Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

Taxonomic notes on the Asian frogs of the tribe Paini (Ranidae, Dicroglossinae): 1. Morphology and synonymy of Chaparana aenea (Smith, 1922), with proposal of a new statistical method for testing homogeneity of small samples

Alain Dubois [a] & Annemarie Ohler [a]

[a] Reptiles et Amphibiens, Département Systématique & Evolution , Muséum national d'Histoire naturelle , Paris, France

[b] Reptiles et Amphibiens, USM 0602, Département Systématique & Evolution , Muséum national d'Histoire naturelle , 25 rue Cuvier, 75005 Paris, France E-mail:

Published online: 21 Feb 2007.

To cite this article: Alain Dubois & Annemarie Ohler (2005) Taxonomic notes on the Asian frogs of the tribe Paini (Ranidae, Dicroglossinae): 1. Morphology and synonymy of Chaparana aenea (Smith, 1922), with proposal of a new statistical method for testing homogeneity of small samples, Journal of Natural History, 39:20, 1759-1778, DOI: 10.1080/00222930400023735

To link to this article: http://dx.doi.org/10.1080/00222930400023735

Journal of Natural History, 2005; 39(20): 1759–1778

Taxonomic notes on the Asian frogs of the tribe Paini (Ranidae, Dicroglossinae): 1. Morphology and synonymy of *Chaparana aenea* (Smith, 1922), with proposal of a new statistical method for testing homogeneity of small samples

ALAIN DUBOIS & ANNEMARIE OHLER

Reptiles et Amphibiens, Département Systématique & Evolution, Muséum national d'Histoire naturelle, Paris, France

(Accepted 4 November 2004)

Abstract
The species from northern Vietnam described as *Rana fansipani* Bourret, 1939 is shown to be a synonym of the species from northern Thailand described as *Rana aenea* Smith, 1922. The male secondary sex characters of this species are described in detail for the first time. Combined with a few other characters, they allow this species to be distinguished from the closely related *Rana unculuanus* Liu, Hu and Yang, 1960 from southern China. Both species should be placed in a subgenus *Chaparana (Chaparana)*, a member of the tribe Paini of the subfamily Dicroglossinae of the Ranidae. In this study, we propose a new statistical method for testing homogeneity of small samples: this consists of considering the values obtained for each specimen and for each regression factor score as morphometric characteristics of this specimen within the frame of this analysis; these values, or some of them, can be used to compare subgroups of specimens by non-parametric tests such as the Mann–Whitney *U* test.

Keywords: *Anura*, Chaparana, Chaparana aenea, Chaparana fansipani, Chaparana unculuanus, *China, Dicroglossinae, male secondary sex characters, Paini, Ranidae, statistical method, Thailand, Vietnam*

Introduction

This is the first of a series of papers dealing with the taxonomy of the frogs of the tribe Paini, a rather poorly-known group of frogs living, mostly in running waters, in the mountains of South and South-East Asia (Himalayas, mountains of northern Indochina and southern China) (Dubois 1976, 1992).

Bourret (1939) established a new subgenus *Chaparana* and a new species *Rana (Chaparana) fansipani* for a single specimen of torrent frog collected on mount Fan Si Pan

Correspondence: Alain Dubois, Reptiles et Amphibiens, USM 0602, Département Systématique & Evolution, Muséum national d'Histoire naturelle, 25 rue Cuvier, 75005 Paris, France. Email: adubois@mnhn.fr

ISSN 0022-2933 print/ISSN 1464-5262 online
DOI: 10.1080/00222930400023735

in northern Vietnam. In subsequent years, no other specimen was referred to this species, whose status remained unclear. Dubois (1977) re-examined the holotype and pointed to several inaccuracies in Bourret's (1939, 1942) descriptions. He suggested that this species was close to the group for which he had earlier (Dubois 1975) erected the subgenus *Paa* of the genus *Rana*, but his conclusion about the taxonomic allocation of this species remained prudent, as the holotype and only known specimen was a juvenile male: as in other cases of frog species named on the basis of single juvenile specimens (see e.g. Ohler and Dubois 1999), taxonomic allocation of the species was difficult due to the absence in this specimen of male secondary sex characters. Later, Dubois (1992) suggested that, by its external morphological characters, the species *Rana fansipani* appeared closest to *Rana aenea* Smith, 1922 from Thailand (a species described on the basis of two juvenile female specimens) and *Rana unculuanus* Liu, Hu and Yang, 1960 from Yunnan (China), and he grouped these three species in a subgenus *Chaparana (Chaparana)*. In doing so, he assumed that these three species had similar male secondary sex characters, i.e. the presence of spines in the anal region, although this character had actually been observed only in the Chinese species.

