on fingers and toes only slightly enlarged (<2× base of phalanges); (12) feet fully webbed to base of distal phalanges; (13) subarticular tubercles and inner metatarsal tubercle large, projecting; (14) terminal phalanges oblong, somewhat pointed.

COMPARISONS: *Rana leporipes* superficially resembles other Asian cascade ranids, including *Huia nasica*, *Rana andersonii*, *R. archotaphus*, *R. chalconota*, *R. chloronota*, *R. grahami*, *R. graminea*, *R. hainanensis*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica* and *R. tiannensis* (table 12). *Rana leporipes* is unique among all of the above species in having a white supratympanic fold, webbing that only reaches the distal phalanx (not the disk), and oblong, somewhat rounded distal phalanges (T-shaped in others, unknown for *R. hejiangensis*, *R. junlianensis*, and *R. kwangwuensis*). The absence of banding on the legs distinguishes *R. leporipes* from all species listed here, except *R. livida* (present or absent in *R. chalconota* and *R. hosii*). The presence of a dorsolateral fold also distinguishes it from *R. andersonii*, *R. chloronota*, *R. hainanensis*, *R. hejiangensis*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica*, and *R. tiannensis*. Whereas *Huia nasica* has an olive-brown dorsum, *R. leporipes* is dark green. *Rana hainanensis* further differs from *R. leporipes* in its size (SVL *R. hainanensis* 103 mm) and relative lengths of fingers (II < IV < I for *R. hainanensis*, I = II for *R. leporipes*). *Rana junlianensis* has brown lip bands. *Rana andersonii* has a rough, olive-brown dorsum. *Rana grahami* has pustules on the dorsum and flanks and no digital disks. *Rana schmackeri* has a smooth, heavily spotted dorsum. *Rana tiannensis* has a rough, brown dorsum with large, prominent lateral granulations. Both *Rana chalconota* and *R. archotaphus* possess an outer metatarsal tubercle, but *R. leporipes* does not. *Rana hosii* can be distinguished

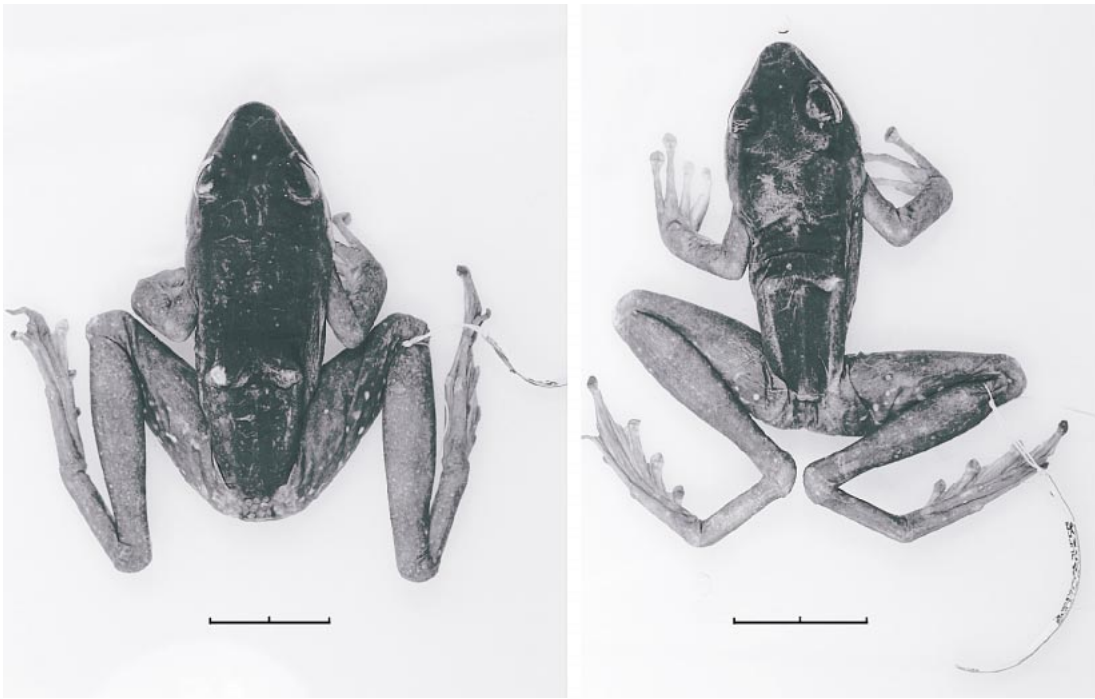

Fig. 9. Dorsal view of *Rana livida*: adult female (BMNH 1889.3.25.47) (**left**); neotype, adult female (BMNH 1889.3.25.48) (**right**). Scale equals 5 mm.

from *R. leporipes* by its feeble tarsal folds. *Rana chloronota* differs from *R. leporipes* in that it is larger (*R. chloronota* female SVL 80–100 mm) and it has a different digital formula (II < I < IV < III for *R. chloronota*). Dorsum of *R. livida* is uniform (flanks a different color for *R. leporipes*).

REMARKS: The original description of *R. leporipes* reported extensive variation in snout–vent length (52–102 mm) and lacked any description of secondary sex characters. The single male specimen of *R. leporipes* is significantly larger than males of *R. chloronota* (93 mm vs. a maximum of 53 mm). However, it is unclear how the male was sexed, as nuptial excrescences and gular pouches are not mentioned. Bourret (who did not indicate whether he had seen the type series) thought the male was an incorrectly identified female and that Werner's (1930) frogs were all females spanning a range of varying degrees of maturity. We are also skeptical about any males, although this cannot be confirmed, as the type series has been lost.

Rana livida (Blyth, 1856)
Figures 6E, F, 7E, F, 9

Rana livida (Boulenger, 1887)

NEOTYPE: BMNH 1889.3.25.48 an adult female from Thagata Juwa, Village on the hills southwest of Mt. Mooleyit, Dawna Mountains, Myanmar (400–500 m), by M.L. Fea in early 1887.

DIAGNOSIS: *Rana livida*, a member of the subgenus *Odorrana* (sensu Fei et al. 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL females 89.4, 97.1 mm; (3) vomerine teeth in rows oblique to choanae; (4) lip-stripe white, extending across upper lip, terminating in glandule above insertion of arm; (5) head broad, snout rounded in dorsal view, bluntly rounded in profile; (6) tympanum round, distinct, TMP:EYE 0.41;

(7) supratympanic fold weak; (8) dorsal skin smooth to flanks, pustules dorsal to cloaca, dorsolateral folds absent, venter smooth; (9) dorsum uniform brown in preservative; forelimbs and hindlimbs lighter brown, without transverse bars; (10) median callous pad on finger III to proximal tubercle; (11) disks on fingers and toes enlarged (>2× base of phalanges); (12) feet fully webbed to disks, weak lateral fringes on I and V to terminal phalanges; (13) subarticular tubercles and inner metatarsal tubercle distinct, conical; (14) terminal phalanges T-shaped; (15) xiphisternum large, deeply notched posteriorly; (17) eggs white.

COMPARISONS: *Rana livida* superficially resembles other Asian cascade ranids, including *Huia nasica*, *Rana andersonii*, *R. archotaphus*, *R. chalconota*, *R. chloronota*, *R. grahami*, *R. graminea*, *R. hainanensis*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, *R. margaretae*, *R. schmackeri*, *R. sinica*, and *R. tiannensis* (table 12). The smooth, uniformly colored dorsum further distinguishes *R. livida* from all of the above species. The unpigmented eggs of *R. livida* distinguish it from *H. nasica*, *Rana andersonii*, *R. chalconota*, *R. grahami*, *R. junlianensis*, *R. margaretae*, and *R. schmackeri*, which are white with melanic poles. *Huia nasica* differs from *R. livida* in its longer, more pointed head, and smaller females (SVL 67 mm). *Rana hainanensis* further differs from *R. livida* in relative lengths of fingers (II < IV < I < III for *R. hainanensis*, II < I < IV < III for *R. livida*). *Rana hejiangensis* differs from *R. livida* in its relative finger size (II < I < III < IV) and smaller digital disks. *Rana andersonii* has a rough, olive-brown dorsum and small disks on fingers. *Rana grahami* has pustules on the dorsum and flanks (vs. smooth in *R. livida*) and slightly swollen digital tips. *Rana junlianensis* has brown lip bands. *Rana kwangwuensis* has small digital disks. *Rana schmackeri* has a smooth, heavily spotted dorsum. *Rana tiannensis* has a rough brown dorsum with large, prominent lateral granulations. *Rana chalconota* differs from *R. livida* by having coarsely shagreened dorsum, distinct dorsolateral folds, pointed snout, smaller SVL (females 46–59 mm), and an outer metatarsal tubercle. In *R. archotaphus*, webbing (toe IV) reaches base of distal subarticular tubercle (*R. livida*, webbing to base of disk), females are smaller (SVL 59–62 mm), and it has an outer metatarsal tubercle. *Rana sinica* differs from *R. livida* in lacking a lip-stripe, and in having smaller mature females (*R. sinica* holotype 66.6 mm), an indistinct, skin-covered tympanum (distinct and uncovered in *R. livida*), nares halfway between the eye and tip of the snout (nearer the snout in *R. livida*), and a different finger formula (I < II < IV for *R. sinica*, II < I < IV for *R. livida*). *Rana hosii* differs from *R. livida* by its obtusely pointed head (rounded in *R. livida*), dorsolateral folds, occasional bands on arms and legs, and feeble tarsal folds (dorsolateral and tarsal folds absent in *R. livida*). *Rana chloronota* differs from *R. livida* with its solid-colored dorsum and dark sides (uniform in *R. livida*), transverse bars on the limbs (absent in *R. livida*), smooth dorsum, flanks granular (slightly granulose on the posterior thighs in *R. livida*), and absence of white mottling on the flanks (present in *R. livida*). *Rana leporipes* differs from *R. livida* in having smaller digital disks, a white supratympanic fold, weak dorsolateral fold, and webbing that only reaches the distal phalanges (*R. livida* to base of the disk). *Rana graminea* further differs from *R. livida* with its nearly vertical (versus concave) loreal region and depressed head.

DESCRIPTION: Head length greater than head width (103%), head width 35% of SVL, length 37% of SVL; snout short, protruding beyond margin of lower jaw, rounded in dorsal view, bluntly rounded in profile; eye large, prominent, 72% snout length; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold weak, swollen rim of tissue dorsal to tympanum; tympanum round, distinctly visible, 44% of EYE. Choanae ovoid; vomerine dentigerous processes prominent, oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately one-third its length.

Forearm robust; fingers moderately short, slender; hands 29% of SVL, relative lengths

of fingers II < I < IV < III; ventromedial callous pad on III to proximal tubercle; disks greatly expanded (>2× base of phalanges), relative pad size II < I < IV < III; circummarginal grooves present ventrally; terminal phalanges T-shaped; subarticular tubercles prominent, rounded. Hindlimbs moderately robust; tibia length 68% of SVL; FTL 85% of SVL; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet fully webbed to base of toe disk, lateral fringes on I and V to terminal phalanges; toes long, slender, with large, obliquely rounded disks, relative pad size I = II = III > IV > V; ventral circummarginal grooves present; subarticular tubercles prominent, conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum large, deeply notched posteriorly.

Skin on dorsum smooth to flanks; dorsolateral fold absent; small tubercles posteroventral to tympanum; granules dorsal cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

COLOR IN PRESERVATIVE: Dorsum uniform dark brown to flanks, some white spots and mottling on flank; prominent lip-stripe white; tympanum brown; posterior surface of thighs light brown with white spots, no transverse banding; venter creamy white; ventral side of limbs creamy white; webbing dark gray.

SECONDARY SEX CHARACTERS: BMNH 1889.3.25.47, an adult female bears white eggs. No male specimens were studied.

MEASUREMENTS OF NEOTYPE (in mm): SVL 89.4; SNT 14.2; HDL 32.8; HDW 31.6; EYE 10.2; IOD 8.0; TMP 4.5; TEY 2.8; HND 25.5; FPL 3.2; TIB 60.8; FTL 76.2; TPL 2.6.

MEASUREMENTS OF REFFERED SPECIMEN (BMNH 1889.3.25.47): SVL 97.1; SNT 16.7; HDL 36.1; HDW 33.4; EYE 11.9; IOD 9.2; TMP 4.6; TEY 4.1; HND 28.8; FPL 3.3; TIB 63.8; FTL 75.6; TPL 2.7.

DISTRIBUTION AND ECOLOGY: The range of *R. livida* is unclear. The type material is lost and the locality information has been poorly recorded. Much confusion exists in its taxonomy. The only confirmed locality is that of the neotype and maps do not show Thagata Juwa village, as indicated in by Feae. Mount Mooleyit is currently found on maps as Mulayit Taung (16°N, 98°30′E). The closest villages to Mulayit Taung are Kyeik-ywa, Daukkat-ywa, and Kyeik-don, to the west, and Mawkhi and Huthi, near the Thai border to the east.

REMARKS: Male *R. chloronota* are substantially smaller than females and they posses paired subgular pouches and a larger tympanum. Presumably, male *R. livida* have the same attributes. Blyth (1852) appears to have included males in his original description; many of the specimens that Theobold assumed to be juveniles have whiter lip-stripes and a relatively large tympanum that is closer to the eye than in females. Although the color is not recorded in life, Blyth (1856) reported that *R. livida* is ''uniform dusky-plumbeous above, probably dull olive green when alive.'' Boulenger (1920) recorded measurements of two *R. livida* females from Thagata, Tenasserim. It is not clear whether these two specimens are the same as those described above.

Rana sinica Ahl, 1925

Figure 10

HOLOTYPE: ZMB 9785 an adult female from China.

DIAGNOSIS: *Rana sinica* is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL of single mature female is 66.6 mm, males unknown; (3) vomerine teeth in rows oblique to choanae; (4) lip-stripe absent; (5) head not broad, snout rounded in dorsal view; (6) tympanum round, indistinct, covered by a layer of skin, TMP:EYE 0.52; (7) supratympanic fold weak; (8) dorsal skin smooth flanks weakly granular, dorsolateral folds absent, venter smooth; (9) dorsum bronze-green with irregular indistinct spots and blue-gray flanks, legs with black bands; cloacal region marbled black with white; (10) median callous pad on finger III almost to proximal tubercle; (11) disks on fingers and toes slightly enlarged (<2× base of phalanges); (12) feet fully webbed on II, III, IV; I and V without lateral web fringes, webbing light gray in alcohol; (13) subarticular tubercles and inner metatarsal tubercle distinct, conical; (14) terminal phalanges are slightly rounded; (15) xiphisternum not large, shallow notch posteriorly; (16) male secondary sexual charac-

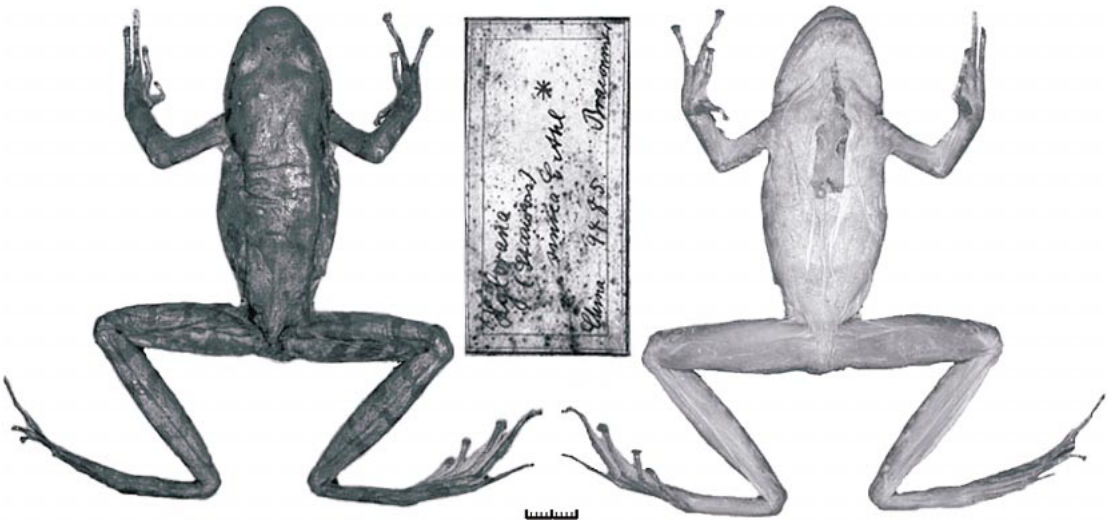

Fig. 10. Holotype of *Rana sinica* (ZMB 9785), dorsal view (**left**), ventral view (**right**). Scale equals 5 mm.

teristics unknown; (17) eggs yellow (in alcohol).