In 1997, while doing field work on the Fan Si Pan, the Frontier field staff (see Dubois and Ohler 1998, p 2) collected three frog specimens (MNHN 1999.5818, 1999.5820–5821) that proved to be adult males of *Chaparana fansipani* (Ohler et al. 2000). These specimens are devoid of spines in the vent region, but on the other hand they show black cornified spines on the throat, the chest and the first three fingers, thus closely resembling several species of the subgenus *Paa (Paa)*, as redefined by Dubois (1992). Comparison of these specimens and of the holotype of *Rana fansipani* with the type-specimens of *Rana aenea* and additional specimens from Thailand referred to this species further suggests that these two nominal species are nothing but synonyms: the species they belong to should therefore be known as *Chaparana aenea* (Smith, 1922). The present paper is first devoted to a redescription of the holotype of *Rana aenea* Smith, 1922 and the description of an adult breeding male of this species from northern Vietnam, topotype of *Rana fansipani* Bourret, 1939. The species *Chaparana aenea* (Smith, 1922) is then compared with its close relative *Chaparana unculuanus* (Liu, Hu and Yang, 1960). Both for the intraspecific and interspecific comparisons, we propose a new method of comparison between two small samples, based on the results of a principal component analysis. This method may prove useful for statistical morphometric comparisons between samples when only small samples are available for measurement, a common situation in amphibian taxonomy.

Material and methods

Specimens studied are from the following collections: Natural History Museum, London, UK (BMNH); Chengdu Institute of Biology, Academia Sinica, Chengdu, Sichuan, China (CIB); Malcolm A. Smith collection (MAS), now housed in the BMNH collection; Muséum national d'Histoire naturelle, Paris, France (MNHN); Naturhistorisches Museum, Wien, Austria (NMW).

Specimens were sexed using their external characters (in the case of adult breeding males) or through a slight lateral incision in order to see the gonad: the state of development of the latter and its ducts allowed two ontogenetic stages to be distinguished, juvenile and adult, as explained in detail by Dubois (1976, p 31–33).

Two specimens were described in detail using the same format and methodology as in several of our previous works on Asian anurans (Dubois and Ohler 1998, 1999, 2000, 2001; Ohler and Dubois 1999; Ohler et al. 2000, 2002; Bossuyt and Dubois 2001;

Delorme and Dubois 2001; Dubois et al. 2001; Veith et al. 2001). The webbing formulae are given according to Myers and Duellman (1982).

Measurements of specimens were taken with a slide calliper to the nearest 0.1 mm, or, for values below 5 mm, with an ocular micrometer to the nearest 0.01 mm. The list and description of measurements are given in the Appendix.

Univariate morphometric comparisons between samples were made using the non-parametric Mann–Whitney *U* test and the Kruskal–Wallis test (Zar 1984). Besides, we performed multivariate factor analyses based on these measurements, using principal component analysis (PCA) with varimax rotation as implemented in the SPSS software (SPSS Inc. 1999, p 426). Special problems are posed for the taxonomic allocation of specimens and for morphometric sample comparisons in the case of small or very small samples (Ohler and Dubois 1999). Here we propose a new method for such comparisons. Because of small sample sizes and because multivariate normal distribution cannot be assumed, it is not appropriate to use a parametric test for the significance of a difference between cluster centroids obtained by PCA (Sneath and Sokal 1973, p 287). However, the values obtained for each specimen and for each regression factor score can be used as morphometric characteristics of this specimen within the frame of this analysis. Therefore we used some of these values (actually only those of the first three regression factor scores) to compare subgroups of specimens by the Mann–Whitney *U* test. Subgroups were composed according to four possible criteria: taxonomic allocation (for the interspecific comparisons); and geographical origin, sex and ontogenetic stage (for intraspecific comparisons). For the three kinds of intraspecific subgroups we corrected for multiple comparisons using Bonferroni correction: $\alpha' = \alpha/k$, with $\alpha = 0.05$ and $k = 3$. However, the use of Bonferroni correction reduces the possibility of detecting differences, and in the case of comparison of populations it does not guarantee a ''prudent'' interpretation of the results (Perneger 1998). So usage of such a correction should not be automatic, but needs to be in agreement with biological plausible results. We did not apply this correction to the comparisons within a series of regression factor scores, as a significant result in one of these comparisons is enough to document the existence of a difference between groups (see Perneger 1998).

Descriptions of specimens referred to the species *Chaparana (Chaparana) aenea* (Smith, 1922)

Holotype of Rana aenea *Smith, 1922 (Figure 1a–c)*

Smith (1922) described *Rana aenea* on the basis of two juvenile female specimens: (1) MAS 5821 (SVL 35 mm), which was clearly designated as ''type'' (we would now write ''holotype'') and shown in his Figure 1 (reproduced in Bourret 1942, p 277), and (2) MAS 5822 (SVL 38 mm), designated as paratype. Both specimens were later deposited in the collection of the British Museum (Natural History), now the Natural History Museum, London. Following is a detailed redescription of the holotype.

Holotype: BMNH 1947.2.2.31 (ex BMNH 1922.7.4.4, ex MAS 5821), juvenile female, collected in May 1920 by a native collector at Doi Chang (19°23′N, 98°52′E), on the border of Chiang Mai and Mae Hong Son Provinces, Thailand (then ''northern Siam''), about 1500 m altitude. This specimen has been dried up and is in rather bad condition.

Size and general aspect. (1) Specimen of rather small size (SVL 35.2 mm), body rather slender.

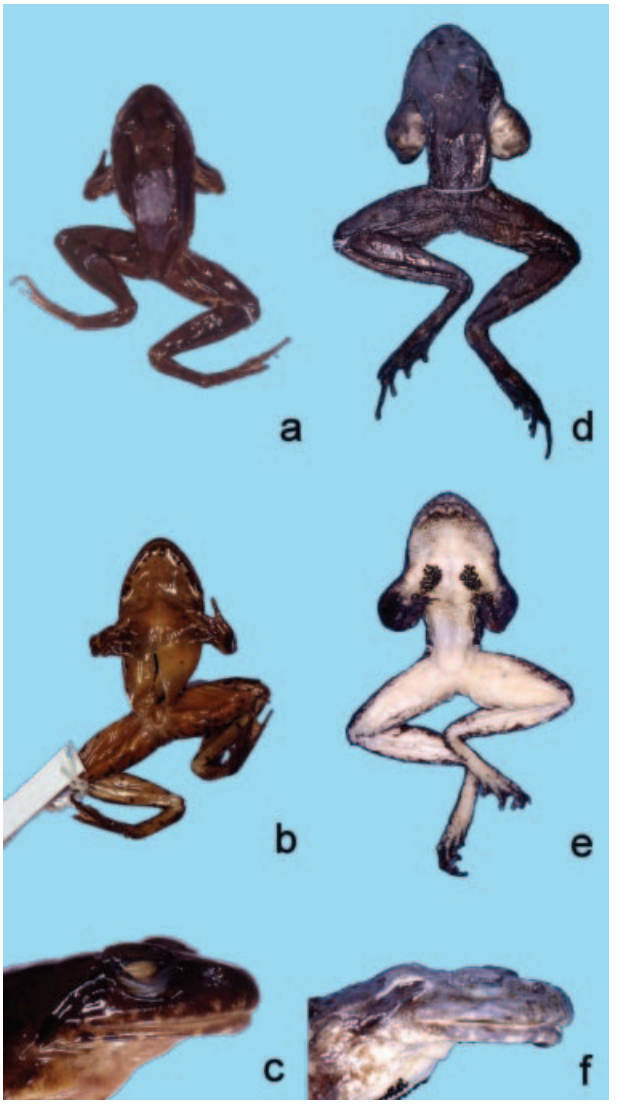

Figure 1. *Chaparana aenea* (Smith, 1922). (a–c) BMNH 1947.2.2.31 (ex BMNH 1922.7.4.4, ex MAS 5821), holotype of *Rana aenea* Smith, 1922, juvenile female from Doi Chang, Thailand: (a) whole body in dorsal view; (b) whole body in ventral view; (c) head in right lateral view. (d–f) MNHN 1999.5821, topotype of *Rana (Chaparana) fansipani* Bourret, 1939, adult male from Fan Si Pan, Vietnam: (d) whole body in dorsal view; (e) whole body in ventral view; (f) head in right lateral view.

Head. (2) Head of medium size, slightly longer (HL 14.4 mm; MN 11.5 mm; MFE 8.9 mm; MBE 5.3 mm) than wide (HW 14.2 mm), convex. (3) Snout rounded, very slightly protruding, its length (SL 5.53 mm) longer than horizontal diameter of eye (EL 4.51 mm). (4) Canthus rostralis rounded, loreal region slightly concave, obtuse in cross-section. (5) Interorbital space flat, smaller (IUE 2.63 mm) than upper eyelid (UEW 3.19 mm) and internarial distance (IN 4.50 mm); distance between front of eyes (IFE 6.3 mm) more than one-half of distance between back of eyes (IBE 10.5 mm). (6) Nostrils closer to eye (EN 2.38 mm) than to tip of snout (NS 3.25 mm). (7) Pupil horizontal oval, very dilated.

(8) Tympanum (TYD 2.63 mm) distinct, rounded, much wider than half of eye; tympanum–eye distance (TYE 1.25 mm) less than half its diameter. (9) Pineal ocellus absent. (10) Vomerine ridges present, bearing teeth, between posterior parts of choanae, with an angle of 45° to body axis, slightly closer to each other than to choanae, slightly longer than distance between them. (11) Tongue not examined. (12) Supratympanic fold distinct, from eye to shoulder. (13) Parotoid glands absent. (14) Cephalic ridges absent. (15) Co-ossified skin absent.

Forelimbs. (16) Arm short (FLL 7.5 mm), shorter than hand (HAL 8.2 mm), not enlarged. (17) Fingers long, rather thin (TFL 3.78 mm). (18) Relative length of fingers, shortest to longest: I=II<IV<III. (19) Tips of fingers slightly swollen, without discs. (20) Fingers without dermal fringes; webbing absent. (21) Subarticular tubercles prominent, rounded, single, all present. (22) Prepollex oval, very prominent, exceptionally developed laterally (with a digit aspect); palmar tubercles indistinct; supernumerary tubercles absent.

Hindlimbs. (23) Shank more than four times longer (TL 21.1 mm) than wide (TW 4.8 mm), longer than thigh (FL 18.9 mm) and than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 18.9 mm). (24) Toes long, thin; toe IV rather long (FTL 14.4 mm), more than one-third of distance from base of tarsus to tip of toe IV (TFOL 29.4 mm). (25) Relative length of toes, shortest to longest: I<II<V<III<IV. (26) Tips of toes swollen, without discs. (27) Webbing moderate: I 0—2 II 0—2⅓ III 0—2½ IV 2½—1 V (WTF 3.38 mm; WFF 3.81 mm; WI 3.00 mm; WII 2.88 mm; MTTF 9.16 mm; MTFF 9.89 mm; TFTF 6.98 mm; FFTF 7.56 mm). (28) Dermal fringe along toe V well developed, from tip of toe to almost level of first subarticular tubercle. (29) Subarticular tubercles prominent, oval, simple. (30) Inner metatarsal tubercle long, prominent; its length (IMT 2.19 mm) about twice length of toe I (ITL 4.25 mm). (31) No tarsal ridge. (32) No outer metatarsal tubercle; no supernumerary tubercles; no tarsal tubercle.