COMPARISONS: *Rana sinica* superficially resembles other Asian cascade ranids, including *Huia nasica*, *Rana andersonii*, *R. archotaphus*, *R. chalconota*, *R. chloronota*, *R. grahami*, *R. graminea*, *R. hainanensis*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, *R. livida*, *R. margaretae*, *R. schmackeri* and *R. tiannensis* (table 12). Unlike the species listed above, *R. sinica* has a layer of skin overlying its tympanum and its terminal phalanges are slightly rounded (not T-shaped; *R. leporipes* has oblong, somewhat rounded distal phalanges). The absence of a lip-stripe in *R. sinica* further differentiates it from *H. nasica*, *R. archotaphus*, *R. chalconota*, *R. chloronota*, *R. grahami*, *R. graminea*, *R. hejiangensis*, *R. hosii*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, and *R. livida*. Eggs of *H. nasica*, *Rana andersonii*, *R. chalconota*, *R. grahami*, *R. junlianensis*, *R. margaretae*, and *R. schmackeri* are white with melanic poles, whereas those of *R. sinica* are immaculate. The smooth green dorsum further distinguishes *R. sinica* from *H. nasica*, *R. andersonii*, *R. jingdongensis*, *R. grahami*, *R. graminea*, *R. leporipes*, *R. schmackeri*, and *R. tiannensis*. *Huia nasica* has an olive-brown dorsum (*R. sinica* green). *Rana hainanensis* further differs from *R. sinica* in its size (mean female SVL *R. hainanensis* 103 mm) and relative lengths of fingers (II < IV < I for *R. hainanensis*, I < II < IV for *R. sinica*). *Rana andersonii* has a rough, olive-brown dorsum. *Rana hejiangensis* has smaller males (SVL 47 mm) and a different finger formula (II < I < III) than *R. sinica*. *Rana julianensis* and *R. kwangwuensis* differ from *R. sinica* in their relative finger formula (II < I < IV). *Rana jingdongensis* possesses vertical lip bands, large toe disks, and is fully webbed to all disks. *Rana graminea* differs from *R. sinica* in that its nares is closer to the tip of the snout than to the eye (halfway in *R. sinica*), and it has a different finger formula (II = I < IV for *R. graminea*). *Rana margaretae* further differs from *R. sinica* in having larger females (SVL 78–88 mm). *Rana grahami* has pustules on the dorsum and flanks and no digital disks (only slightly swollen tips). *Rana schmackeri* has a smooth, heavily spotted dorsum. *Rana tiannensis* has a rough, brown dorsum with large, prominent lateral granulations. *Rana chalconota* differs from *R. sinica* by having distinct dorsolateral folds, a pointed snout (vs. rounded), and an outer metatarsal tubercle. In *R. archotaphus* the outer metatarsal tubercle

is present. *Rana hosii* differs from *R. sinica* by its dorsolateral folds and feeble tarsal folds (absent in *R. sinica*). *Rana chloronota* differs from *R. sinica* in being larger (SVL for adult females 80–100 mm for *R. chloronota*), having nostrils closer to the tip of the snout than the eye (halfway for *R. sinica*), and a different digital formula (II < I < IV < III for *R. chloronota*). *Rana leporipes* also differs from *R. sinica* by having a white supratympanic fold (not colored in *R. sinica*). *Rana livida* has a solid-colored dorsum with white spots on its sides (flanks a different color for *R. sinica*, lacking spots), and it lacks transverse bands on the arms and legs (present in *R. sinica*).

DESCRIPTION OF HOLOTYPE: HDL greater than HDW (132%), HDW 26% of SVL, HDL 34% of SVL; snout short, rounded in dorsal view; protruding beyond margin of lower jaw, rounded in lateral view, EYE prominent, smaller than SNT, IOD broader than EYE and upper eyelid. Top of head flat; canthus rostralis rounded; loreal region steeply concave; nostril about one-half the distance from eye to tip of snout; supratympanic fold weak; tympanum round, indistinct, covered by layer of skin; TMP 52% of EYE in females. Choanae ovoid; vomerine dentigerous processes prominent, oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for part of its posterior length.

Forearm robust; relative lengths of fingers I < II < IV, III < snout; ventromedial callous pad on III almost to proximal tubercle; disks slightly expanded (<2× base of phalanges); circummarginal grooves present ventrally; terminal phalanges rounded; subarticular tubercles conical. Hindlimbs moderately robust; extend 15 mm beyond snout when adpressed; TIB 59% of SVL; FTL 30% of SVL; toe II is longer than all others, III = IV; inner tarsal fold absent; feet fully webbed to base of toe disk on II, III, and IV, I and V without external fringes; toes long, slender, with slight, rounded disks; ventral circummarginal grooves present; subarticular tubercles prominent, conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum small, with a shallow notch posteriorly.

Skin on dorsum smooth, flanks with slight granulations; dorsolateral fold absent; small tubercles posteroventral to tympanum; granules on thighs and around cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

COLOR IN LIFE (in preservative): Dorsum green (bronze-green to brown), flanks gray (blue-gray to light brown); loreal region black (dark blackish brown), lip-stripe absent; dorsal limbs and digits brown with dark brown transverse bands; posterior surface of thighs black with white marbling; venter creamy white; ventral side of limbs creamy yellow; webbing marbled white on dark brown (brown).

SECONDARY SEXUAL CHARACTERS: The female holotype has large, immaculate yellow eggs (possibly white in life).

MEASUREMENTS OF HOLOTYPE (in mm): SVL 66.6; HDL 22.5; HDW 17.6; EYE 8.2; IOD 13.4; TMP 4.2; TIB 39.4; femur 33.7; FTL 33.7.

REMARKS: The holotype is the only known specimen of *R. sinica*; all others are lost. This redescription is based on the original description by Ahl (1925) with amendments and additions based on our examination of the holotype. Ahl described the holotype as a male, but it is clearly a gravid female. As well, Ahl described a frog with large finger and toe pads. Although the condition of the specimen did not allow for accurate pad measurements to be made, the enlarged pads on the holotype are not as large as those on other species in the *Rana chloronota* complex. This species differs significantly from the other members of the *Rana chloronota* complex in preservative, but presumably has superficial resemblances in life. Ahl (1925) believed that *R. sinica* was closely related to *Staurois natator*.

Rana bacboensis, new species

(Previously referred to as species 2, ''Black Egg'')

Figures 11D, 12E, F, 13B

HOLOTYPE: (ROM field no. 13171) ROM 29534 an adult female from the Khe Moi River, approximately 24 km west of Con Cuong

Fig. 11. Members of the *Rana chloronota* complex. (**A**) Male and female and (**B**) male *R. chloronota*, Nghe An Province, Vietnam. **C.** *R. graminea*, male, Hainan Island, China, (NLO field series 26375). **D.** *R. bacboensis*, new species, holotype, a female from Nghe An Province, Vietnam. (**E**) Female holotype and male paratype in amplexus, and (**F**) juvenile paratype of *R. daorum*, new species, Lao Cai Province, Vietnam.

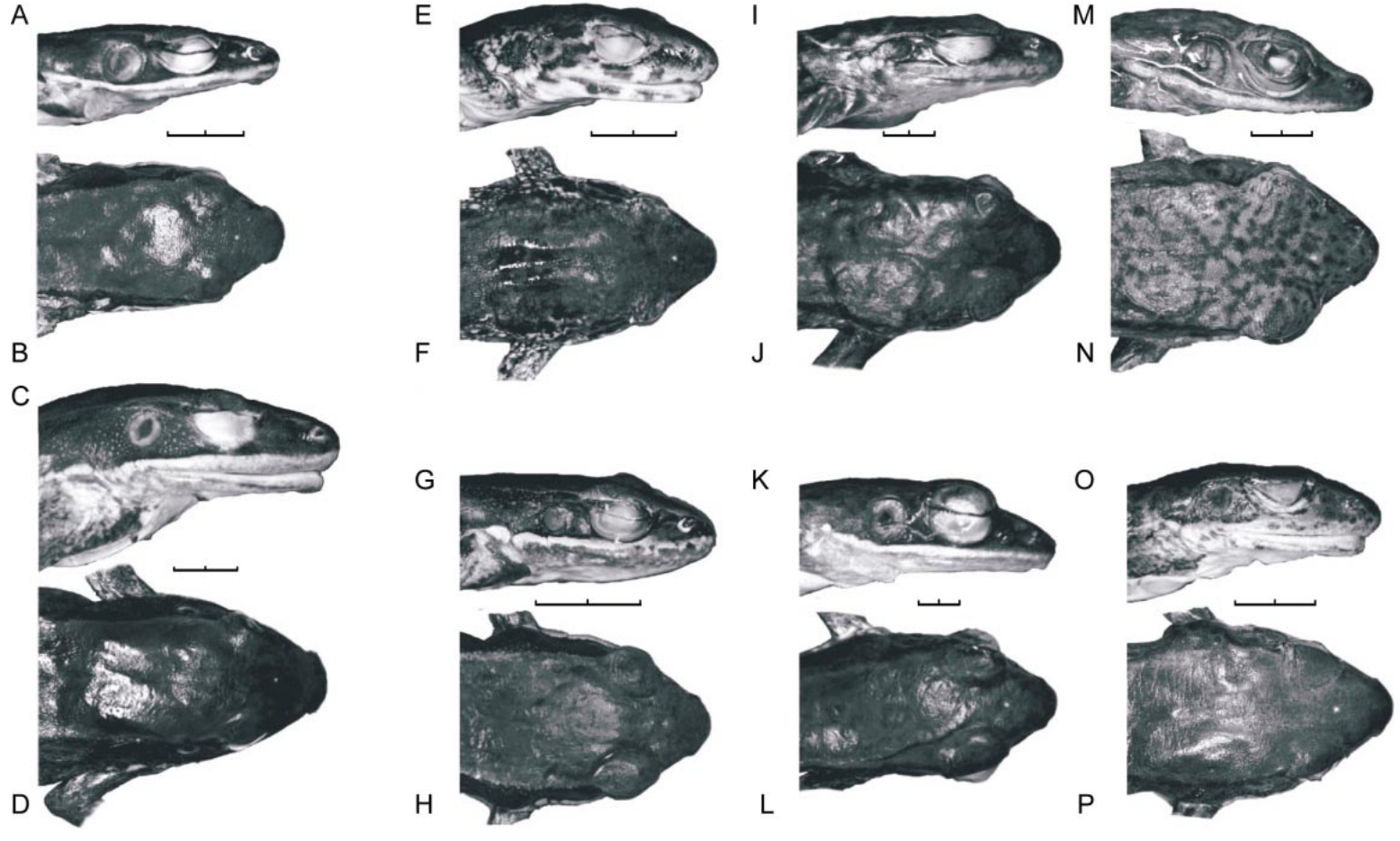

Fig. 12. Heads of members of the *Rana chloronota* complex in lateral and dorsal views: (**A, B**) *Rana chloronota*, male (ROM 26402), and (**C, D**) female (ROM 26406); paratypes of (**E, F**) *Rana bacboensis*, new species (ROM 29529); (**G, H**) *Rana daorum*, new species (ROM 38538); (**I, J**) *Rana hmongorum*, new species (ROM 39891); (**K, L**) *Rana morafkai*, new species (ROM 39906); (**M, N**) *Rana banaorum*, new species (ROM39941); and (**O, P**) *Rana megatympanum*, new species (ROM 26398).

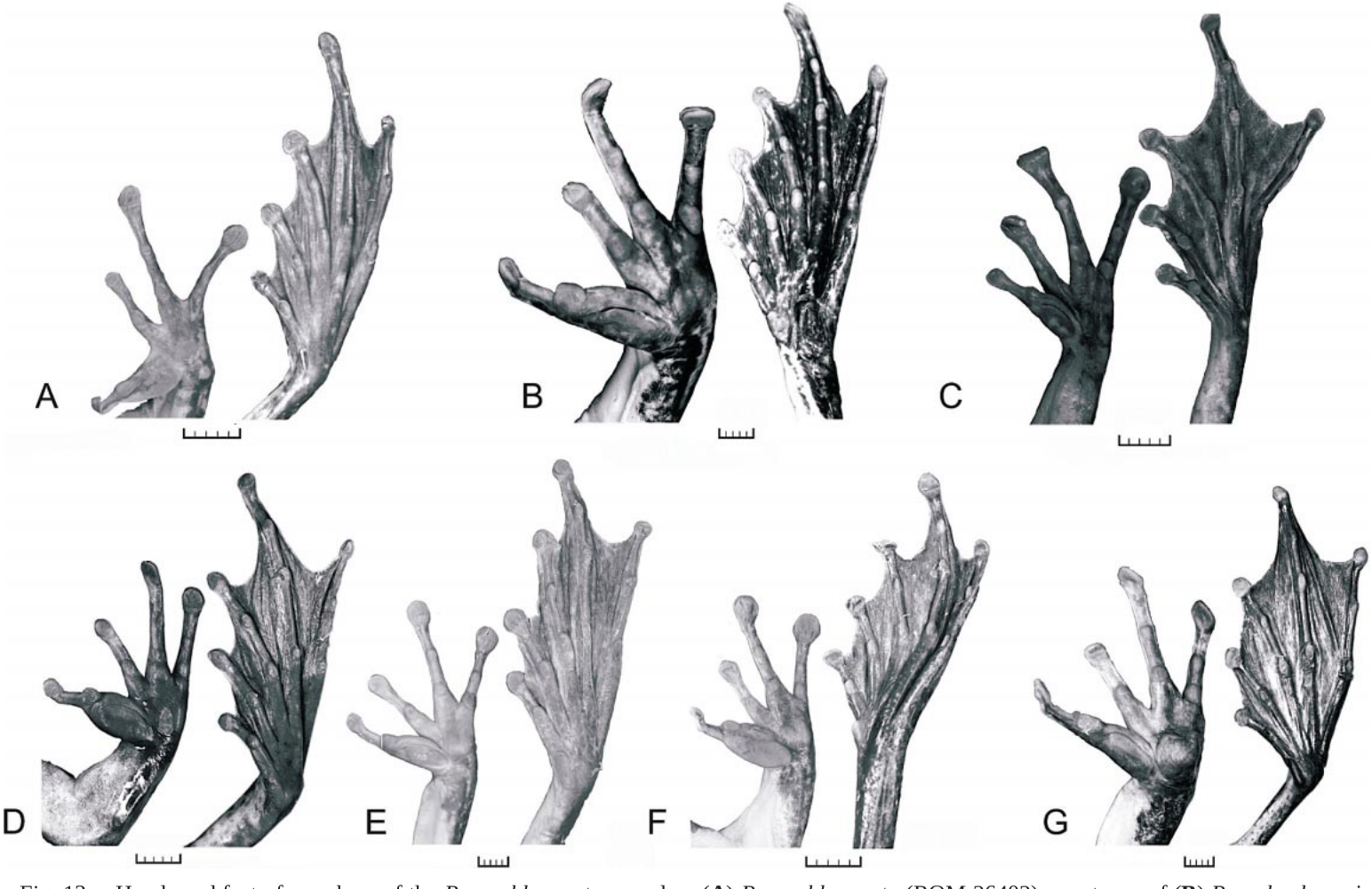

Fig. 13. Hands and feet of members of the *Rana chloronota* complex: (**A**) *Rana chloronota* (ROM 26402); paratypes of (**B**) *Rana bacboensis*, new species (ROM 29529); (**C**) *Rana daorum*, new species (ROM 38538); (**D**) *Rana hmongorum*, new species (ROM 26379); (**E**) *Rana morafkai*, new species (ROM 39906); (**F**) *Rana banaorum*, new species (ROM 39941); and (**G**) *Rana megatympanum*, new species (ROM 26398). Scale equals 5 mm.

village, Con Cuong District, Nghe An Province, Vietnam (18°56′30″N, 104°48′35″E) collected 24 October 1994 by I.S. Darevsky, L.A. Lowcock, R.W. Murphy, and N.L. Orlov. The holotype had leg and liver tissue removed shortly after it was euthanised.

PARATYPES: ROM 29531–29533, all females, collected with holotype on 24 October 1994 by I.S. Darevsky, L.A. Lowcock, R.W. Murphy, and N.L. Orlov; ROM 26404, a female collected at the type locality by A. Lathrop, R.W. Murphy, and N. Orlov on 5 June 1995; ROM 26357–26358, adult females collected from the type locality on 5 June 1995 by A. Lathrop, R.W. Murphy, and N.L. Orlov; ROM 29359, a female, from Ba Be Lake, Ba Be Lake National Park, Bac Kan Province (formerly Cao Bang Province), Vietnam (22°25′05″N, 105°38′05″E), collected by R.H. Bain on 24 May 1995 at the outflow on the south side of Ba Be Lake; ROM 29526–29530, all females, from Na Hang Nature Reserve, Tuyen Quang Province, Vietnam (22°21′54″N, 105°25′40″E) approximately 15 km from Pac Ban village collected by R.W. Murphy and A. Lathrop between 25 and 30 May 1996; AMNH A-161248, a female, from Hieng Stream, Chau Khe Commune, Con Cuong District, Nghe An Province, Vietnam (19°02′17″N, 104°42′06″E, elevation 300 m) collected on 29 April 1998 by N.Q. Truong; FMNH 255611 (adult female), 255612 (adult male) along the Khe Chat Stream, Pu Mat Nature Reserve, Con Cuong District, Nghe An Province, Vietnam (18°56′N, 104°45′E, elevation 300 m) on 8 September 1998 by Bryan L. Stuart.

DIAGNOSIS: *Rana bacboensis*, a member of the subgenus *Odorrana* (sensu Fei et al., 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL of males 54.9 mm, means of females 96 mm (82–105 mm); (3) vomerine teeth present in rows oblique to choanae; (4) vertical black stripes on upper lip (especially under eye), light colored glandule above insertion of arm; (5) head broad, bluntly rounded in profile; (6) tympanum circular, distinct, TMP:EYE 0.43 in females, 0.66 in the male; (7) supratympanic fold weak; (8) dorsal skin shagreened, becoming granular laterally, dorsolateral fold absent; venter smooth; (9) dorsum brown with black blotches; forelimbs and hindlimbs with transverse bands of distinct blotches to tips of digits; (10) median callous pad on base of fingers II and III to proximal tubercle; (11) disks on fingers and toes enlarged ($<2\times$ base of phalanges); (12) feet fully webbed to disks, but as a fringe from distal subarticular tubercle of IV, slight lateral fringes on toes I and V to terminal phalanges, webbing marbled brown on white; (13) subarticular tubercles distinct, conical; inner metatarsal tubercle distinct, ovoid; (14) terminal phalanges T-shaped; (15) xiphisternum large, deeply notched posteriorly; (16) male with velvety nuptial pad on thumb, paired gular pouches, no pectoral spines; (17) eggs black.

COMPARISONS: *Rana bacboensis* is one of the larger species of cascade ranids (SVL female 81–105 mm). It can be distinguished from all other cascade ranids of Southeast Asia by its dark, pigmented eggs (immaculate white or white with melanic pole in other species) (table 12). Its black vertical lip-bars distinguish it from *R. archotaphus*, *R. chalconota*, *R. chloronota*, *R. grahami*, *R. graminea*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. kwangwuensis*, *R. leporipes*, *R. livida*, *R. schmackeri*, *R. sinica*, and *Huia nasica*. The brown dorsum with dark spots distinguishes it from *R. archotaphus*, *R. chalconota*, *R. chloronota*, *R. grahami*, *R. graminea*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, *R. margaretae*, *R. schmackeri*, and *R. sinica*, all of which have a predominantly green dorsum. The presence of gular pouches in males differentiates *R. bacboensis* from *R. andersonii*, *R. chalconota*, *R. grahami*, *R. hainanensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, and *R. margaretae*. *Huia nasica* has a smooth, olive-brown dorsum with lighter flanks (*R. bacboensis* is shagreened and uniformly brown with black spots both on the dorsum and flanks), and adult females are smaller than those of *R. bacboensis* (67 mm vs. >80 mm). The absence of an outer metatarsal tubercle and the large female SVL also distinguishes *R. bacboensis* from *R. archotaphus* and *R. chalconota* (female SVL 81–105 mm for *R. bacboensis*, 59–62 mm and 46–59 mm for *R. archotaphus* and *R. chalconota*, respectively). The absence of dorso-

lateral folds distinguishes *R. bacboensis* from *R. chalconota*, *R. graminea*, *R. hosii*, and *R. leporipes* (pustules on the dorsum of *R. grahami* sometimes form a dorsolateral fold). *Rana bacboensis* has webbing to the base of the toe pad distinguishing it from *R. leporipes* (webbing to distal phalanx). *Rana sinica* can further be distinguished from *Rana bacboensis* by its indistinct, skin-covered tympanum, and different finger formula (I < II < IV for *R. sinica*, II < I < IV for *R. bacboensis*). *Rana bacboensis* shares a superficial resemblance to *R. tiannensis*, another large brown cascade ranid, but differs in having shagreened dorsal skin with small lateral granulations (dorsum of *R. tiannensis* is rough with large, prominent lateral granulations) and smaller toe disk than finger disk (the opposite condition of *R. tiannensis*). *Rana bacboensis* most closely resembles *R. hainanensis*, *R. jingdongensis*, and *R. andersonii*. *Rana bacboensis* further differs from *R. hainanensis* in its relative lengths of fingers (II < IV < I < III for *R. hainanensis*) and by its shagreened skin (smooth for *R. hainanensis*). *Rana bacboensis* also differs from *R. jingdongensis* in profile of its snout shape (rounded or obtusely pointed in *R. jingdongensis* versus rounded in *R. bacboensis*) and texture of skin (*R. jingdongensis* dorsum scattered with tubercles and large warts, lips and sides of heads with white spines, all absent in *R. bacboensis*). *Rana bacboensis* also differs from *R. andersonii* in its head shape (obtusely pointed in *R. andersonii*) and absence of ventral spines in the males.

DESCRIPTION OF HOLOTYPE: A gravid female (ROM 29534), head length greater than width (127%), head width 34% of SVL, length 43% of SVL; snout short, protruding beyond margin of lower jaw, rounded in dorsal view, bluntly rounded in profile; eye large, prominent, 81% of snout length; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold barely evident, curving posteroventrally from posterior corner of eye to a level above insertion of arm; tympanum round, distinctly visible, separated from eye by distance equal to TMP:EYE 0.62. Choanae ovoid; vomerine dentigerous processes prominent, slightly oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately one-half its length.

Forearms moderately robust; fingers moderately short, slender; hands 27% of SVL, relative lengths of fingers II < I < IV < III; ventromedial callous ridge on fingers II and III prominent, extending to proximal tubercle; disks expanded (<2× base of phalanges), relative pad size II < I < IV < III, pad length (III) 75% of pad width; ventral circummarginal grooves present; terminal phalanges T-shaped; subarticular tubercles conical. Hindlimbs moderately robust; tibia length 60% of SVL; foot length 62% of SVL; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet fully webbed to disks, but as a fringe from distal subarticular tubercle of IV, lateral fringes on toes I and V to terminal phalanges; toes long, slender, with large, rounded triangular disks, relative pad size I = II = III > IV ≫ V, pad width (IV) 85% of pad length, circummarginal grooves present; subarticular tubercles prominent, conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum large, deeply notched posteriorly.

Skin on dorsum shagreened with heavy granulations, leathery in alcohol preservation; dorsolateral folds absent; small tubercles anterior and posterior to tympanum; flanks with small granulations and large pustules; distinct granules on posterior thighs and around cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

COLOR IN LIFE (in preservative): Dorsum, flanks, and loreal region brown (brownish gray) with small black spots, becoming larger on the flanks; upper and lower lips creamy yellow with vertical black bars; dorsal limbs and digits brown with black transverse bands; webbing on feet marbled white and dark brown (black); venter creamy white, sometimes with light spotting on belly, chest, and chin; iris golden, margin of pupil outlined in a striking yellow and red border.

SECONDARY SEXUAL CHARACTERS: The holotype possesses large, black eggs (2 mm in

diameter). The lone male paratype has gular pouches, thickened forearms, and thick white nuptial pads.

MEASUREMENTS OF HOLOTYPE (in mm): SVL 95.1; SNT 12.0; HDL 41.0; HDW 32.2; EYE 9.7; IOD 6.4; TMP 6.0; TEY 5.0; HND 25.6; FGR 21.8; FPL 2.8; FPW 3.7; TIB 56.8; FTL 59.6; TPL 2.4; TPW 2.0.

VARIATION OF PARATYPES: Variation in all type material is given in table 15.

MEASUREMENTS OF FEMALE PARATYPES (in mm, n = 6, ROM 29359, 29526–29530): SVL 95.8 mm ± 6.4 (81.8–105.1); SNT 13.8 ± 1.4 (10.8–15.6) ; HDL 46.4 ± 3.5 (43.5–51.2); HDW 35.4 ± 2.9 (34.1–39.6); EYE 9.8 ± 0.5 (9.4–10.8); IOD 7.9 ± 1.7 (5.8–11.0); TMP 5.3 ± 0.6 (4.0–6.0); TEY 4.9 ± 0.7 (3.6–6.0); HND 25.5 ± 2.8 (18.6–30.3); FGR 20.8 ± 2.3 (14.0–24.1); FPL 3.0 ± 0.3 (2.4–3.6); FPW 3.5 ± 0.6 (2.6–4.3); TIB 58.6 ± 3.7 (50.5–66.2); FTL 70.2 ± 7.8 (55.8–79.1).

MEASUREMENTS OF MALE PARATYPE (in mm, FMNH 255611): SVL 54.9, SNT 8.8, HDL 28.0, HDW 18.1, EYE 6.6, IOD 6.1, TMP 4.4, TEY 1.8, HND 16.5, FPL 2.4, FPW 1.8, TIB 32.4, FTL 45.4, TPL 2.4, TPW 1.6.

ETYMOLOGY: The specific name, derived from Bac Bo, the Vietnamese name for northern Vietnam (often referred to as Tonkin), reflects this species' distribution.

DISTRIBUTION AND ECOLOGY: *Rana bacboensis* occurs in forested montane river systems across northern Vietnam. These rivers vary from shallow and slow moving to torrential and deep. Specimens may be found on boulders and logs, both in and around the water and in the adjacent forest. Radiographs revealed that females feed on large invertebrates, including small freshwater crabs. Females were collected in April–May and October. The holotype, collected in October, has fully developed ova, and two females (ROM 26358, 29529) collected in the spring have undeveloped ova suggesting a fall breeding season. No calls are associated with this species. The tadpoles are unknown.

REMARKS: Cascade ranids bearing white eggs lay them under rocks, sheltered from the sunlight (Pope, 1931; ROM field notes, 1996). In contrast, the black eggs of *R. bacboensis* might be found where they are exposed to sunlight to promote development, a requirement for some species with melanic eggs (Duellman and Trueb, 1986).

Rana daorum, new species

(Previously referred to as species 4, "Small")

Figures 11E, F, 12G, H, 13C

HOLOTYPE: (ROM field no. 19047) ROM 26381 an adult female from approximately 5 km NW of Sa Pa village, near O Qui Ho Pass, Lao Cai Province, Vietnam (22°22′09″N, 103°50′14″ E, elevation 1400 m) collected on 7 May 1995 along a waterfall beside the road by A. Lathrop and B. Hubley at approximately 1930 hours.

PARATYPES: ROM 26382–26397, all males, collected with the holotype, 7 May 1995 by A. Lathrop and B. Hubley at 1030 hours; ROM 38500–38530, 38532–38540, 38542–43, 38546–38561 collected between 30 April and 15 May 1999 in the vicinity of the type locality approximately 12 km northwest of Sa Pa Village near the O Qui Ho Pass (22°20′58″N, 103°46′14″E, elevation 1900 m) by R.O. de Sá, C.T. Ho, A. Lathrop, T. Mason, R.W. Murphy, and N.L. Orlov. ROM 38547 is a subadult; ROM 38503, 38507, 38512, 38516, and 38530 are gravid females; ROM 38500, 38517, 38526, and 38538 are nongravid females; and the remaining specimens are males with distended gular pouches.

DIAGNOSIS: *Rana daorum*, a member of the subgenus *Odorrana* (sensu Fei et al., 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL means of males 36 mm (32–38 mm), females 55 mm (53–58 mm); (3) vomerine teeth absent; (4) lip-stripe white, extending across upper lip, terminating in a glandule above insertion of arm; (5) head not broad, snout rounded in dorsal view, rounded in profile; (6) tympanum round, distinct, TMP:EYE of females (0.45) greater than males (0.29); (7) supratympanic fold weak or absent; (8) dorsal skin smooth, granular near cloaca and tympanum, dorsolateral fold covered with small white granules, ventral skin smooth; (9) dorsum green occasionally with black spots, flanks brown with at least one large white glandular spot;

fore- and hindlimbs goldish brown, with mottling or indistinct transverse bands; (10) median callous pad on proximal two-thirds of fingers II and III; (11) disks on fingers and toes greatly enlarged (>2× base of phalanx), finger pads larger than toe pads; (12) feet fully webbed to disks, but as a fringe from distal subarticular tubercle of IV, lateral fringes on I and V to terminal phalanges, webbing mottled brown; (13) subarticular tubercles and inner metatarsal tubercle distinct, conical; (14) terminal phalanges T-shaped; (15) xiphisternum narrow, forked posteriorly; (16) males with nuptial pads on thumb, paired gular pouches, pectoral spines absent; (17) eggs large, white.

COMPARISONS: Though bearing a superficial resemblance to other cascade ranids of Southeast Asia, *R. daorum* is distinct (table 12) by the absence of vomerine teeth, females with larger TMP:EYE than males, and the presence of at least one large white spot on each flank. Its noticeably smaller SVL, dorsolateral folds formed by white granules, and solid, bright green dorsum immediately distinguishes it from *H. nasica*, *R. andersonii*, *R. archotaphus*, *R. bacboensis*, *R. chloronota*, *R. grahami* (whose dorsal pustules sometimes form a fold), *R. graminea*, *R. hainanensis*, *R. hejiangensis*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica*, and *R. tiannensis*. The entirely white eggs of *R. daorum* distinguish it from *Huia nasica*, *Rana andersonii*, *R. chalconota*, *R. grahami*, *R. junlianensis*, *R. margaretae*, *R. schmackeri* (all with white eggs with a melanic pole), and *R. bacboensis* (fully pigmented eggs). The presence of gular pouches in males differentiates *R. daorum* from *R. andersonii*, *R. chalconota*, *R. grahami*, *R. hainanensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, and *R. margaretae*. A distinct and uncovered tympanum also distinguishes *R. daorum* from *R. sinica*. *Rana daorum* can be further distinguished from *R. livida*, *R. chloronota*, *R. maragaretae*, and *R. schmackeri* by its finger formula (II < I < IV for *R. daorum*, I < II < IV for others listed). Although *R. daorum* closely resembles *A. chunganenesis* in size, the presence of white granular dorsolateral folds, and diurnal behavior, *A. chunganensis* is red-brown, has vomerine teeth, and males have a TMP:EYE ratio twice that of *R. daorum*.

DESCRIPTION OF THE HOLOTYPE: An adult female (ROM 26381), head width 74% of length, length 46% of SVL; snout short, rounded in dorsal view, rounded in profile, protruding beyond margin of lower jaw; eye very large, prominent, 72% of snout; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region vertical, concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold indistinct, slight swelling above tympanum; tympanum round, distinctly visible, separated from eye by distance equal to that of TMP, 41% of EYE. Choanae ovoid; vomerine dentigerous processes absent. Tongue cordiform, distinctly notched posteriorly, free for approximately two-thirds its length.

Forearms robust; fingers moderately short, slender, hand 28% of SVL, relative lengths of fingers I < II < IV < III, ventromedial callous pad on fingers II and III for two-thirds length of finger; disks greatly expanded (>2× base of phalanges), relative pad size II < I < IV < III, pad length (finger III) equal to pad width, ventral circummarginal grooves present; terminal phalanges T-shaped; subarticular tubercles conical. Hindlimbs moderately robust; tibia length 60% of SVL; foot length 84% of SVL; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet fully webbed to disks, but as a fringe from distal subarticular tubercle of IV, lateral fringe on toe V to terminal phalanx; toes long, slender, with enlarged disks, smaller than those on fingers, relative pad size I = II = III > IV ≫ V, pad width (IV) 83% of length, each pad with ventral circummarginal grooves; subarticular tubercles prominent and conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum narrow, notched posteriorly.

Skin on dorsum smooth, dorsolateral folds prominent in form of granules; small tubercles posteroventrally to tympanum, distinct granules on flanks and dorsum to cloaca; cloacal opening unmodified, directed posteriorly at upper level of thighs.

COLOR IN LIFE (in preservative): Dorsum green (livid blue), flanks brown (brown) and

green (gray), each a prominent white spot; granules of dorsolateral fold golden (white); lip-stripe white (silvery white) from nostril to above insertion of arm; tympanum dark brown; loreal region dark brown (black); dorsal surfaces of limbs mottled brown and yellow with indistinct dark brown (black) transverse bands; posterior surface of thighs yellow with brown (black) mottling; webbing marbled white (translucent) and dark brown; venter creamy white; iris golden, pupil outlined in a striking yellow and red border.

SECONDARY SEXUAL CHARACTERS: Gravid females have immaculate white eggs. They are approximately 1.5 times larger than males. Males have a proportionally smaller tympanum than females (TMP:EYE for males 0.29, for females 0.45). The EYE:SNT is also greater in females (0.72) than it is in males (0.51). Males have velvety nuptial pads extending across thumb, and paired gular pouches located at the angles of the jaw. Pectoral spines are absent.

MEASUREMENTS OF HOLOTYPE (in mm): SVL 55.7; SNT 7.8; HDL 25.4; HDW 18.8; EYE 5.6; IOD 5.6; TMP 2.3; TEY 2.4; HND 15.5; FGR 13.9; FPL 2.8; FPW 2.8; TIB 33.6; FTL 47.0; TPL 2.3; TPW 1.9.

VARIATION OF PARATYPES: The loreal region on some specimens varies from dark brown to green. The large white spot on the flanks is sometimes accompanied by smaller ones. Flanks also have varying degrees of white mottling. The venter of some specimens has light mottling on the chest and chin. Variation in all type material is given in table 15.

MEASUREMENTS OF FEMALE PARATYPES (in mm, n = 8, ROM 38500, 38503, 38507, 38512, 38516, 38517, 38526, 38530): SVL 55.0 ± 1.2 (53.3–57.6); SNT 7.3 ± 0.5 (6.8–8.3); HDL 17.8 ± 1.6 (16.7–19.4); HDW 17.2 ± 0.6 (15.6–17.6); EYE 5.8 ± 0.4 (5.3–6.4); IOD 10.0 ± 1.7 (10.0–11.3); TMP 2.5 ± 0.2 (2.3–3.0); FPW 2.3 ± 0.3 (1.8–2.8); TIB 34.3 ± 1.3 (32.7–36.4); TPW 2.3 ± 0.3 (1.8–2.8).

MEASUREMENTS OF MALE PARATYPES (in mm, n = 7, ROM 26383, 26386, 26387, 26389, 26390, 26392, 26394): SVL 36.2 ± 1.2 (34.8–38.1); SNT 4.5 ± 0.4 (4.0–4.9); HDL 18.4 ± 1.7 (16.5–21.0); HDW 12.3 ± 0.6 (11.1–13.0); EYE 4.2 ± 0.6 (3.2–5.2); IOD 3 ± 0.4 (2.3–3.6); TMP 1.1 ± 0.2 (1.0–1.9); TEY 0.6 ± 0.2 (0.2–1.0); HND 10.1 ± 0.6 (9.0–11.1); FGR 9.0 ± 0.3 (8.5–9.6); FPL 1.7 ± 0.3 (1.2–2.0); FPW 2.0 ± 0.2 (1.7–2.2); TIB 22.1 ± 1.3 (19.1–23.5); FTL 29.7 ± 4.4 (27.1–40.4); TPL 1.6 ± 0.2 (1.2–1.7); TPW 1.4 ± 0.1 (1.2–1.6).

ETYMOLOGY: The specific name is a patronym for the Đao people (pronounced ''zao'') of northern Vietnam.

DISTRIBUTION AND ECOLOGY: This species is known from the vicinity of Sa Pa village, Lao Cai Province in northern Vietnam. The photograph of a froglet of *R. livida* (in Karsen et al., 1998) also documents the occurrence of *R. daorum* in Hong Kong. The distinctive granular dorsolateral fold of *R. daorum* is clearly visible in the misidentified frog.

In early May, male Vietnamese *R. daorum* are actively calling by 1000 hours on partially submerged rocks in cascades as well as in vegetation adjacent to the streams. Females, although not as common, can be found slightly farther away from streams in more dense vegetation. One male (ROM 26394) was found in amplexus with the holotype (fig. 6E).

REMARKS: *Rana daorum* differs substantially from *R. graminea* (Boulenger, 1899; Bourret, 1942) despite having a dorsolateral fold. Its small, forked xiphisternum differs from the large, deeply notched element of other members in the *Rana chloronota* complex and the subgenus *Odorrana* (sensu Fei et al., 1990) and more closely resembles that of male *Huia nasica* (Yang, 1991b). *Huia nasica* shares range, habitat and morphological similarities with the *Rana chloronota* complex: greatly expanded finger and toe disks, tremendous sexual dimorphism in size, white eggs, paired gular pouches, and a high chirp-like call (Boulenger, 1920; Pope, 1931; Bourret, 1942).

Rana hmongorum, new species

(Previously referred to as species 3, ''Speckled'')

Figures 14A, 12I, J, 13D

HOLOTYPE: (ROM field no. 19055) ROM 26376 an adult female approximately 5 km

NW of Sa Pa village, near O Qui Ho Pass, Lao Cai Province, Vietnam (22°20′09″N, 103°50′14″E, elevation 1400 m) collected 30 April 1995 by A. Lathrop and B. Hubley between 1900 and 2100 hours. The holotype had leg and liver tissue removed shortly after it was euthanised.