Skin. (33) Dorsal and lateral parts of head and body smooth, with very small ridges (blood vessels) on flanks. (34) Dorsolateral folds present, not prominent, narrow, continuous until the rear of back. (35) Dorsal parts of limbs smooth, with very small ridges (blood vessels). (36) Ventral parts of head, body and limbs smooth, with some transverse folds on venter. (37) No macroglands.

Coloration in alcohol. (38) Dorsal and lateral parts of head and body: uniform brown with several darker bands and spots (a band between eyes, spots on anterior part of eyelids, a band from eye to snout, a band enclosing tympanum and around it, and a band along anterior third of latero-dorsal fold); clearer spots on upper lip, and clear triangle on tip of snout; flanks darker in their upper than in their lower part, with distinct small darker spots everywhere. (39) Dorsal parts of limbs: brown, with two darker bands on forelimb and four narrow bands on each hindlimb. (40) Ventral parts: throat orange with brown marblings and numerous darker spots on margins; chest and belly yellow orange; thighs orange; back of thighs brown with clearer spots and with darker spots similar to those of flanks; webbing marbled brown and cream.

Female sex characters. (41) Oviduct not seen. (42) Ovary juvenile, with white ovocytes (diameter roughly 0.5 mm).

Topotype of Rana (Chaparana) fansipani *Bourret, 1939 (Figure 1d–f)*

MNHN 1999.5821, adult male, collected by the field staff of Frontier Vietnam on 23 November 1997, in Yi Li Ho (1460 m; 22°18′N, 103°50′E) on Fan Si Pan, Lao Cai Province, Vietnam.

Size and general aspect. (1) Specimen of rather large size (SVL 74.6 mm), body robust.

Head. (2) Head of large size, wider (HW 30.1 mm) than long (HL 27.3 mm; MN 23.1 mm; MFE 18.0 mm; MBE 11.4 mm), flat. (3) Snout rounded, very slightly protruding, its length (SL 11.3 mm) longer than horizontal diameter of eye (EL 7.7 mm). (4) Canthus rostralis rounded, loreal region concave, obtuse in cross-section. (5) Interorbital space flat, smaller (IUE 4.7 mm) than upper eyelid (UEW 5.4 mm) and internarial distance (IN 8.4 mm); distance between front of eyes (IFE 11.2 mm) more than one-half of distance between back of eyes (IBE 17.9 mm). (6) Nostrils closer to eye (EN 4.5 mm) than to tip of snout (NS 7.1 mm). (7) Pupil not observed. (8) Tympanum indistinct. (9) Pineal ocellus absent. (10) Vomerine ridges present, bearing few teeth, between posterior parts of choanae, with an angle of 40° to body axis, slightly closer to each other than to choanae, slightly longer than distance between them. (11) Tongue large, rounded, emarginate. (12) Supratympanic fold prominent, from eye to above shoulder. (13) Parotoid glands absent. (14) Cephalic ridges absent. (15) Co-ossified skin absent.

Forelimbs. (16) Arm short (FLL 20.2 mm), longer than hand (HAL 17.0 mm), enlarged. (17) Fingers short, rather thin (TFL 7.6 mm). (18) Relative length of fingers, shortest to longest: II<I<IV<III. (19) Tips of fingers slightly swollen, without discs. (20) Fingers II and III with dermal fringes; webbing absent. (21) Subarticular tubercles prominent, rounded, single, all present. (22) Prepollex oval, very prominent, exceptionally developed laterally (with a shovel aspect); one flat, oval palmar tubercle; supernumerary tubercles absent.

Hindlimbs. (23) Shank four times longer (TL 48.4 mm) than wide (TW 12.8 mm), longer than thigh (FL 42.0 mm) and than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 42.8 mm). (24) Toes long, rather thin; toe IV rather long (FTL 23.7 mm), more than one-third of distance from base of tarsus to tip of toe IV (TFOL 62.2 mm). (25) Relative length of toes, shortest to longest: I<II<V<III<IV. (26) Tips of toes swollen, without discs. (27) Webbing moderate: I 0—2 II 0—2⅓ III 0—2 IV 2—0 V (WTF 9.74 mm; WFF 9.21 mm; WI 8.68 mm; WII 8.42 mm; MTTF 20.9 mm; MTFF 21.4 mm; TFTF 15.4 mm; FFTF 17.7 mm). (28) Dermal fringe along toe V well developed, from tip of toe to beyond level of first subarticular tubercle. (29) Subarticular tubercles prominent, oval, simple. (30) Inner metatarsal tubercle long, prominent; its length (IMT 5.40 mm) half of length of toe I (ITL 10.40 mm). (31) No tarsal ridge. (32) No outer metatarsal tubercle; no supernumerary tubercles; no tarsal tubercle.