PARATYPES: ROM 26370–26375, 26377–26380, 39235, and 39236 collected in the vicinity of the holotype between 9 and 12 May 1995 by A. Lathrop and B. Hubley. ROM 26380, 39235, and 39236 are males and the remainder females. Additional specimens from the vicinity of the type locality include AMNH A-161480 collected on 27 August 1997 by D.R. Frost and C.J. Raxworthy, and ROM 39867–39896 (22°20′58″N, 103°46′14″E, elevation 1900 m) collected between 30 April and 2 May 1999 by R.O. de Sá, C.T. Ho, A. Lathrop, T. Mason, R.W. Murphy, and N.L. Orlov. Male specimens are ROM 39874–39879, 39888, and 39890–39894; juveniles and subadults ROM 39867, 39868, 39880, 39895, and 39896; all others are females.

DIAGNOSIS: *Rana hmongorum*, a member of the subgenus *Odorrana* (sensu Fei et al., 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL means of males 59 mm (54–65 mm), females 80 mm (74–87 mm); (3) vomerine teeth in rows posteromedial to choanae; (4) lip-stripe yellow, indistinct, extending across upper lip, terminating in a row of glandules; (5) head broad, bluntly rounded in profile; (6) tympanum round, distinct, TMP:EYE in males (0.43) greater than females (0.31); (7) supratympanic fold weak; (8) dorsal skin smooth with pustules becoming more pronounced laterally, pustules may form two dorsolateral lines resembling a fold, ventrum smooth; (9) dorsum and forearms green with black spots, flanks reddish brown with yellowish pustules, transverse bars on fore– and hindlimbs; (10) median callous pad on fingers II and III to proximal tubercle; (11) disks on fingers and toes moderately expanded ($<2\times$ base of phalanges); (12) feet fully webbed to disks, but as a fringe from distal subarticular tubercle of IV, lateral fringes on toes I and V to terminal phalanges, webbing brown-gray; (13) subarticular tubercles distinct, conical; inner metatarsal tubercle ovoid; (14) terminal phalanges T-shaped; (15) xiphisternum large, deeply notched posteriorly; (16) males with nuptial pad; gular pouches and pectoral spines absent; (17) eggs white.

COMPARISONS: *Rana hmongorum* superficially resembles other Asian cascade ranids, including *Huia nasica*, *Rana andersonii*, *R. archotaphus*, *R. bacboensis*, *R. chalconota*, *R. chloronota*, *R. daorum*, *R. grahami*, *R. graminea*, *R. hainanensis*, *R. hejiangensis*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica*, and *R. tiannensis* (table 12). The white eggs of *R. hmongorum* distinguish it from *H. nasica*, *Rana andersonii*, *R. chalconota*, *R. grahami*, *R. junlianensis*, *R. margaretae*, *R. schmackeri* (all with white eggs with a melanic animal pole), and *R. bacboensis* (fully pigmented eggs). The dorsum and flanks with distinct pustules distinguishes *R. hmongorum* from all of the above species, except *R. jingdongensis*, and *R. grahami*; *R. daorum* has two distinct rows of granular dorsolateral folds. Absence of gular pouches further differentiates it from *H. nasica*, *R. archotaphus*, *R. bacboensis*, *R. chloronota*, *R. daorum*, *R. graminea*, *R. junlianensis*, *R. kwangwuensis*, *R. schmackeri*, and *R. tiannensis*. *Rana hmongorum* has an indistinct yellow lip-stripe distinguishing it from all other cascade ranids above, except *R. chalconota*, *R. jingdongensis*, *R. junlianensis*, and *R. grahami*. The presence of webbing to the base of the toe pad distinguishes *R. hmongorum* from *R. leporipes* (webbing to distal phalanx) and *R. archotaphus*. Larger females and the absence of an outer metatarsal tubercle further distinguish *R. hmongorum* from *R. archotaphus* (female SVL 59–62 mm) and *R. chalconota* (SVL 46–59 mm). Absence of ventral spines in males differentiates *R. hmongorum* from *R. andersonii*, *R. grahami*, *R. jingdongensis*, *R. junlianensis*, *R. margaretae*, and *R. schmackeri*. *Rana sinica* is further differentiated from *R. hmongorum* by its indistinct, skin-covered tympanum, the relative length of its digits (I < II < IV for *R. sinica*, II < I < IV for *R. hmongorum*), and its rounded distal phalanges (T-shaped in *R. hmongorum*). *Huia nasica* is different in that it has a smooth, olive-brown dorsum, a longer head and smaller size (67 mm vs. >75 mm for

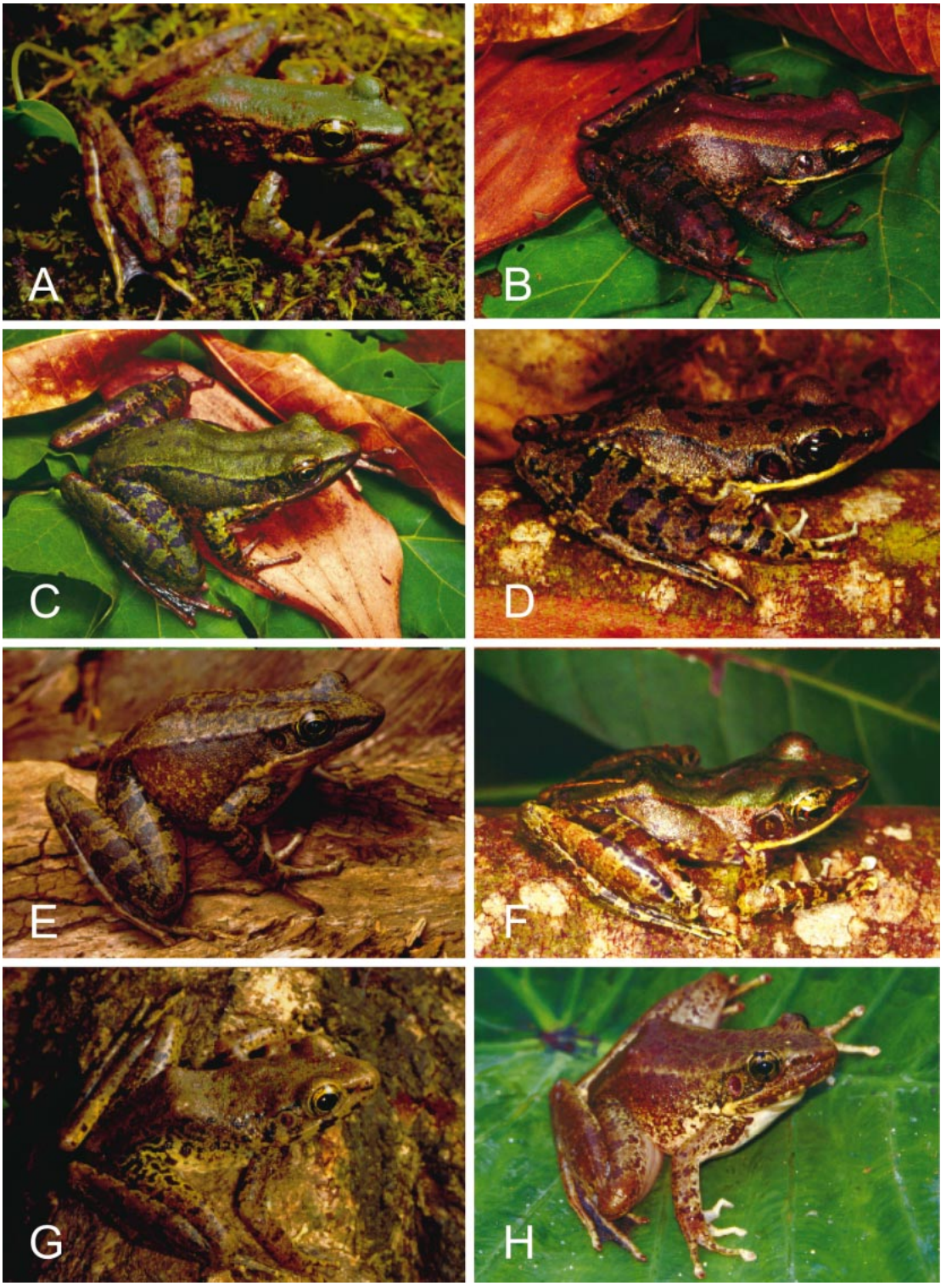

Fig. 14. Members of the *Rana chloronota* complex from Vietnam. **A.** Paratype of *R. hmongorum*, new species, male from Lao Cai Province. (**B**) Female, brown (night) phase, (**C**) female, green (day)

females, 44–49 mm vs. 54–59 for males). The small male of *R. hmongorum* further distinguishes it from *R. jingdongensis*, *R. junlianensis*, *R. andersonii*, and *R. grahami* (SVL 62–81 mm for *R. jingdongensis*, 70–80 mm for *R. andersonii*, 66–84 mm for *R. grahami*). The relative length of fingers further distinguishes it from *R. hainanensis* (II < IV < I < III) and *R. hejiangensis* (II < I < III < IV).

DESCRIPTION OF THE HOLOTYPE: ROM 26376, an adult female, head length greater than width (136%), head width 36% of SVL, length 49% of SVL; snout short, protruding beyond margin of lower jaw, rounded in dorsal view, bluntly rounded in profile; eye large, prominent, 88% of snout length; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold indistinct, slight swelling above the tympanum; tympanum round, distinctly visible, separated from eye by distance equal to TMP, 26% of EYE. Choanae ovoid; vomerine dentigerous processes prominent, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately one-half its length.

Forearms robust; fingers relatively short, slender, hands 25% of SVL, relative lengths of fingers II < I < IV < III; ventromedial callous pad on fingers II and III to proximal tubercle, disks moderately expanded (<2× base of phalanges), relative pad size III > IV > I > II, pad length (III) 85% of pad width; ventral circummarginal grooves on disks present; terminal phalanges T-shaped; subarticular tubercles conical. Hindlimbs moderately robust; tibia length 57% of SVL; foot length 40% of SVL; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet fully webbed to disks, but as a fringe from distal subarticular tubercle of IV, lateral fringes on toes I and V to terminal phalanges; toes long, slender, with large, triangularly rounded disks, relative pad size I = II = III > IV ≫ V, pad width (IV) 78% of pad length, ventral circummarginal grooves present; subarticular tubercles prominent and conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum large, deeply notched posteriorly.

Skin on dorsum smooth with large pustules, particularly on flanks, sacrum, and around cloaca; cloacal opening unmodified, directed posteriorly at upper level of thighs.

COLOR IN LIFE (in preservative): Dorsum green (dark brown) and reddish brown (dark brown) with black spots. Sides reddish brown (gray) and yellow (cream), with some black spotting. Pustules on flanks yellowish white (creamy white), with black around the bases. Cloacal region dark brown (black). Lip-stripe creamy white (gray); dorsal surface of forearms with green (gray) patch; limbs mottled yellow (light brown) and brown (dark brown) with black transverse bands; anterior and posterior surfaces of thighs with brown (dark brown) marbling on yellow (cream); webbing uniformly brown; venter creamy white (creamy yellow). Iris greenish yellow or brown, pupil outlined with a yellow border.

SECONDARY SEXUAL CHARACTERISTICS: Holotype is a gravid female with white eggs, 2 mm diameter. Adult female SVL 135% that of males. Males have slightly larger tympanum than do females, and velvety nuptial pads on thumb. Paired gular pouches and pectoral spines absent. Venter of males varies from immaculate creamy white to darkly mottled brown (gray in preservative).

MEASUREMENTS OF HOLOTYPE (in mm): SVL 86.8; SNT 11.1; HDL 42.3; HDW 31.1; EYE 9.7; IOD 6.4; TMP 2.5; TEY 3.9; HND 22.3; FGR 16.5; FPL 2.3; FPW 2.7; TIB 49.2; FTL 35.0; TPL 3.0; TPW 2.3.

VARIATION OF PARATYPES: Pustules can sometimes form dorsolateral lines, which superficially resemble folds. Pustules can be white. Variation in all type material is given in table 15.

MEASUREMENTS OF FEMALE PARATYPES (in

←

phase, and (**D**) male of *R. morafkai*, new species, from Gia Lai Province. (**E**) Female and (**F**) male of *R. banaorum*, new species, from Gia Lai Province. (**G, H**) female of *R. megatympanum* new species.

mm, n = 9; ROM 26370–26375, 26377–26379): SVL 80.2 ± 4.3 (74.3–86.8); SNT 11.0 ± 0.5 (10.1–11.7); HDL 38.8 ± 1.9 (37.0–41.0); HDW 29.8 ± 1.0 (29.2–31.3); EYE 9.3 ± 1.1 (7.6–10.8); IOD 7.0 ± 0.3 (6.4–7.3); TMP 2.9 ± 0.4 (2.5–3.3); TEY 3.0 ± 0.6 (2.1–3.9); HND 23.2 ± 1.3 (22.1–25.6); FGR 18.6 ± 1.1 (16.5–19.6); FPL 3.0 ± 0.4 (2.3–3.4); FPW 2.6 ± 0.4 (2.0–3.1); TIB 47.6 ± 2.3 (43.1–49.2); FTL 39.6 ± 5.0 (35.0–48.3) TPL 2.8 ± 0.6 (2.0–3.5); TPW 2.4 ± 0.5 (1.9–3.3).

MEASUREMENTS OF MALE PARATYPES (in mm, n = 12; ROM 26380, 30876, 39235, 39236, 39874, 39875, 39877, 39879, 39888, 39891, 39892; AMNH A-161480): SVL 59.4 ± 3.8 (54.7–65.3); SNT 9.4 ± 0.9 (8.7–10.4); HDL 24.0 ± 3.0 (20.7–30.4); HDW 20.0 ± 1.2 (18.9–21.1); EYE 7.3 ± 0.5 (6.7–8.3); IOD 5.3 ± 0.7 (4.3–6.5); TMP 3.0 ± 0.4 (2.4–3.7); TEY 2.5 ± 0.3 (2.2–3.0); HND 17.2 ± 1.4 (14.1–19.4); FGR 13.3 ± 1.2 (12.8–14.8); FPL 2.5 ± 0.5 (1.6–3.6); FPW 2.1 ± 0.6 (1.0–2.4); TIB 38.6 ± 4.5 (33.4–51.2); FTL 47.2 ± 5.7 (30.4–52.1); TPL 2.3 ± 0.4 (1.7–2.9); TPW 1.7 ± 0.4 (0.9–2.2).

ETYMOLOGY: The specific name is a patronym for the Hmong (pronounced ''huh-mung'') people, an ethnic group in the northern montane regions of Vietnam. Their assistance made it possible for us to document the fauna of Hoang Lien Mountains.

DISTRIBUTION AND ECOLOGY: This species is only known only from the vicinity of Mount Fan Si Pan at approximately 1900 m or above. Adults were found along the cascades of a waterfall and along the mossy slopes of a human-made culvert.

Rana morafkai, new species

(Previously referred to as species 5, ''Mottled'')

Figures 12K, L, 13E, 14 B–D

HOLOTYPE: (ROM field no. 7301) ROM 39932, a female from Tram Lap, An Khe District, Gia Lai Province, Vietnam (14°26′39″N, 108°32′97″E, elevation ca. 900 m) collected on 19 June 1996 by R.H. Bain, B. Hubley, A. Lathrop, R.W. Murphy, and N.L. Orlov. The holotype had leg and liver tissue removed shortly after it was euthanised.

PARATYPES: ROM 39904–39911, 39930, 39934, 39937, 39947, and 39949 collected with the holotype between 15 and 19 June 1996 by R.H. Bain, B. Hubley, A. Lathrop, R.W. Murphy, and N.L. Orlov; ROM 39904–39011, and 39937 are males; the remainder are females. ROM 25094–25097, 25099, 25101, 25104–25106, 25108–25111, all males collected in Buon Loi, An Khe District, Gia Lai Province, Vietnam (elevation 700–750 m) by I.S. Darevsky and N.L. Orlov on 11 November 1993.

DIAGNOSIS: *Rana morafkai*, a member of the subgenus *Odorrana* (sensu Fei et al., 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL means of males 43 mm (39–46 mm), females 88 (80–100 mm); (3) vomerine teeth in rows oblique to choanae; (4) yellow-white lip-stripe extending across upper lip, terminating in glandule above insertion of arm; (5) head broad, bluntly rounded in profile; (6) tympanum round, relatively large, distinct, approximately 96% of eye length in males, 71% in females; (7) supratympanic fold weak; (8) dorsal skin smooth or partly shagreened, becoming granular laterally, dorsolateral folds absent; (9) dorsum changing colors between day and night, usually bright green in daylight, brown at night sometimes with black spots; forelimbs and hindlimbs with transverse bars; (10) median callous pad on finger III to proximal tubercle; (11) disks on fingers and toes greatly enlarged (>2× base of phalanges); (12) webbing on feet complete to base of disk in females, sometimes as a fringe on IV; in males to distal tubercle in males, lateral fringes on I and V to terminal phalanges; webbing brown-gray; (13) subarticular tubercles and inner metatarsal tubercle conical, indistinct; (14) terminal phalanges T-shaped; (15) xiphisternum deeply notched posteriorly; (16) males with nuptial pads on thumb, paired gular pouches, pectoral spines absent; (17) eggs white.

COMPARISONS: *Rana morafkai* resembles other Asian cascade ranids, including *Huia nasica*, *Rana andersonii*, *R. archotaphus*, *R. bacboensis*, *R. chalconota*, *R. chloronota*, *R. daorum*, *R. grahami*, *R. graminea*, *R. hain-*

anensis, *R. hejiangensis*, *R. hmongorum*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, *R. livida*, *R. margaretae*, *R. schmackeri*, *R. sinica*, and *R. tiannensis* (table 12). It differs from these cascade ranids (except *R. chalconota*) in having unique nocturnal and diurnal coloration, less distinct subarticular tubercles (all other species bear distinct subarticular tubercles), and a webbing pattern that is unique to each sex (females fully webbed to disk, males to distal subarticular tubercles). Female *R. morafkai* (SVL 80–100 mm) are considerably larger than female *R. archotaphus* (59–62 mm), *R. chalconota* (45–60 mm), *R. daorum* (55–58 mm), and *R. sinica* (holotype 66.6 mm). The presence of a large tympanum in the males (TMP:EYE 0.96) differentiates *R. morafkai* from *H. nasica* (0.5), *R. andersonii* (0.7), *R. chloronota* (0.57), *R daorum* (0.29), *R. grahami* (0.53), *R. graminea* (0.77), *R. hainanensis* (0.66), *R. hmongorum* (0.43), and *R. hejiangensis* (0.5). Its broadly rounded snout distinguishes *R. morafkai* from *H. nasica*, *R. andersonii*, *R. chalconota*, *R. schmackeri* (obtusely pointed snouts in profile), *R. graminea*, and *R. margaretae* (distinctly depressed snouts). The presence of gular pouches differentiates male *R. morafkai* from those of *R. andersonii*, *R. chalconota*, *R. grahami*, *R. hainanensis*, *R. hmongorum*, *R. jingdongensis*, *R. hosii*, and *R. margaretae*. The absence of dorsolateral folds distinguishes *R. morafkai* from *R. chalconota*, *R. daorum*, *R. graminea*, *R. hosii*, *R. junlianensis*, *R. kwangwuensis*, *R. leporipes*, and *R. margaretae* (pustules on the dorsum of *R. grahami* and *R. hmongorum* sometimes form a dorsolateral fold). The absence of an outer metatarsal tubercle distinguishes *R. morafkai* from *R. archotaphus* and *R. chalconota*. The presence of completely white eggs differentiates it from *R. bacboensis* (black eggs), *H. nasica*, *R. andersonii*, *R. chalconota*, *R. grahami*, *R. junlianensis*, *R. margaretae*, and *R. schmackeri* (white eggs with a dark melanic pole). The absence of spinules on the venter distinguishes *R. morafkai* from *R. andersonii*, *R. grahami*, *R. jingdongensis*, *R. junlianensis*, *R. margaretae* and *R. schmackeri*. *Rana sinica* differs from *R. morafkai* by its indistinct and skin-covered tympanum (distinct and uncovered in *R. morafkai*), finger formula (I < II < IV for *R. sinica*, II < I < IV for *R. morafkai*), rounded distal phalanges (T-shaped in *R. morafkai*), and absence of a lip-stripe. *Rana leporipes* has small disks and white supratympanic folds, both distinguishing it from *R. morafkai*. The color pattern and skin texture of specimens of *R. morafkai* may be identical to those of *R. chloronota*; however, the pronounced sexual dimorphism in the tympanum size (TMP:EYE *R. morafkai* males 0.96; females 0.71) differentiates it from all Vietnamese populations of *Rana chloronota* except those from Na Hang (males 0.60, females 0.43).

DESCRIPTION OF THE HOLOTYPE: An adult female (ROM 39932), head width 66% of length, length 50% of SVL; snout short, acutely rounded in dorsal view, bluntly rounded in profile, protruding beyond margin of lower jaw; eye large, prominent, 38% of snout length; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold curving posteroventrally from posterior corner of eye to a level above the insertion of the arm; tympanum round, distinctly visible, separated from eye by distance equal to TMP, 68% of EYE. Choanae ovoid; vomerine dentigerous processes prominent, oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately two-thirds its length.

Forearms moderately robust; fingers moderately short, slender, hands 21% of SVL, relative lengths of fingers II < I < IV < III, ventromedial callous pad on finger III to proximal tubercle, disks greatly expanded (>2× base of phalanges), relative pad size II < I < IV < III, pad width (III) 90% of pad length, ventral circummarginal grooves present; terminal phalanges T-shaped; subarticular tubercles conical. Hindlimbs moderately robust; tibia length 62% of SVL; foot length 82% of SVL; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet fully webbed to toe disk, lateral fringe on I and V to terminal phalanges, toes long, slender, with large, rounded, triangular disks, relative pad size I = II = III > IV ≫ V, pad

width (IV) 80% of pad length, each with ventral circummarginal grooves; subarticular tubercles prominent and conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum large, deeply notched posteriorly.

Skin on dorsum shagreened, light granulations laterally; dorsolateral folds absent; small tubercles posteroventrally to tympanum; prominent granules on flanks and around cloaca; cloacal opening unmodified, directed posteriorly at upper level of thighs.

COLOR IN LIFE (in preservative): Green (livid blue, with dark spots); flanks yellow and gray (cream and gray) with some white mottling posteroventrally; lip-stripe yellow-white (creamy white); loreal region brown (black); tympanum beige with dark brown central ring; limbs above brown with black transverse bands, below creamy yellow with black mottling; thighs marbled yellow and brown; cloacal region black; venter creamy white; iris golden, margin of pupil outlined in a striking yellow and red border.

SECONDARY SEXUAL CHARACTERS: The holotype is a gravid female with creamy white eggs, 2 mm in diameter. Gravid females are approximately twice the SVL of males. Tympanum in males (TMP:EYE 0.96) is larger than in females (0.71). Webbing on females extends to disk, and only to distal subarticular tubercle in males. Males have velvety nuptial pads extending across the thumb, paired gular pouches located at the angle of the jaws, and pectoral spines absent.

MEASUREMENTS OF HOLOTYPE (in mm): SVL 84.4; SNT 14.3; HDL 42.7; HDW 28.2; EYE 5.4; IOD 7.3; TMP 3.7; TEY 4.1; HND 18.0; FGR 14.0; FPL 3.0; FPW 2.7; TIB 52.6; FTL 68.7; TPL 2.9; TPW 2.3.

VARIATION OF PARATYPES: The skin on the dorsum can be smooth or partly shagreened. These frogs are often brown at night, but diurnally they can become green over their entirely body or only dorsally. The dorsum is occasionally colored with black spots. Variation in all type material is given in table 15.

MEASUREMENTS OF FEMALE PARATYPES (in mm, n = 4, ROM 39930, 39934, 39947, 39949): SVL 87.6 ± 6.9 (80.4–99.6); SNT 13.4 ± 1.7 (10.8–15.6); HDL 39.1 ± 2.4 (37.6–38.5); HDW 27.2 ± 1.1 (27.7–28.2); EYE 6.0 ± 0.9 (4.9–7.6); IOD 7.7 ± 0.9 (6.1–9.0); TMP 4.1 ± 0.7 (3.4–5.2); TEY 4.5 ± 1.9 (3.2–8.3); HND 18.8 ± 2.2 (16.7–21.9); FGR 15.0 ± 2.5 (12.2–18.1); FPL 3.5 ± 0.4 (2.8–3.9); FPW 3.0 ± 0.3 (2.7–3.5); TIB 53.5 ± 4.7 (47.4–61.5); FTL 63.0 ± 11.3 (43.3–76.1) TPL 3.1 ± 0.3 (2.5–3.5); TPW 2.9 ± 0.5 (2.3–3.7).

MEASUREMENTS OF MALE PARATYPES (in mm, n =14, ROM 25094–25097, 25099, 25101, 25104–25106, 25108–25111, 39937): SVL 43.2 ± 1.7 (39.2–45.9); SNT 6.8 ± 0.4 (6.2–7.8); HDL 21.3 ± 0.8 (20.5–22.4); HDW 13.8 ± 1.0 (13.2–15.5); EYE 3.5 ± 0.5 (2.5–4.5); IOD 3.9 ± 0.4 (3.2–4.8); TMP 3.3 ± 0.3 (2.8–4.0); TEY 1.2 ± 0.3 (0.8–1.8); HND 11.8 ± 1.4 (9.0–15.6); FGR 9.6 ± 0.8 (7.9–12.0); FPL 1.8 ± 0.3 (1.16–2.3); FPW 1.6 ± 0.2 (1.4–2.0); TIB 26.0 ± 1.5 (22.8–28.4); FTL 27.1 ± 7.7 (17.5–40.9); TPL 1.7 ± 0.2 (1.3–2.0); TPW 1.3 ± 0.1 (1.1–1.7).

ETYMOLOGY: The specific name honors David Joseph Morafka, Research Associate of the Royal Ontario Museum and California Academy of Sciences, in recognition of his unfailing friendship, his unselfish development and perpetuation of multiple, independent research programs, and for his catapulting the careers of many conservation biologists.

DISTRIBUTION AND ECOLOGY: *Rana morafkai* is known only from the Tay Nguyen Plateau of the Central Highlands, Gia Lai Province, Vietnam. It inhabits forested montane river systems. Specimens may be found on or near rapids or waterfalls. In at least May and June, male specimens may have distended gular pouches, indicating that this species breeds in spring.

REMARKS: This species has been previously referred to as *R. livida* by Inger and Chanard (1997) and Inger et al. (1999).

Rana banaorum, new species

(Previously referred to as species 6, ''Southern Big Eye'')

Figures 12M, N, 13F, 14E, F

HOLOTYPE: (ROM field no. 7145) ROM 39944, an adult female from Tram Lap, An Khe District, Gia Lai Province, Vietnam (14°26′39″N, 108°32′97″E), elevation ca. 900

TABLE 15

Variation in Body Proportions for *Rana chloronota* sensu stricto and Vietnamese Species of the *Rana chloronota* Complex Given as Means (in mm) ± 1 SD and ranges

See Materials and Methods for abbreviations.

N	SVL	HDL:HDW	TIB:SVL	IOD:HDL	TMP:EYE	EYE:HDL	SNT:HDL
R. bacboensis Male							
1	54.90	1.54	0.59	0.21	0.66	0.23	0.31
R. bacboensis Female							
6	95.8 ± 6.4	1.31 ± 0.02	0.62 ± 0.02	0.55 ± 0.06	0.43 ± 0.03	0.33 ± 0.03	0.40 ± 0.03
	(81.8–105.1)	(1.27–1.40)	(0.59–0.66)	(0.40–0.63)	(0.36–0.47)	(0.30–0.40)	(0.38–0.55)
R. banaorum Male							
14	50.2 ± 3.7	1.50 ± 0.06	0.61 ± 0.08	0.16 ± 0.01	0.89 ± 0.18	0.15 ± 0.02	0.30 ± 0.03
	(42.5–54.6)	(1.45–1.66)	(0.46–0.80)	(0.14–0.17)	(0.45–1.12)	(0.13–0.18)	(0.12–0.31)
R. banaorum Female							
8	92.7 ± 5.6	1.36 ± 0.17	0.63 ± 0.03	0.19 ± 0.02	0.75 ± 0.08	0.14 ± 0.01	0.33 ± 0.01
	(83.4–98.7)	(1.00–1.44)	(0.59–0.67)	(0.18–0.21)	(0.63–0.87)	(0.12–0.14)	(0.33–0.34)
R. daorum Male							
16	35.5 ± 1.5	1.50 ± 0.05	0.64 ± 0.04	0.18 ± 0.01	0.29 ± 0.06	0.23 ± 0.02	0.24 ± 0.01
	(32.0–38.1)	(1.30–1.66)	(0.52–0.68)	(0.17–0.20)	(0.19–0.38)	(0.20–0.25)	(0.23–0.24)
R. daorum Female							
8	55.0 ± 1.2	1.40 ± 0.10	0.62 ± 0.01	0.17 ± 0.03	0.45 ± 0.02	0.11 ± 0.01	0.30 ± 0.03
	(53.3–57.6)	(0.80–1.12)	(0.62–0.63)	(0.14–0.21)	(0.43–0.47)	(0.11–0.12)	(0.26–0.30)
R. hmongorum Male							
12	59.4 ± 3.8	1.20 ± 0.13	0.65 ± 0.06	0.22 ± 0.04	0.43 ± 0.40	0.31 ± 0.04	0.40 ± 0.06
	(54.7–65.25)	(1.09–1.45)	(0.57–0.82)	(0.15–0.28)	(0.33–0.49)	(0.24–0.35)	(0.30–0.45)
R. hmongorum Female							
9	80.2 ± 4.3	1.30 ± 0.07	0.59 ± 0.02	0.18 ± 0.01	0.31 ± 0.04	0.24 ± 0.01	0.28 ± 0.01
	(74.3–86.8)	(1.27–1.39)	(0.57–0.62)	(0.17–0.18)	(0.26–0.36)	(0.20–0.25)	(0.27–0.28)
R. morafkai Male							
14	43.2 ± 1.7	1.54 ± 0.07	0.60 ± 0.03	0.18 ± 0.03	0.96 ± 0.13	0.18 ± 0.02	0.32 ± 0.02
	(39.2–45.9)	(1.35–1.77)	(0.54–0.65)	(0.15–0.23)	(0.78–1.27)	(0.17–0.21)	(0.30–0.37)
R. morafkai Female							
4	87.6 ± 6.9	1.44 ± 0.08	0.61 ± 0.02	0.20 ± 0.01	0.71 ± 0.20	0.15 ± 0.02	0.34 ± 0.02
	(80.4–99.6)	(1.36–1.51)	(0.59–0.63)	(0.16–0.21)	(0.53–1.07)	(0.13–0.18)	(0.28–0.36)
R. chloronota Male							
57	46.2 ± 2.7	1.44 ± 0.09	0.64 ±0.03	0.20 ± 0.08	0.57 ± 0.13	0.28 ± 0.07	0.31 ± 0.11
	(41.5–53.5)	(1.05–1.65)	(0.59–0.71)	(0.10–0.44)	(0.48–0.85)	(0.20–0.40)	(0.26–0.59)
R. chloronota Female							
95	92.3 ± 7.0	1.32 ± 0.08	0.64 ± 0.10	0.20 ± 0.05	0.48 ± 0.15	0.24 ± 0.06	0.39 ± 0.03
	(78.3–101.7)	(1.14–1.53)	(0.51–0.71)	(0.14–0.45)	(0.37–0.99)	(0.12–0.29)	(0.20–0.44)
R. megatympanum Male							
4	52.3 ± 3.4	1.42 ± 0.04	0.63 ± 0.04	0.20 ± 0.01	1.20 ± 0.30	0.15 ± 0.02	0.31 ± 0.02
	(48.6–55.2)	(1.37–1.46)	(0.59–0.67)	(0.18–0.21)	(0.96–1.54)	(0.12–0.17)	(0.31–0.36)
R. megatympanum Female							
10	100.7 ± 4.2	1.28 ± 0.07	0.63 ± 0.03	0.19 ± 0.02	0.51 ± 0.05	0.23 ± 0.01	0.33 ± 0.01
	(93.6–105.3)	(1.21–1.35)	(0.57–0.69)	(0.16–0.21)	(0.44–0.58)	(0.22–0.25)	(0.33–0.35)

m, collected on 15 June 1996 by R.H. Bain, A. Lathrop, R.W. Murphy, and N.L. Orlov. The holotype had leg and liver tissue removed shortly after it was euthanised.

PARATYPES: Four males (ROM 39912–39913, 39915–39916) and eight females (ROM 39899–39901, 39928, 39929, 39931, 39936, and 39941) collected with holotype between 15 and 29 June 1996 by R.H. Bain, A. Lathrop, R.W. Murphy, and N.L. Orlov. ROM 39716–39720, 39920–39922, and 39924–39926 (males); 39942 (subadult) from the Cha River, Buon Loi, An Khe District, Gia Lai Province, Vietnam (elevation ca. 900 m), collected on 27 June 1996 by R.H. Bain and N.L. Orlov. ROM 39700, and 39702–39705 males from Krong Pa, An Khe District, Gia Lai Province, Vietnam (14°20′29″ N, 108°28′46″E, elevation 850 m), collected on 13–25 August 1997 by C.T. Ho, A. Lathrop, L.A. Lowcock, R.W. Murphy, and N.L. Orlov. ROM 25084–25086, 25100, 25102, and 25103 (males) collected from Buon Loi, An Khe District, Gia Lai Province, Vietnam (elevation ca. 700–750 m), 5 November 1993 by I.S. Darevsky and N.L. Orlov.

DIAGNOSIS: *Rana banaorum*, a member of the subgenus *Odorrana* (sensu Fei et al., 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL means of males 50 mm (42–55 mm), females 93 mm (83–99 mm); (3) vomerine teeth in rows oblique to choanae; (4) white lip-stripe extending across upper lip, terminating in glandule above insertion of arm; (5) head broad, bluntly rounded in profile; (6) tympanum round, distinct, very large, TMP:EYE in males (0.89) greater than females (0.75); (7) supratympanic fold weak; (8) dorsal skin shagreened, becoming granular laterally, with slight dorsolateral folds; (9) dorsum usually brown with yellow and black spots, sometimes green with black spots; legs brown, lightly banded; (10) median callous pad on fingers II, and III to proximal tubercle; (11) disks on fingers and toes greatly enlarged (>2× base of phalanges); (12) feet fully webbed to disks, except medial side of IV, where it reaches disk as a fringe, lateral fringes on I and V to terminal phalanges, webbing brown; (13) subarticular tubercles and inner metatarsal tubercle distinct, conical; (14) terminal phalanges T-shaped; (15) xiphisternum large, deeply notched posteriorly; (16) males with nuptial pads, paired gular pouches, pectoral spines absent; (17) eggs white.