Skin. (33) Dorsal and lateral parts of head smooth, back smooth with indistinct glandular warts, flanks granular. (34) Dorsolateral folds present, not prominent, narrow, continuous until the rear of back. (35) Dorsal parts of limbs smooth. (36) Ventral parts of head, body and limbs smooth bearing horny spinules and with some transverse folds on belly. (37) No macroglands.

Coloration in alcohol. (38) Dorsal and lateral parts of head and body: greyish brown with several darker bands and spots (a mid-dorsal chevron, a band from eye to snout, a band enclosing tympanum and around it, and a band along anterior third of latero-dorsal fold); clearer spots on upper lip, and clear triangle on tip of snout; flanks darker in their upper than in their lower part, with some darker spots. (39) Dorsal parts of limbs: brown, with indistinct darker bands; posterior part of thigh dark brown with white marbling. (40) Ventral parts: throat whitish with brown spots on margins; chest, belly and thighs whitish; webbing greyish brown.

Male secondary sex characters. (41) Large-sized, blackish nuptial spines present on prepollex, fingers I–III, chest and throat, forming two separate pads on finger I and prepollex and two widely separated plates of tightly connected spines on chest. Table I gives the numbers of spines in these different places. (42) Forearms distinctly enlarged. (43) Vocal sacs and slits absent.

Other specimens referred to the species Chaparana aenea *(Smith, 1922)*

To our knowledge, beside the two specimens described in detail above, only 11 other specimens referable to this species are known, which are briefly discussed below. Table II gives the measurements of the 13 specimens here discussed, and Figure 2 shows the known localities of this species in China, Thailand and Vietnam, as well as areas of known occurrence of the closely related species *Chaparana unculuanus* (see below).

Specimens from Thailand

BMNH 1974.1113 (ex MAS 5822). Juvenile (SVL 38.6 mm), paratopotype of *Rana aenea* from Doi Chang. This specimen, slightly larger than the holotype, has similar characters.

MNHN 1989.0712 (Figure 3a–c). Non-breeding adult male (SVL 77.4 mm) from Doi Inthanon (18°35′N, 98°28′E), Chiangmai Province, Thailand. Except for its absence of secondary sex characters, this specimen is very similar to the three adult males from Fan Si Pan mentioned above and below. The major differences between them are: the complete absence of nuptial spines on fingers, breast and throat and the absence of enlargement of the forearms, as in the Vietnamese specimen MNHN 1999.5818. The ventral colour pattern is similar in all specimens, but the specimen from Doi Inthanon has a rather clear fawn dorsal colour, whereas the males from Fan Si Pan are dark brown on the back: this difference may be related to nycthemeral colour variation, as specimens collected at night

Table I. Numbers of spines in various parts of body in three adult breeding males of *Chaparana aenea* (Smith, 1922) collected on mount Fan Si Pan (Vietnam), topotypes of *Rana fansipani* Bourret, 1939.

Specimen number	Metacarpal tubercle	First finger	Second finger	Third finger	Breast	Maximum total
MNHN 1999.5818	20/19	98/109	32/36	3/7	35/31	207
MNHN 1999.5820	12/15	76/89	27/23	10/8	31/32	173
MNHN 1999.5821	21/21	93/91	34/29	19/20	42/44	212

For each item, the table gives the number of spines on the left side of the body followed by that on the right side: e.g. 20/19. The maximum total given in the last column is the total of the maximum value for each item on either the left or the right side of the body (see Dubois 1976, p 59; Dubois and Matsui 1983, p 900–901).

Table II. Measurements (in mm) of the 13 specimens here referred to the species *Chaparana (Chaparana) aenea* (Smith, 1922).