COMPARISONS: Among Asian cascade ranids, *R. banaorum* is most similar to sympatric *R. morafkai* and particularly *R. chloronota* but it can be anatomically distinguished from both by its dorsolateral folds (table 12). *Rana banaorum* can further be distinguished from *R. morafkai* by its larger males (SVL 42–55 mm, versus 39–45 mm). Some *Rana banaorum* males have indistinct, microscopic spinules on the dorsal surface of the leg extending to the feet, forming a ''saw-tooth'' formation along the lateral edge of toe V, which is present only to a slight degree or absent in *R. chloronota*. Its broad, rounded snout differs from the obtusely pointed snouts of *H. nasica*, *R. andersonii*, *R. chalconota*, and *R. schmackeri* and from the depressed snouts of *R. graminea* and *R. margaretae*. A white lip-stripe differentiates *R. banaorum* from *R. andersonii*, *R. bacboensis*, *R. grahami*, *R. hainanensis*, *R. hmongorum*, *R. jingdongensis*, *R. junlianensis*, *R. margaretae*, *R. sinica*, *R. schmackeri*, and *R. tiannensis*. The gular pouches of *R. banaorum* distinguish it from *R. andersonii*, *R. chalconota*, *R. grahami*, *R. hainanensis*, *R. hmongorum*, *R. hosii*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, and *R. margaretae*. The dorsolateral folds of *R. banaorum* distinguish it from *H. nasica*, *R. andersonii*, *R. bacboensis*, *R. chloronota*, *R. hainanensis*, *R. hejiangensis*, *R. jingdongensis*, *R. junlianensis*, *R. kwangwuensis*, *R. morafkai*, *R. livida*, *R. schmackeri*, *R. sinica*, and *R. tiannensis*; the dorsolateral folds of *R. daorum* are composed of distinct white granules, and dorsolateral pustules sometimes form folds on *R. grahami* and *R. hmongorum*. The absence of an outer metatarsal tubercle immediately differentiates *R. banaorum* from *R. archotaphus* and *R. chalconota*. The presence of white eggs differentiates *R. banaorum* from *R. bacboensis* (black eggs), *Huia nasica*, *R. andersonii*, *R. chalconota*, *R. grahami*, *R. junlianensis*, *R. margaretae* and *R. schmackeri* (white eggs with a dark melanic pole). The absence of spinules on the venter distinguishes *R. banaorum* from *R. ander-*

sonii, *R. grahami*, *R. jingdongensis*, *R. junlianensis*, *R. margaretae*, and *R. schmackeri*. *Rana banaorum* further differs from *Huia nasica* by its larger females (83–99 mm vs. 67 mm in *H. nasica*). It is further differentiated from *R. sinica* by its uncovered, distinct tympanum (indistinct, covered by skin in *R. sinica*), large disks (small in *R. sinica*) and its relative finger lengths (I < II < IV for *R. sinica*, II < I < IV for *R. banaorum*) and T-shaped distal phalanges (rounded in *R. sinica*). *Rana leporipes* further differs from *R. banaorum* with its white supratympanic fold (not colored in *R. banaorum*), webbing to distal phalanges (webbing to disks in *R. banaorum*), and T-shaped distal phalanges (oblong, somewhat rounded in *R. leporipes*).

DESCRIPTION OF HOLOTYPE: ROM 39944, an adult female, head width 78% head length, length 46% SVL; snout short, acutely rounded in dorsal view, bluntly rounded in profile, protruding beyond margin of lower jaw; eye large, prominent, 50% snout length; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold curving posteroventrally from posterior corner of eye to a level above the insertion of arm; tympanum very large, round, distinctly visible, separated from eye by distance equal to TMP, 80% of eye length. Choanae ovoid; vomerine dentigerous processes prominent, oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately two-thirds its length.

Forearms moderately robust; fingers moderately short, slender, hands 23% SVL, relative finger lengths II < I < IV < III, ventromedial callous pad on fingers II and III to proximal tubercle, disks greatly expanded (>2× base of phalanges), relative pad size II < I < IV < III, pad length (III) 94% of pad width, ventral circummarginal grooves present; terminal phalanges T-shaped; subarticular tubercles conical. Hindlimbs moderately robust; tibia length 65% SVL; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet very large, 82% of SVL, fully webbed to terminal phalanges except the inner side of IV where the webbing reaches the disk as a fringe; lateral fringe on toes I and V to terminal phalanges; toes long, slender, with large, rounded triangular disks; relative pad size I = II = III > IV > V, pad length (IV) equals pad width; each pad with ventral circummarginal grooves; subarticular tubercles prominent and conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum large, deeply notched posteriorly.

Skin on dorsum shagreened, with small pustules on flanks; dorsolateral folds weak; small tubercles posteroventral to tympanum; prominent granules on flanks and around cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

COLOR IN LIFE (in preservative): Dark brown (olive-brown, beige), flanks gray with yellow spots (white spots); lip-stripe brown anteriorly and creamy white from level of the eye posteriorly (white); loreal dark brown (black); tympanum beige with dark brown central ring; iris golden brown; dorsal limbs grayish brown with black banding; cloacal region dark brown (black); webbing marbled white on dark brown (uniformly brown); venter creamy white, ventral surfaces of limbs creamy yellow with black mottling.

SECONDARY SEXUAL CHARACTERS: The holotype is a gravid female with immaculate white eggs (2 mm in diameter). Gravid females have an SVL nearly twice that of males (mean SVL female, 93 mm; male 50 mm). Male TMP:EYE (0.89) is larger than females (0.75). Males have velvety nuptial pads on the thumb and paired gular pouches located at the angle of jaw. Pectoral spines are absent.

MEASUREMENTS OF HOLOTYPE (in mm): SVL 98.0; SNT 13.5; HDL 45.4; HDW 35.6; EYE 6.8; IOD 7.4; TMP 5.4; TEY 4.7; HND 22.7; FGR 19.4; FPL 3.1; FPW 3.3; TIB 63.7; FTL 80.0; TPL 3.4; TPW 3.4.

VARIATION OF PARATYPES: The skin on the dorsum varies from smooth to shagreened with small pustules on flanks. The lip-stripe varies from creamy yellow (white in alcohol) throughout its length to brown anteriorly and creamy white from the level of the eye posteriorly. The dorsal skin is variable from light green to dark brown (olive, brown, beige, or livid blue in alcohol) with or without large

black spots. Variation in all type material is given in table 15.

MEASUREMENTS OF FEMALE PARATYPES (in mm, n = 8, ROM 39899–39901, 39928, 39929, 39931, 39936, and 39941): SVL 92.7 ± 5.6 (83.4–98.7); SNT 13.8 ± 1.6 (12.4–16.8); HDL 43.8 ± 3.2 (37.5–48.8); HDW 30.6 ± 1.5 (26.7–33.4); EYE 6.1 ± 0.7 (4.7–6.9); IOD 8.2 ± 0.9 (6.8–10.1); TMP 4.5 ± 0.6 (3.5–5.6); TEY 4.5 ± 0.6 (3.5–5.2); HND 22.3 ± 2.8 (17.5–25.0); FGR 18.2 ± 2.8 (12.9–20.8); FPL 3.4 ± 0.4 (2.8–4.3); FPW 3.1 ± 0.2 (2.8–3.5); TIB 58.1 ± 3.2 (52.7–63.7); FTL 68.0 ± 7.0 (58.3–78.0) TPL 3.4 ± 0.6 (2.3–4.3); TPW 2.8 ± 0.4 (2.4–3.4).

MEASUREMENTS OF MALE PARATYPES (in mm, n = 14, ROM 25084–25086, 25100, 25102, 25103, 39912, 39913, 39915, 39916, 39920–39922, 39924): SVL 50.5 ± 3.7 (42.5–54.6); SNT 7.4 ± 1.5 (3.1–8.7); HDL 26.1 ± 1.4 (24.6–28.1); HDW 17.4 ± 0.6 (17.8–18.3); EYE 4.0 ± 0.5 (3.1–5.1); IOD 3.8 ± 0.4 (3.4–4.7); TMP 3.5 ± 0.6 (2.0–4.7); TEY 1.7 ± 0.6 (0.9–3.6); HND 14.0 ± 1.2 (11.8–16.0); FGR 11.1 ± 1.1 (9.2–12.7); FPL 1.9 ± 0.3 (1.4–2.6); FPW 1.6 ± 0.2 (1.4–2.0); TIB 30.6 ± 4.6 (24.1–43.6); FTL 32.6 ± 6.8 (23.3–42.7); TPL 1.9 ± 0.4 (1.3–2.4); TPW 1.5 ± 0.3 (1.1–2.1).

ETYMOLOGY: The specific name is a patronym for the Ba Na people, an ethnic group living on the Tay Nguyen Plateau (Central Highlands) of south-central Vietnam where this species occurs.

DISTRIBUTION AND ECOLOGY: *Rana banaorum* is known only from the Tay Nguyen Plateau of the Central Highlands, Gia Lai Province, Vietnam. It inhabits forested montane river systems on or near rapids or waterfalls of primary and disturbed second growth. In May and June males have tight, leathery gular pouches, suggesting that they are not calling and that the breeding season occurs during some other time.

REMARKS: Inger and Chanard (1997) and Inger et al. (1999) noted that specimens of *Rana chloronota* (as *R. livida*) from An Khe have more pronounced dorsolateral folds than elsewhere in Vietnam. These frogs do not fit Bourret's (1942) interpretation of *R. graminea* as a ''northern variety'' of *R. chloronota*. These differences likely reflect the occurrence of three sympatric species of the *R. chloronota* complex from this region. Some male *R. banaorum* have indistinct, microscopic spinules on the dorsal surface of the leg extending to the feet, forming a ''saw-tooth'' formation along the lateral edge of toe (seen in FMNH specimens that are not part of the type series).

Rana megatympanum, new species

(Previously referred to as species 7, ''Large'')

Figures 12O, P, 13G, 14G, H

HOLOTYPE: (ROM field no. 12999) ROM 39684, a gravid adult female from Khe Moi River, approximately 24 km west of Con Cuong village (by road), Con Cuong District, Nghe An Province, Vietnam (18°56′30″N, 104°48′35″E) found between 24 and 29 October 1994 by I.S. Darevsky, L.A. Lowcock, R.W. Murphy, and N.L. Orlov. The holotype had leg and liver tissue removed shortly after it was euthanised.

PARATYPES: Eight females (ROM 39263, 39685–39691) collected with holotype between 24 and 29 October 1994 by I.S. Darevsky, L.A. Lowcock, R.W. Murphy, and N.L. Orlov. Four males (ROM 39237–39240) from Na Hang Nature Reserve, Tuyen Quang Province, Vietnam (22°21′54″N, 105°25′40″E) found along waterfalls between 26 and 27 May 1996 by A. Lathrop and R.W. Murphy between 193 and 0200 hours. ROM 26398–26400 Con Cuong District, Nghe An Province, Vietnam (18°56′30″N, 104°48′35″E), collected 5 June 1995 by B. Hubley, A. Lathrop, R.W. Murphy, and N.L. Orlov.

DIAGNOSIS: *Rana megatympanum*, a member of the subgenus *Odorrana* (sensu Fei et al., 1990), is characterized by a combination of the following attributes: (1) body dorsoventrally compressed; (2) SVL means of males 52 mm (48–55 mm), females 100 mm (93–105 mm); (3) vomerine teeth in rows oblique to choanae; (4) yellow lip-stripe present in males, absent or indistinct in females; (5) head broad, bluntly rounded in profile; (6) tympanum round, distinct, TMP:EYE in males enormous (1.20), greater than in females (0.51); (7) supratympanic fold weak; (8) dorsal skin shagreened, dorsolateral folds present only in males; (9) dorsum olive to

brown sometimes with black spots; flanks marbled yellow and brown-gray; forelimbs and hindlimbs barred; (10) ventromedial callous pad on fingers II, III, and IV to proximal tubercle, fringes on fingers II, III, and IV; (11) disks on fingers and toes greatly enlarged (>2× base of phalanges); (12) feet fully webbed to toe disk, lateral fringes on I and V to terminal phalanges, webbing brown; (13) subarticular tubercles and an internal metatarsal tubercle distinct, conical; (14) terminal phalanges T-shaped; (15) xiphisternum large, deeply notched posteriorly; (16) males with nuptial pads, paired gular pouches, pectoral spines absent; (17) eggs white.

COMPARISONS: *Rana megatympanum* superficially resembles other Asian cascade ranids, including *Huia nasica*, *Rana andersonii, R. archotaphus, R. bacboensis, R. banaorum, R. chalconota, R. chloronota, R. daorum, R. grahami, R. graminea, R. hainanensis, R. hejiangensis, R. hmongorum, R. hosii, R. morafkai, R. jingdongensis, R. junlianensis, R. kwangwuensis, R. leporipes, R. livida, R. margaretae, R. schmackeri, R. sinica*, and *R. tiannensis* (table 12). It can be differentiated from all other *Odorrana* by the enormous sexual dimorphism in tympanum size (TMP:EYE 1.20 in males, 0.51 in females). Male *R. megatympanum* have a yellow lip-stripe and females have an indistinct or absent yellow lip-stripe, differentiating it from *H. nasica*, *R. archotaphus, R. banaorum, R. chalconota, R. chloronota, R. daorum, R. graminea, R. hejiangensis, R. hosii, R. morafkai, R. leporipes*, and *R. livida* (all with white lip-stripes); *R. andersonii, R. bacboensis, R. hainanensis, R. jingdongensis, R. margaretae*, and *R. tiannensis* have vertical lip-bars; *R. junlianensis* has a yellow lip-stripe with brown lip-bars; *R. schmackeri* has no lip-stripe or vertical lip-bars. The broad, rounded snout differentiates *R. megatympanum* from *H. nasica, R. andersonii, R. chalconota*, and *R. schmackeri* (obtusely pointed) and from *R. graminea* and *R. margaretae* (depressed). Its gular pouches distinguish *R. megatympanum* from *R. andersonii, R. chalconota, R. grahami, R. hainanensis, R. hmongorum, R. hosii, R. jingdongensis, R. junlianensis, R. kwangwuensis*, and *R. margaretae*. Dorsolateral folds immediately differentiate male *R. megatympanum* from *R. andersonii, R. bacboensis, R. chloronota, R. hainanensis, R. hejiangensis, R. morafkai, R. jingdongensis, R. junlianensis, R. kwangwuensis, R. livida, R. schmackeri, R. sinica*, and *R. tiannensis*. The dorsolateral fold of male *R. megatympanum* differs from that of *R. daorum*, which is composed of minute white granules, *R. hmongorum* and *R. grahami*, whose dorsolateral pustules sometimes form a dorsolateral fold, and *R. banaorum* and *R. chalconota*, which have folds that are distinct and continuous, extending to the groin. The olive brown coloration with black spots of *R. megatympanum* differentiates it from *H. nasica* (olive-brown dorsum, lighter brown laterally) and from *R. archotaphus, R. chalconota, R. chloronota, R. daorum, R. graminea, R. hejiangensis, R. hmongorum, R. hosii, R. jingdongensis, R. junlianensis, R. kwangwuensis, R. leporipes, R. margaretae, R. schmackeri, R. sinica* (all with green). *Rana megatympanum* lacks an external metatarsal tubercle present in *R. archotaphus* and *R. chalconota*. Absence of ventral spines in male *R. megatympanum* separates them from *R. andersonii, R. grahami, R. jingdongensis, R. junlianensis, R. margaretae*, and *R. schmackeri*. The presence of white eggs differentiates *R. megatympanum* from *H. nasica, R. andersonii, R. chalconota, R. grahami, R. junlianensis, R. margaretae, R. schmackeri* (white eggs with melanic poles), and *R. bacboensis* (eggs completely melanic). *Rana megatympanum* differs from *R. sinica* by its distinct, uncovered tympanum (indistinct and covered with a layer of skin in *R. sinica*), its disk size (small in *R. sinica*), its relative finger lengths (I < II < IV for *R. sinica*, II < I < IV for *R. megatympanum*), and its T-shaped distal phalanges (rounded in *R. sinica*). *Rana megatympanum* can be distinguished from *R. leporipes* by its webbing (only to the basal end of the distal phalanx in *R. leporipes*, to the disk in *R. megatympanum*), supratympanic fold (colored white in *R. leporipes*), and its T-shaped distal phalanges (oblong, somewhat rounded in *R. leopripes*). *Rana megatypmanum* also differs from *R. hejiangensis* by its finger formula (II < I < III < IV for *R. hejiangensis*), and by its large disks (small for *R. hejiangensis*). *Rana megatympanum* closely resembles *R.*

andersonii, *R. hainanensis*, *R. jingdongensis*, and *R. tiannensis*. In addition, *R. megatympanum* differs from *R. andersonii* in that its males are smaller (53–78 mm for males of *R. andersonii*), and its finger and toe-disks are relatively larger. *Rana megatympanum* differs from *R. hainanensis* in its smaller SVL (*R. hainanensis* males 49–62 mm, females 75–122 mm, *R. megatympanum* males 48–55 mm, females 93–105 mm) and its relative finger lengths (II < IV < I < III for *R. hainanensis*, II < I < IV < III for *R. megatympanum*). *Rana megatympanum* further differs from *R. jingdongensis* by its smaller males (*R. jingdongensis* SVL 62–81 mm) and skin (*R. jingdongensis* dorsum scattered with tubercles and large warts, lips and sides of heads with white spines, all absent in *R. megatympanum*). *Rana megatympanum* most closely resembles *R. tiannensis*, another large brown cascade ranid, but differs from it by having shagreened dorsal skin with small lateral granulations (dorsum of *R. tiannensis* is rough with large, prominent lateral granulations), and toe disks are smaller than those on fingers (the opposite condition of *R. tiannensis*).

DESCRIPTION OF HOLOTYPE: ROM 39684, a gravid female, head width 77% of head length, length 50% of SVL; snout short, acutely rounded in dorsal view, bluntly rounded in profile, protruding beyond margin of lower jaw; eye very large, prominent, 73% of snout length; eyelid broader than interorbital distance. Top of head flat; canthus rostralis rounded; loreal region concave; lip flared just anterior to orbit; nostril about three-fourths distance from eye to tip of snout; supratympanic fold curving posteroventrally from posterior corner of eye to a level above the insertion of arm; tympanum round, distinctly visible, separated from eye by distance equal to TMP, 52% of EYE. Choanae ovoid; vomerine dentigerous processes prominent, oblique, posteromedial to choanae, each bearing numerous teeth. Tongue cordiform, distinctly notched posteriorly, free for approximately two-thirds its length.

Forearms moderately robust; fingers moderately short, slender, hands 27% of SVL, relative lengths of fingers II < I < IV < III, lateral fringes on finger II, III, and IV, with median callous pads to proximal tubercle; disks greatly expanded (>2× base of phalanges), relative pad size II < I < IV < III, pad width (III) 87% of pad length, ventral circummarginal grooves present; terminal phalanges T-shaped; subarticular tubercles conical. Hindlimbs moderately robust; tibia length 69% of SVL; foot length 53% of SVL; relative toe lengths I < II < III < V < IV; inner tarsal fold absent; feet fully webbed to base of toe pads, lateral fringes on I and V to terminal phalanges; toes long, slender, with large, rounded triangular disks, relative pad size I = II = III > IV ≫ V, pad width (IV) 75% of pad length, each with ventral circummarginal grooves; subarticular tubercles prominent and conical; inner metatarsal tubercle ovoid, long; outer metatarsal tubercle absent.

Xiphisternum large, deeply notched posteriorly.

Skin on dorsum shagreened, becoming increasingly granular laterally; dorsolateral folds absent; small tubercles posteroventral to tympanum; prominent granules on flanks and around cloaca; cloacal opening unmodified, directed posteriorly, at upper level of thighs.

COLOR IN LIFE (in preservative): Dorsum olive-brown, flanks yellow and brown-gray (gray to olive); lip-stripe absent (tympanum beige with dark brown center ring); loreal brown (black); iris gold; top one-third red, dorsal limbs brown with black banding (brown); posterior surface of thighs brown with black marbling (cloacal region black, thighs gray with white mottling); webbing marbled white on dark brown (brown on white); venter creamy white (creamy yellow with black mottling).

SECONDARY SEXUAL CHARACTERS: The eggs of the holotype are creamy white and 2 mm in diameter. Adult females have SVL approximately twice that of males. Males have a yellow lip-stripe, and females either lack one or have an indistinctly yellow lip. Males also possess a weak dorsolateral fold, whereas females do not. Males have a larger tympanum than females, velvety nuptial pads extending across the thumb, paired gular pouches located at the angle of the jaw, and no pectoral spines.

MEASUREMENTS OF HOLOTYPE (in mm): SVL 93.6; SNT 15.0; HDL 46.5; HDW 35.7;

EYE 10.8; IOD 6.8; TMP 5.6; TEY 4.1; HND 25.7; FGR 19.6; FPL 3.0; FPW 2.6; TIB 65.0; FTL 49.7; TPL 3.2; TPW 2.4.

VARIATION OF PARATYPES: Variation in all type material is given in table 15.

MEASUREMENTS OF FEMALE PARATYPES (in mm, n = 10, ROM 26398–26400, 39685–39691): SVL 100.3 ± 4.2 (93.6–105.3); SNT 14.8 ± 0.8 (13.8–16.5); HDL 45.1 ± 3.3 (41.3–47.6); HDW 35.2 ± 0.7 (34.1–35.7); EYE 10.2 ± 0.7 (9.3–11.6); IOD 8.8 ± 1.0 (6.8–10.0); TMP 5.3 ± 0.4 (4.6–5.9); TEY 4.7 ± 0.3 (4.1–5.0); HND 25.2 ± 2.5 (20.6–29.7); FGR 21.0 ± 1.0 (19.6–22.6); FPL 3.5 ± 0.6 (2.8–4.4); FPW 3.0 ± 0.5 (2.5–3.8); TIB 63.0 ± 3.3 (55.8–67.7); FTL 72.0 ± 12.1 (49.7–88.0) TPL 3.4 ± 1.0 (1.9–5.2); TPW 2.8 ± 0.4 (2.2–3.4).

MEASUREMENTS OF MALE PARATYPES (in mm, n = 4, ROM 39237–39240): SVL 52.3 ± 3.4 (48.6–55.2); SNT 8.7 ± 0.8 (8.3–9.6); HDL 28.0 ± 1.4 (24.6–27.1); HDW 18.5 ± 0.8 (18.0–19.1); EYE 4.1 ± 0.9 (3.17–4.6); IOD 5.0 ± 0.5 (4.7–5.6); TMP 4.7 ± 0.3 (4.3–5.1); TEY 1.7 ± 0.3 (1.5–2.0); HND 15.2 ± 0.4 (14.8–15.5); FGR 12.5 ± 0.4 (12.2–13.0); FPL 2.0 ± 0.5 (1.6–2.5); FPW 1.9 ± 0.4 (1.4–2.3); TIB 32.7 ± 0.4 (32.3–33.1); FTL 38.3 ± 7.3 (29.9–42.8) TPL 1.8 ± 0.6 (1.3–2.5); TPW 1.6 ± 0.1 (1.5–1.6).

ETYMOLOGY: The specific name is a noun in opposition, derived from the Latin prefix ''mega'' (meaning very large) and ''tympanum'', in reference to the relatively large tympanum of this species.

DISTRIBUTION AND ECOLOGY: *Rana megatympanum* is known from northern and north-central Vietnam. It occurs in montane rivers that vary from shallow and slow moving to torrential and deep. It may be found on boulders and logs, both in and around the water as well as in the adjacent forest. Radiographs revealed that large invertebrates (both insects and crustaceans) form part of the diet. Vocalizations and tadpoles are unknown.

REMARKS: The dorsolateral fold and very large tympanum of male *R. megatympanum* potentially make it Bourret's (1942) ''northern form'' of *R. chloronota* (= *R. graminea*). However, *R. graminea* is bright green above (Boulenger, 1899) in contrast to the olive-brown dorsum of *R. megatympanum*.

KEY TO VIETNAMESE SPECIES IN THE *RANA CHLORONOTA* COMPLEX

The *Rana chloronota* complex in Vietnam includes species that are dorsoventrally compressed with long legs. Snout–vent length of females is approximately twice that of males (table 14). The dorsum may be green, brown, or a combination thereof; dorsum usually smooth, sometimes shagreened, often becoming more rugose laterally. Tympanum is distinct. Venter is entirely smooth. Legs with transverse bands or mottled with indistinct bands, posterior surface of thighs marbled yellow and black. An outer metatarsal tubercle is absent. Disks on fingers and toes well dilated, with ventral circummarginal grooves. Webbing is complete or nearly so, extending to most distal tubercle or to base of toe pad (as a fringe in some species). Males have velvety nuptial pads.

VARIABLE CHARACTERS: Lip-stripe is present in most species and is usually white. Vomerine teeth, if present, are in rows oblique to the internal choanae. Males usually have paired gular pouches. Eggs completely pigmented or unpigmented.

HABITAT: Ubiquitous throughout highland waterways of Southeast Asia. Found in and around water, including the forest floor and canopy of surrounding forests. Commonly found perched on rocks beside or among the cascades.

1. Dorsolateral fold distinct, composed of small gold (white in preservative) granules; noticeably smaller than other cascade ranids (males 35 mm, females 55 mm), large white lateral spot, and vomerine teeth absent . . . . . *R. daorum*
– Dorsolateral fold not as above or granules absent 2
2. Indistinct glandular dorsolateral folds present 3
– Dorsolateral folds absent 4
3A. Lip-stripe indistinct yellow or absent in females, yellow in males; male tympanum 120% of eye length, 51% for females; skin completely shagreened, brown, and snout–vent length notably large (males 52 mm, females 100 mm) . . . *R. megatympanum*
3B. White lip-stripe present in both males and females; dorsum green to olive, shagreened or incompletely smooth, flank gray; male tympanum 89% eye, females 75%; SVL males 50 mm, females 93 mm . . . . . *R. banaorum*

3C. Dorsum bright green with or without black spots, completely smooth; flank brownish; male tympanum 77% eye, females 56%; SVL males 46 mm, females 94 mm . . . . . *R. graminea*

4. Dorsum completely smooth; dorsum bright green, vomerine teeth present, white lip-stripe present, eggs immaculate, and SVL females 93 mm, males 46 mm . . . . . *R. chloronota*

– Dorsum in part smooth and shagreened, or with heavy granulations 5

5. Dorsum with heavy granulations; skin heavily granulated laterally and on pelvis, dorsum bright green with black spots, males without gular pouches, SVL females 80 mm, males 60 mm . . . . . *R. hmongorum*

– Dorsum shagreened or in part smooth . . . 6

6. Black vertical bar on lip; dorsum shagreened, brown with some black spots, lip bands black, extend vertically across mandible, (white lip-stripe absent), webbing marbled white on dark brown to toes, eggs pigmented black, SVL 95 females, 55 mm males) . . . . . *R. bacboensis*

– No black vertical bar on lip; dorsum shagreened or incompletely smooth, color variable green to brown in daylight, changing to brown at night, white lip-stripe present, webbing brown, eggs immaculate white, SVL females 88 mm, males 43 mm . . . . . *R. morafkai*

DISCUSSION

The discovery of a high degree of diversity in the *R. chloronota* complex in a small area is astonishing given that the species group has been studied for more than 145 years. The historical confusion regarding the identification of *Rana chloronota* is a result of several factors: the loss of type material, the disparate localities of sampling areas, and the presence of multiple cryptic species (both sympatric and allopatric). *Rana chloronota* inhabits a large portion of its historically recognized range, although the ranges of other species in the complex appear to be more restricted than *R. chloronota*. Interestingly, multiple species of the complex are usually found in sympatry in Vietnam (and presumably elsewhere). As many as three species can be found in the same stream on a given evening. One or two of the following four species from northern Vietnam occur sympatrically with *R. chloronota*: *R. bacboensis*, *R. hmongorum*, *R. daorum*, and *R. megatympanum*. Two species from the Central Highlands of Vietnam also occur sympatrically with *R. chloronota*: *R. banaorum* and *R. morafkai*.

The amphibian diversity in Southeast Asia is underestimated. Given that three of the new species (*R. bacboensis*, *R. daorum*, and *R. hmongorum*) are distinct in their gross morphology and that many areas remain unsurveyed or poorly explored, we predict that the amphibian diversity in Indochina is grossly underestimated; since the review of Vietnamese amphibians by Inger et al. (1999), the number of recorded species has increased by more than 50% to 154 species, including those described herein (Orlov et al., 2002). Museum specimens have not always been studied with close attention to morphological detail. This raises the likelihood that previously undescribed species in the *R. chloronota* complex will be found, both in the wild and in current museum collections.

At every surveyed location in Vietnam at least two, and sometimes three, species of the *Rana chloronota* complex occur sympatrically. Fixed diagnostic characters differentiate these sympatric species. If these criteria are extended to allopatric populations across the vast range of *R. chloronota*, additional species are recognizable. This concordant approach would be beneficial to the elucidation of species within other problematic species complexes such as *Polypedates leucomystax* (e.g., Narins et al., 1998; Inger, 1999), *P. dugritei* (e.g. Orlov et al., 2001), *Limnonectes blythii* (e.g., Emerson, 1998), and *L. kuhlii* (e.g., Inger, 1999). Furthermore, the complexity of the alpha taxonomy is exacerbated by the absence of phylogenetic data of Southeast Asian ranids.

Implications for Conservation

The occurrence of multiple species in the *Rana chloronota* complex has important implications for conservation. Montane forests across Southeast Asia are increasingly threatened by human pressure (Wege et al., 1999). *Rana chloronota* was presumed to be relatively secure from threat when it was consid-

ered to be a single, widespread species. However, as a complex of species with unknown, but presumably smaller ranges, the complex may be much more susceptible to habitat degredation and pressures. Other similar species complexes are equally at risk and they require urgent study and international collaboration to ensure that they can be identified in a timely manner.

The *Rana chloronota* complex is potentially useful as a biomonitor of forest health. These frogs are harvested for food by some ethnic groups in Vietnam (and by Chinese farmers), but are avoided by other groups (Nguyen, 2000). Local people are aware of their toxic skin; in our experience, the Vietnamese do not prefer these frogs as food given a choice. In contrast, *R. chloronota* is referred to as ''green chicken'' in southeastern Yunnan Province, China. These frogs must be skinned, thoroughly cleaned, and sometimes decapitated before being consumed. Cognizant of conservation, Chinese farmers only eat ''adult'' frogs (females) and leave ''juveniles'' (males) to sustain the resource (Murphy and Orlov, personal obs.).

The skin secretions likely make *Odorrana* unpalatable and possibly even dangerous to other would-be predators. Snake stomach contents across Southeast Asia have not included *R. chloronota* and yet they have included other large ranids (Bourret, 1936; Pope, 1935). Consequently, if the *R. chloronota* complex experiences low hunting and harvesting pressure in an area where resource use by humans is otherwise intense, their population status could be a useful indicator of the health of the montane forest. That said, almost nothing is known about the natural history of the complex. Their breeding habits have not been reported. Their feeding habits are poorly known. The composition and source of their skin toxins is unknown. Even their distributions are uncertain.

ACKNOWLEDGMENTS

Collecting and export permits were made available through Vietnam's Institute of Ecology and Biological Resources, Hanoi, and the Forestry Protection Department, Ministry of Agriculture and Rural Development, Vietnam. Hong Kong specimens were acquired under permits to Michael M. Lau. Laotian specimens were acquired under permits to Bryan Stuart by the Ministry of Agriculture and Forestry, Vientiane. Agriculture Canada issued import permits for frozen tissues and preserved specimens deposited in the ROM, whereas the United States Fish and Wildlife Service issued permits for frozen tissues and preserved specimens deposited in the AMNH and FMNH. All collecting and euthanasia of specimens were performed under approved animal use protocols.

This study is based on work supported by the Natural Sciences and Engineering Research Council (NSERC) of Canada grant A3148 to R.W.M.; the National Science Foundation under grant no. 98–70232 to the Center for Biodiversity and Conservation at the American Museum of Natural History; the generous assistance of the ROM Sciences Fieldwork Fund, the ROM Future Fund, the ROM Foundation, the Department of ROM Volunteers, Department of Zoology of the University of Toronto, and Cathay Pacific Airlines to R.W.M.; a University of Toronto Open Masters Fellowship and American Museum of Natural History Collections Study Grant to R.H.B.; Deutsche Wissenschaftliche Gesellshaft Grant (Zoological Museum of Hamburg University) for N.L.O. Bryan Stuart's collections were made possible by support from the National Geographic Society grant no. 6247–98 to Harold Heatwole.

We thank Eleanor J. Sterling for her continued support of this project. We are grateful to Nguyen Van Sang, Pham Duc Tien, Khuat Dang Long, Nguyen Tien Hiep, and the late Cao Van Sung of the IEBR for their invaluable assistance with on-site arrangements. We are further indebted to Nguyen Quang Truong, Leslie A. Lowcock, Tom Mason, Rafael O. de Sá, and Brad Hubley for their valuable assistance in the field. Chen Liqiao provided access to unpublished data, and Ned Gilmore provided information regarding specimen holdings at the Academy of Natural Sciences, Philadelphia. For permission to study specimens under their care, we thank Harold K. Voris and Robert F. Inger (FMNH), Charles W. Myers and Darrel R. Frost (AMNH), Mark Wilkinson and Barry Clarke (BMNH), and Rainer Guenther (ZMB). We also thank the AMNH library

staff, particularly Mary DeJong and Amanda Bielskas. For invaluable assistance during museum visits, we thank Linda S. Ford and Margaret Arnold (AMNH), Alan Resetar and James B. Ladonski (FMNH), and Frank Tillack (ZMB). We thank Roman Khalikov for imaging assistance. We thank Bryan Stuart for granting us permission to study and include recent collections from Laos in our study.

Chunmei Huang, Xiao-Chun Wu, Ho-Ling Poon, and Jinzhong Fu provided translations of Chinese descriptions, and Nasreen Rahman and Johan Lindell did the same for German publications. For reading and commenting on the manuscript, we are grateful to Charles W. Myers, Robert F. Inger, Darrel R. Frost, Meredith J. Mahoney, Julian Faivovich, and Taran Grant. Each provided critical insights in their reviews and subsequent discussions. Ignoring or altering their advice was done so at our risk.

REFERENCES

Ahl, E. 1925 (1927). Ueber vernachlässigte Merkmale bei Fröschen. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin 1925(1–10): 40–47.

Anderson, J. 1871. On some Indian Reptiles. Proceedings of the Zoological Society of London 1871: 149–211.

Blyth, E. 1852. Proceeding of the Society for April. Journal of the Asiatic Society of Bengal 21: 351–356.

Blyth, E. 1856. Report for the October meeting, 1855. Journal of the Asiatic Society of Bengal 25(7): 711–723.

Boring, A.M. 1932. A list of Fukien Amphibia and Reptilia. First Annual Report of the Marine Biological Association of China: 99–124.

Boulenger, G.A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. London: Trustees of the British Museum, 495 pp.

Boulenger, G.A. 1887. An account of the reptiles and batrachians obtained in Tenasserim by M.L. Feae, of the Genoa Civic Museum. Annali dell Museo Civico di Storia Naturale di Genova, ser. 2, 4: 474–486, 3 pls.

Boulenger, G.A. 1890. The Fauna of British India, including Ceylon and Burma. Reptilia and Batrachia. London: Taylor and Francis, 541 pp., 142 figs.

Boulenger, G.A. 1899. On the reptiles, batrachians, and fishes collected by the late Mr. John Whitehead in the interior of Hainan. Proceedings of the Zoological Society of London 1899: 956–962, 4 pls.

Boulenger, G.A. 1918. Remarks on the batrachian genera *Cornufer*, Tschudi, *Platymantis*, Gthr., *Simonantis*, g.n., and *Staurois*, Cope. Annals and Magazine of Natural History, ser. 9(1): 372–375.

Boulenger, G.A. 1920. A monograph of the south Asian, Papuan, Melanesian, and Australasian frogs of the genus *Rana*. Records of the Indian Museum 20: 1–126.

Bourret, R. 1936. Les serpentes de l'Indochine. Toulouse: Henri Basuyau & Companie, 2 vols., 646 pp.

Bourret, R. 1942. Les batrachians de l'Indochine. Hanoi, Vietnam: Gouvernment General de L'Indochine, Hanoi, Vietnam, 547 pp.

Chanda, S.K., I. Das, and A. Dubois. 2000. Catalogue of amphibian types in the collection of the Zoological Survey of India. Hamadryad 25(2): 100–128.

Davis, J.I., and K.C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. Systematic Biology 41(4): 421–435.

Dubois, A. 1992. Notes sur la classification des Ranidae (Amphibiens: Anoures). Bulletin Mensuel de la Société Linnéenne de Lyon 61(10): 305–352.

Dubois, A., and A.M. Ohler. 2000. Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 1. Nomenclatural status and type-specimens of the nominal species *Rana limnocharis* Gravenhorst, 1829. Alytes 18(1–2): 15–50.

Duellman, W.E. 1993. Amphibian species of the World: additions and corrections. Lawrence, KS: Allen Press, 670 pp.

Duellman, W.E. and L. Trueb. 1986. Biology of the Amphibians. Baltimore, Md: Johns Hopkins Press, 114 pp.

Emerson, S.B. 1998. Male secondary sexual characteristics, sexual selection, and molecular divergence in fanged ranid frogs of Southeast Asia. Zoological Journal of the Linnean Society 122: 537–553.

Emerson, S.B., and D. Berrigan. 1993. Systematics of Southeast Asian ranids: multiple origins of voicelessness in the subgenus *Limnonectes* (Fitzinger). Herpetologica 49(1): 22–31.

Faith, D.P., and P.S. Cranston 1991. Could a cladogram this short have arisen by chance alone? On permutation tests for cladistic structure. Cladistics 7: 1–28.