	Doi Chang, Thailand		Doi Inthanon, Thailand			Fan Si Pan, Vietnam						Pu Hoat, Vietnam	Luchun, China
	Juv. female BMNH 1922.7.4.4	Juv. BMNH 1974.1113	Adult male MNHN 1989.0712	Juv. MNHN 1989.0713	Juv. male MNHN 1989.0714	Juv. male MNHN 1948.0139	Adult male MNHN 1999.5821	Adult male MNHN 1999.5820	Adult male MNHN 1999.5818	Juv. male MNHN 1999.5998	Juv. male MNHN 1999.5819	Juv. female MNHN 2000.9018	Juv. male MNHN 2001.0277
SVL	35.2	38.6	77.4	23.7	40.5	54.5	74.6	64.7	69.1	49.8	28.4	38.8	39.2
HW	14.2	15.0	31.2	9.2	16.6	22.0	30.1	25.7	25.8	19.5	11.9	15.6	15.2
HL	14.4	15.7	28.8	9.6	16.2	21.0	27.3	25.9	25.5	18.8	11.5	15.0	15.4
MN	11.5	13.3	23.2	8.2	13.1	17.2	23.1	19.7	20.4	14.9	10.0	12.1	12.6
MFE	8.9	10.4	19.2	6.5	11.0	14.2	18.0	16.2	16.3	12.0	8.0	9.5	10.8
MBE	5.3	6.7	12.0	3.4	6.3	8.7	11.4	9.9	10.3	7.2	4.9	5.4	6.4
IFE	6.3	7.2	12.5	5.1	7.6	8.6	11.2	10.2	11.6	8.8	5.1	7.2	7.9
IBE	10.5	11.2	18.5	7.1	12.3	14.8	17.9	15.6	17.4	12.9	8.2	11.1	11.1
IN	4.50	4.50	8.68	3.44	5.19	5.7	8.4	7.24	7.63	5.83	3.95	4.93	5.25
NS	3.25	6.49	7.90	2.72	4.74	3.7	7.1	6.05	6.84	4.90	3.29	3.82	4.34
EN	2.38	2.56	4.21	1.81	2.59	4.0	4.5	4.08	3.68	2.66	2.07	2.46	2.79
EL	4.51	5.19	8.16	3.37	5.12	5.7	7.7	6.97	7.76	6.42	3.63	4.80	5.19
TYD	2.63	2.38	3.82	0.84	2.07	2.9	nm	1.84	2.76	1.43	1.10	2.07	2.07
TYE	1.25	1.69	4.74	0.97	1.94	3.7	nm	3.55	4.21	3.24	1.62	1.94	1.62
IUE	2.63	2.75	6.58	2.14	3.24	4.4	4.7	3.16	5.40	3.89	2.98	3.11	2.98
UEW	3.19	3.63	5.79	2.40	3.89	4.2	5.4	5.92	5.79	4.41	2.59	3.95	3.56
SL	5.53	5.54	12.11	4.54	4.80	8.4	11.3	9.74	10.92	8.10	5.39	6.97	7.63
FLL	7.5	8.2	19.0	4.8	8.8	13.0	20.2	17.0	18.8	10.9	6.2	8.2	8.9
HAL	8.2	8.3	18.9	5.8	9.6	12.7	17.0	14.5	15.5	11.4	6.3	8.8	9.3
TFL	3.78	4.56	9.1	3.05	5.0	6.4	7.6	8.0	7.4	5.5	3.24	4.87	4.7
TL	21.1	23.7	49.6	14.1	25.9	34.8	48.4	40.9	41.9	28.3	16.5	22.9	24.0
TW	4.8	nm	17.3	2.8	6.7	11.0	12.8	10.6	11.1	6.9	3.7	6.2	4.9
FL	18.9	22.0	47.3	13.3	24.7	34.5	42.0	36.9	40.7	26.6	15.3	20.3	22.6
TFOL	29.4	nm	66.5	19.8	36.5	49.0	42.2	55.3	57.9	42.2	22.5	32.8	32.9
FOL	18.9	22.3	46.5	12.9	21.2	32.0	42.8	37.5	38.3	28.7	15.2	21.2	21.9
FTL	14.4	11.6	25.7	7.4	12.0	18.5	23.7	20.8	21.5	16.3	8.2	12.0	12.5
IMT	2.19	2.44	6.32	1.62	2.27	3.7	5.40	4.74	5.26	2.92	1.69	2.27	2.53
ITL	4.25	4.69	9.74	2.98	5.12	7.3	10.40	8.55	9.74	7.00	3.44	5.12	4.80
WTF	3.38	3.75	8.55	2.07	4.80	5.79	9.74	7.24	7.90	4.99	2.92	3.69	4.21
WFF	3.81	4.00	7.63	2.01	4.99	6.05	9.21	6.58	8.82	5.70	2.72	3.82	4.34

Table II. *(Continued)*.

	Doi Chang, Thailand		Doi Inthanon, Thailand			Fan Si Pan, Vietnam						Pu Hoat, Vietnam	Luchun, China
	Juv. female BMNH 1922.7.4.4	Juv. BMNH 1974.1113	Adult male MNHN 1989.0712	Juv. MNHN 1989.0713	Juv. male MNHN 1989.0714	Juv. male MNHN 1948.0139	Adult male MNHN 1999.5821	Adult male MNHN 1999.5820	Adult male MNHN 1999.5818	Juv. male MNHN 1999.5998	Juv. male MNHN 1999.5819	Juv. female MNHN 2000.9018	Juv. male MNHN 2001.0277
WI	3.00	3.19	8.03	2.01	3.89	4.74	8.68	6.32	7.37	3.95	2.33	3.18	3.82
WII	2.88	3.19	7.37	1.75	4.34	5.00	8.42	5.79	7.24	4.34	2.07	3.11	3.68
MTTF	17.0	18.7	21.2	6.55	12.9	15.0	20.9	16.4	18.7	14.6	8.29	11.3	11.32
MTFF	18.4	19.5	24.4	7.13	14.6	18.6	21.4	16.0	20.3	16.2	8.55	11.6	12.11
TFTF	13.0	16.5	20.4	5.90	11.1	14.1	15.4	14.3	15.5	13.2	6.84	9.9	9.34
FFTF	14.1	16.8	20.2	6.16	10.5	14.0	17.7	15.4	14.0	12.5	7.11	9.5	10.26

Juv., juvenile (as defined in Dubois 1976, p 31–33); nm, measurement not taken on this specimen. Of the 36 measurements, only 32 are available for all 13 specimens and were used for the principal component analysis of Figure 5 and Table III.