Fei, L. 1999. Atlas of amphibians of China. Zhengzhou: Henan Publishing House of Science and Technology, 432 pp. [in Chinese]

Fei, L., C-y. Ye, and C. Li. 2001. Descriptions of two new species of the genus *Odorrana* in China (Anura: Ranidae). Acta Zootaxonomica Sinica 26(1): 108–114.

Fei, L., C.-y. Ye, and Y.-z. Huang. 1990. Keys to Chinese Amphibians. Chongqing: Chongqing Branch, Science and Technology Materials Press, 364 pp. [in Chinese]

Fellowes, J.R., and C.-h. Hau. 1997. A faunal survey of nine forest reserves in tropical south China, with a review of conservation priorities in the region. Hong Kong, China: Kadoorie Farm and Botanic Garden, 152 pp.

Frost, D.R. 1985. Amphibian species of the world: a taxonomic and geographic reference. Lawrence, KS: Association of Systematic Collections and Allen Press, 732 pp.

Frost, D.R. 2002. Amphibian species of the world: an online reference, v. 2.21 (15 July 2002). Electronic database available at http://research.amnh.org/herpetology/amphibia/index.html. New York: American Museum of Natural History.

Fu, J., and R.W. Murphy. 1999. Discriminating and locating character covariation: an application of permutation tail probability analyses. Systematic Biology 48: 380–395.

Günther, A. 1875. Third report on the collections of Indian amphibians and reptiles obtained by the British Museum. Proceedings of the Zoological Society of London 1875: 567–577, pls. lxiii–lxvi.

Hair, J.F., R.E. Anderson, R.L. Tatham, and W.C. Black. 1995. Mulivariate data analysis, 4th ed. Englewood Cliffs, NJ: Prentice Hall, 768 pp.

Hallowell, E. 1861. Report upon the reptilia of the north Pacific exploring expedition, under command of Capt. John Rogers, U.S.N. Proceeding of the Acadamey of Natural Science of Philadelphia 12: 480–510.

Inger, R.F. 1956. Morphology and development of the vocal sac apparatus in the African frog *Rana* (Ptychadena) *porosissima* Steindachner. Journal of Morphology 99(1): 57–72.

Inger, R.F. 1996. Commentary on a proposed classification of the family Ranidae. Herpetologica 52(2): 241–246.

Inger, R.F. 1999. Distribution of amphibians of southern Asia and adjacent islands. *In* W.E. Duellman (editor), Patterns of distribution of amphibians: a global perspective. Baltimore, MD: Johns Hopkins University Press, 445–482.

Inger, R.F., and T. Charnard. 1997. A new species of ranid frog from Thailand, with comments on *Rana livida* (Blyth). Natural History Bulletin of the Siam Society 45: 65–70.

Inger, R.F., N.L. Orlov, and I.S. Darevsky. 1999. Frogs of Vietnam: a report on new collections. Fieldiana: Zoology (new series) 92: 1–46.

International Commission on Zoological Nomenclature. 1999. International code of zoological nomenclature, 4th ed. London: The International Trust for Zoological Nomenclature, 306 pp. [in English and French]

Jerdon, T.C. 1870. Notes on Indian herpetology. Proceedings of the Asiatic Society of Bengal 1870: 66–85.

Karsen, S.J., M.W.-n. Lau, and A. Bogadek. 1998. Hong Kong Amphibians and Reptiles, 2nd ed. Hong Kong: Urban Council, 136 pp.

Lathrop, A., R.W. Murphy, N. Orlov, and C.T Ho. 1998a. Two new species of *Leptolalax* (Anura: Megophryidae) from northern Vietnam. Amphibia-Reptilia 19: 253–267.

Lathrop, A., R.W. Murphy, N. Orlov, and C.T Ho. 1998b. Two new species of *Leptobrachium* (Anura: Megophryidae) from the Central Highlands of Vietnam. Russian Journal of Herpetology 5(1): 51–60.

Li, C., C.-y. Ye, and L Fei. 2001. Taxonomic studies of *Odorrana andersonii* in China (Anura: Ranidae). Acta Zootaxonica Sinica 26(2): 234–238.

Li, W.-H., and Z.-Y. Wang. 1985. Karyotype of *Rana livida*. Acta Herpetologica Sinica, Chengdu 4(1): 56.

Liu, C.e.-c., and S-c. Hu. 1961. Tailless amphibians of China. Peking: Science Press, xvi + 364 pp, 28 pls. [in Chinese]

Malnate, E.V. 1971. A catalog of primary types in the herpetological collections of the Academy of Natural Sciences, Philadelphia (ANSP). Proceedings of the Academy of Natural Sciences of Philadelphia 123: 345–375.

Matsui, M. 1994. A taxonomic study of the *Rana narina* complex, with description of three new species (Amphibia: Ranidae). Zoological Journal of the Linnean Society 11: 385–415.

Matsui, M., H. Ota, M. Lau, and A. Bogadek. 1995. Cytotaxonomic studies of three ranid species (Amphibia: Anura) from Hong Kong. Japanese Journal of Herpetology 16(1): 12–18.

Murphy, R.W. 1993. The phylogenetic analysis of allozyme data: invalidity of coding alleles by presence/absence and recommended procedures. Biochemical Systematic Ecology 21: 25–38.

Murphy, R.W., and C.B. Crabtree. 1985. Evolutionary aspects of isozyme patterns, number of loci, and tissue-specific gene expression in the prairie rattlesnake, *Crotalus viridis viridis* Herpetologica 41: 451–470.

Murphy, R.W., and K.D. Doyle. 1998. Phylophenetics: frequencies and polymorphic characters

in genealogical estimation. Systematic Biology 47: 737–761.

Murphy, R.W., L.A. Lowcock, C. Smith, I.S. Darevsky, N.L. Orlov, R.D. MacCulloch, and D.E. Upton. 1997. Flow cytometry in biodiversity surveys: methods, utility, and constraints. Amphibia-Reptilia 18(1): 1–13.

Murphy, R.W., J.W. Sites Jr., D.G. Buth, and C.H. Haufler. 1996. Proteins: isozyme electrophoresis. *In* D.M. Hillis, C. Moritz and B.K. Mable (editors), Molecular Systematics: 41–120. Sunderland, MA: Sinauer Associates.

Narins, P.M., A.S. Feng, H.-S. Yong, and J. Christensen-Dalsgaard. 1998. Morphological, behavioral, and genetic divergence of sympatric morphotypes of the treefrog *Polypedates leucomystax* in Peninsular Malaysia Herpetologica 54: 129–142.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

Nguyen, V.S., and T.C. Ho. 1996. Danh Luc Bo Sat Va Ech Nhai Viet Nam [The reptiles and amphibians of vietnam]. Ha Noi: Nha Xuat Ban Khoa Hoc Va Ky Thu At, 264. [in Vietnamese]

Nguyen, Q.T. 2000. Amphibian uses in Vietnam. Froglog no. 38.

Nixon, K.C., and Q.D. Wheeler. 1990. An amplification of the phylogenetic species concept. Cladistics 6: 211–223.

Ohler, A., O. Marquis, S. Swan, and S. Grosjean. 2000. Amphibian biodiversity of Hoang Lien Nature Reserve (Lao Cai Province, northern Vietnam) with descriptions of two new species. Herpetozoa 13(1): 71–87.

Orlov, N.L, A. Lathrop, R.W. Murphy, and T.C. Ho. 2001. New records of frogs of the family Rhacophoridae (Anura: Amphibia) in the north part of the Hoang Lien Mountains (Mount Fan Si Pan, Sa Pa district, Lao Cai Province), Vietnam. Russian Journal of Herpetology 8(1): 17–44.

Orlov, N.L., R.W. Murphy, N.B. Ananjeva, S.A. Ryabov, and T.C. Ho. 2002. Herpetofauna of Vietnam, a checklist. Part I. Amphibia. Russian Journal of Herpetology 9(2): 81–104.

Pope, C.H. 1931. Notes on amphibians from Fukien, Hainan, and other parts of China. Bulleetin of the American Museum of Natural History 61(8): 397–611, 10 pls.

Pope, C.H. 1935. Reptiles of China. Natural history of Central Asia vol.10. New York: American Museum of Natural History, 604 pp., 27pls.

Rogers, J.S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics 7213: 145–153.

Smith, M.A. 1921. New or little-known reptiles and batrachians from southern Annam (Indo-China). Proceedings of the Zoological Society of London 1921: 423–440, 2 pls., 2 figs.

Smith, M.A. 1930. The Reptilia and Amphibia of the Malay Peninsula. Bulletin of the Raffles Museum 1930(3): xviii + 1–149.

Smith, M.A. 1931. The Fauna of British India, Including Ceylon and Burma: Reptilia and Amphibia, vol. 1. London: Taylor and Francis, 185 pp, 2 pls.

StatSoft. 1995. STATISTICA ver. 5.0. Tulsa, OK: StatSoft.

Stuart, B.L. 1999. Amphibians and Reptiles. *In* J.W. Duckworth, R.E. Salter and K. Khounboline (editors), Wildlife in Lao PDR: 1999 status report. Vientianne, Lao PDR: IUCN–The World Conservation Union, Wildlife Conservation Society, Centre for Protected Area and Watershed, 43–68, annex 3, 6.

Swofford, D.L., and R.B. Selander. 1989. BIOSYS 1.7: a computer program for the analysis of allelic variation in genetics. Urbana–Champaign: University of Illinois.

Tabachnick, B., and L.S. Fidell. 1989. Using multivariate statistics, 2nd ed. New York: Harper and Row, 509 pp.

Taylor, E.H. 1962. The amphibian fauna of Thailand. University of Kansas Scientific Bulletin 43(8): 265–599, errata.

Theobold, W. 1860. Herpetology. *In* F. Mason (editor), Burmah. Its people and natural productions; or Notes on the nation's fauna, flora, and minerals of Tenasserim, Pegu and Burmah with systematic catalogues of the known mammals, birds, fish, reptiles, insects, mollusks, crustaceans, annelids, radiates, plants and minerals with vernacular names: 291–325. London: T.S. Ranney, Rangoon and Trubner & Co.

Vindelov, L., I.J. Christensen, N. Keiding, M. Spang-Thomsen, and N.I. Nissen. 1982. Long-term storage of samples for flow cytometric DNA analysis. Cytometry 3: 317–322.

Wege, D.C., A.J. Long, M.K. Vinh, V.V. Dung and J.C. Eames (editors). 1999. Expanding the protected areas network in Vietnam for the twenty-first century: an analysis of the current system with recommendations for equitable expansion. Birdlife Vietnam Report no.6. Hanoi: Birdlife International. Also online: http://www.wing-wbsj.or.jp/~vietnam/pdf/report6.pdf.

Wei, G., N. Xu, D. Li, G.-f. Wu and X.-q. Song. 1993. Karyotype, C-band and Ag-NORs study of three stink frogs. Asiatic Herpetological Research 5: 45–50.

Werner, F. 1930. *Rana leporpies*, a new species of frog from south China. Lignan Science Journal 9(1, 2): 45–47, pl. 49.

White House, Office of the Press Secretary. 2000. (1 May 2000) Statement by the President regarding the United States decision to stop degrading global positioning system accuracy. The White House, Washington, D.C.: Press Release (available online: http://www.ngs.noaa.gov/fgcs/info/sans_SA/).

Yang, D.-T. (editor). 1991a. Amphibian fauna of Yunnan. Beijing: China Forestry Press, iv + 259 pp. [in Chinese]

Yang, D.-T. 1991b. Phylogenetic systematics of the *Amolops* group of ranid frogs of southeastern Asia and the Greater Sunda Islands. Fieldiana: Zoology 63: 1–42.

Zhao, E.-M. 1994. A historical review and evaluation of the partitioning of the ranid genus *Rana* (Amphibia: Salientia). Sichuan Journal of Zoology 13(3): 111–115.

Zhao, E.M., and K. Adler. 1993. Herpetology of China. Contribution to herpetology no. 10. St. Louis, MO: Society for the Study of Amphibians and Reptiles, 522 pp.

Ziegler, T. 2002. Die Aamphibien und Reptilien eines Tieflandfeuchtwald-Schutzgebietes in Vietnam. Münster: NTV Wissenschaft, 342 pp.

Ziegler, T., and J. Kohler. 2001 *Rhacophorus orlovi*, sp. n., ein neuer Ruderfrosch aus Vietnam (Amphibia: Anura: Rhacophoridae). Sauria 23(3): 37–46.

APPENDIX 1

Specimens Examined

Rana chloronota: Vietnam; Tam Dao, Vinh Phu Province: (females) ROM 26411–264416, 39248–39249, 39313–39315, 39338; (males) ROM 26433, 39348–39350, 39353–39354, 39357–39358, 39360, 39361, 39364; Ba Be National Park, Bac Kan Province (formerly Cao Bang Province): (females) ROM 26348–26356, 26367; (males) ROM 26360–26366, 26368, 26369, 39362; Na Hang Nature Reserve, Pac Ban, Tuyen Quang Province: (females) ROM 39278–39284, 39286, 39287; (males) ROM 39755, 39757, 39759, 39760, 39767, 39774, 39775; Con Cuong Region, Nghe An Province: (females) ROM 26405, 39260–39262, 39264–39271, 39276, 39277; (males) ROM 26401–26403, 39272–39275; Gia Lai Province: (females) ROM 26422, 26424, 26425, 26427, 26428; (males) ROM 26420; Lang Bien Plateau (female) FMNH 83223; China; Hong Kong: (female) ROM 39243; (males) ROM 39241, 39242, 39244, 39245; Lao PDR: FMNH 256493; India; Darjeeling: ROM 14057, 14058, BMNH 1947.2.28.4, 1947.2.28.6, 1947.2.28.12; Assam: FMNH 72416, 74158; *Rana graminea*: China; Fujian Province: AMNH A29973–29991, A28543–28545, 28612; Hainan Island: BMNH 1947.2.27.96, 1947.2.27.97; NLO Field Series 26375; *Rana livida*: Myanmar; Tenasserim: BMNH 1889.3.25.47, 1889.3.25.48; *Rana sinica*: China; undisclosed: ZMB 9785; *Rana bacboensis*: Vietnam; Ba Be National Park, Bac Kan Province (formerly Cao Bang Province): (female) ROM 29359; Na Hang Nature Reserve, Pac Ban, Tuyen Quang Province: (females) ROM 29526–29530; Con Cuong Region, Nghe An Province: (females) ROM 26404, 29531–29534, 26357, 26358, AMNH A-161248, FMNH 255611; (male) FMNH 255612; *Rana daorum*: Sa Pa and vicinity, Lao Cai Province: (females) ROM 26381, 38500, 38503, 38507, 38512, 38516, 38517, 38526, 38530, 38538; (males) ROM 26382–26397, 38501, 38502, 38504–38506, 38508–38511, 38513–38515, 38518–38525, 38527–38529, 38532–38537, 38539, 38540, 38542–38543, 38546, 38548–38561; (juveniles and subadults) ROM 38547; *Rana hmongorum*: Sa Pa and vicinity, Lao Cai Province: (females) ROM 26370–26379, 39867–39873; AMNH A-161480; (males) ROM 26380, 39235, 39236, 39874–39879, 39890–39894; (juveniles and subadults) ROM 39868, 39880–39889, 39895, 39896; *Rana morafkai*: Gia Lai Province: (females) ROM 39930, 39932, 39934, 39947, 39949; (males) ROM 25094–25097, 25099, 25101, 25104–25106, 25108–25111, 39904–39911, 39937; *Rana banaorum*: Gia Lai Province: (females) ROM 39899–39901, 39928, 39929, 39931, 39936, 39941, 39944; (males) ROM 25084–25086, 25100, 25102, 25103, 39700, 39702–39705, 39716–39720, 39912, 39913, 39915, 39916, 39920–39922, 39924–39926; (subadult) ROM 39942; *Rana megatympanum*: Na Hang Nature Reserve, Pac Ban, Tuyen Quang Province: (males) ROM 39237–39240; Con Cuong Region, Nghe An Province: (females) ROM 26398–26400, 39263, 39684–39689, 39691; (males) ROM 39690.

APPENDIX 2

ISOZYME LOCI ASSAYED AND BUFFER SYSTEMS USED TO RESOLVE THEM

Buffer abbreviations are as follows: tris-citrate II, TC 8; tris-citrate III, WTC; amine-citrate (Morpholine), CT 6.3, CT 6.5, CT 6.7; tris-citrate/borate, Plk 8.7; lithium borate, LiOH; tris-borate-EDTA, EBT.

Isozyme	Locus abbreviation/ EC number	Buffer system
Adenylate kinase	Ak-A (E.C. 2.7.4.3)	CT 6.5
Aspartate aminotransferase	mAAT-A (E.C. 2.6.1.1)	TC 8, Plk 8.7
Creatine kinase	CK-C (E.C. 2.7.3.2)	CT 6.3, CT 6.7, TC 8
Dipeptidase-A	PEP-A (E.C. 3.4.13.11)	Plk 8.7
Fumarate hydrogenase	FUMH-A (E.C. 4.2.1.2)	TC 8, Plk 8.7
Glucose-6-phosphate isomerase	GPI-A (E.C. 5.3.1.9)	TC 8, Plk 8.7
Glutamate dehydrogenase	GTDH-A (E.C. 1.4.1.2)	WTC
Isocitrate dehydrogenase	IDH-A (E.C. 1.1.1.42)	TC 8, CT 6.3
L-lactate dehydrogenase	LDH-A (E.C. 1.1.1.27)	TC 8
L-lactate dehydrogenase	LDH-B (E.C. 1.1.1.27)	TC 8, Plk 8.7
Malate dehydrogenase	mMDH-A (E.C. 1.1.1.37)	CT 6.3, TC 8, Plk 8.7, CT 6.5
Malate dehydrogenase	sMDH-A (E.C. 1.1.1.37)	TC 8
Malate dehydrogenase (NADP+)	MDHP-A (E.C. 1.1.1.40)	WTC, Plk 8.7, LiOH,
Phosphoglucomutase	PGM-A (E.C. 5.4.2.2)	CT 6.3, TC 6.7, Plk 8.7, CT 6.5
Superoxide dismutase	sSOD-A (E.C. 1.15.1.1)	EBT, Plk 8.7

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://library.amnh.org. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).