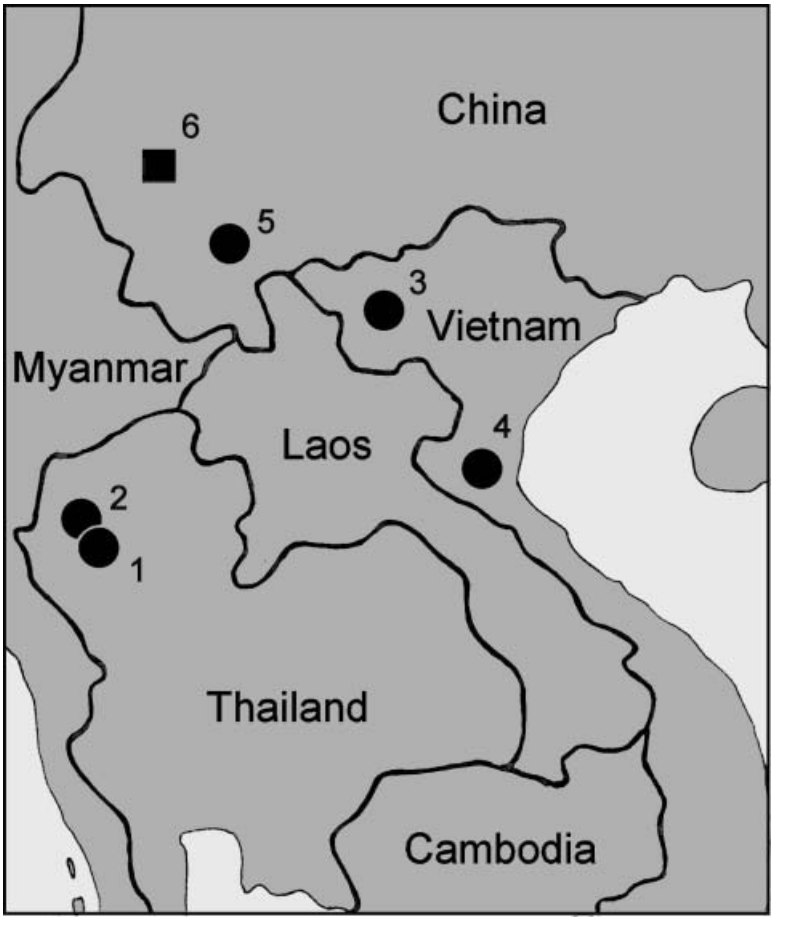

Figure 2. Map showing the localities of specimens studied of the species *Chaparana aenea* (Smith, 1922) (circles) and *Chaparana unculuanus* (Liu, Hu and Yang, 1960) (square). 1, Doi Chang, Thailand; 2, Doi Inthanon, Thailand; 3, Fan Si Pan, Vietnam; 4, Pu Hoat, Vietnam; 5, Luchun, China; 6, Jingdong, China.

are darker than specimens collected during the day. This specimen is clearly adult, and its absence of spines on the fingers and chest indicates that it was not collected during the breeding season. However, its first finger is notably enlarged, and this finger and the prepollex show structures which correspond to basements of spines.

MNHN 1989.0713. Juvenile female (SVL 23.7 mm) from same locality as previous frog. This specimen is very similar in general aspect to both holotypes of *Rana aenea* and *Rana fansipani*.

MNHN 1989.0714. Juvenile male (SVL 40.5 mm) from same locality as both previous specimens, and very similar to them.

Specimens from Vietnam

MNHN 1948.0139 (Figure 3d–f). Juvenile male (SVL 54.5 mm), holotype of *Rana fansipani*, collected in August 1938 by René Bourret on Fan Si Pan mountain (22°19′N,

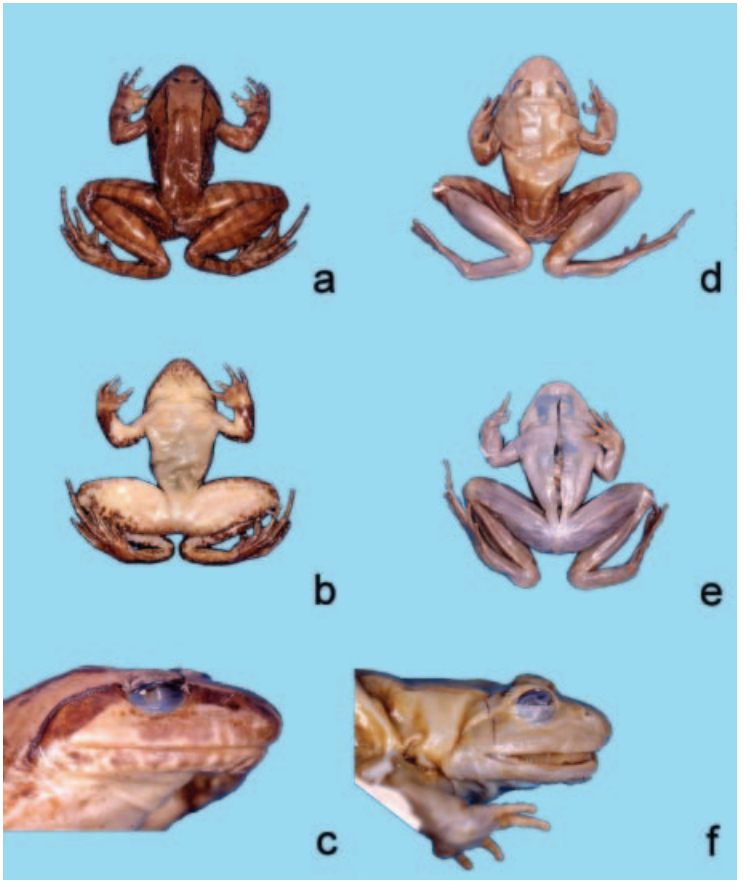

Figure 3. *Chaparana aenea* (Smith, 1922). (a–c) MNHN 1989.0712, non-breeding adult male from Doi Inthanon, Chiangmai Province, Thailand: (a) whole body in dorsal view; (b) whole body in ventral view; (c) head in right lateral view. (d–f) MNHN 1948.0139, holotype of *Rana (Chaparana) fansipani* Bourret, 1939, juvenile male from Fan Si Pan, Vietnam: (d) whole body in dorsal view; (e) whole body in ventral view; (f) head in right lateral view.

103°47′E), Sa Pa District, Lao Cai Province, Vietnam. This specimen was described in detail by Dubois (1977), who wondered whether this frog, clearly a male, was juvenile, subadult or adult. It is very similar in all its characters to the three adult males collected in 1997–1998 on the same mountain, except for its absence of male secondary sex characters: given its much smaller size (SVL 54.5 mm versus 64.7–74.6 mm in the three adult males), it is now clear that it is not adult, nor even subadult, but juvenile, hence its absence of any secondary sex character. This specimen is also very similar in all its characters to the lectotype and paralectotype of *Rana aenea* mentioned above.

MNHN 1999.5820. Adult male (SVL 64.7 mm), topotype of *Rana fansipani* Bourret, 1939, collected on 17 November 1997 at Cat Cat (1280 m; 22°19′N, 103°49′E), on Fan Si Pan mountain, Vietnam. This second specimen is very similar to the specimen MNHN 1999.5821 described in detail above. The major differences between them are the secondary sex characters that are less developed in MNHN 1999.5820: the spines on the

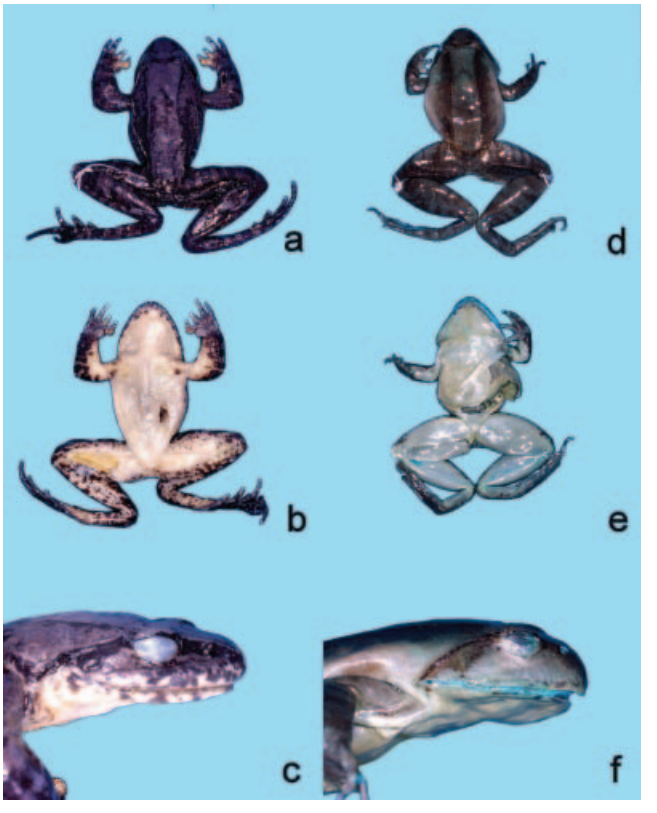

Figure 4. (a–c) *Chaparana aenea* (Smith, 1922), MNHN 1999.5818, topotype of *Rana (Chaparana) fansipani* Bourret, 1939, adult male from Fan Si Pan, Vietnam: (a) whole body in dorsal view; (b) whole body in ventral view; (c) head in right lateral view. (d–f) *Chaparana unculuanus* (Liu, Hu and Yang, 1960), MNHN 2001.0280, adult female from Jingdong Xian, Yunnan, China: (d) whole body in dorsal view; (e) whole body in ventral view; (f) head in right lateral view.

breast are large and blackish, but isolated from each other and less numerous (Table I); on the throat, blackish spines are distinct, but small; the forearms are distinctly enlarged.

MNHN 1999.5818 (Figure 4a–c). Adult male (SVL 69.1 mm), topotype of *Rana fansipani* Bourret, 1939, collected on 1 August 1998 at Ban Khoang (1500 m; 22°23′N, 103°48′E), on Fan Si Pan mountain, Vietnam. This specimen is similar to the other two adult males mentioned above, but in a better condition of preservation. The secondary sex characters are similar to those of MNHN 1999.5820, but the blackish horny covering of the nuptial spines is lost on the breast and on the fingers, and the spines are less numerous (Table I). No spines are present on the throat, and the forearms are not enlarged.

MNHN 1999.5819. Juvenile male (SVL 28.4 mm) from O Qui Ho (1625 m; 22°23′N, 103°47′E), on Fan Si Pan mountain, Vietnam. Its size is smaller but its morphology and colour pattern are similar to those of the adults from the same mountain.

MNHN 1999.5998. Juvenile male (SVL 49.8 mm) from Fan Si Pan mountain (1700 m; 22°23′N, 103°47′E), Vietnam. This specimen is similar in colour pattern to the other specimens.

MNHN 2000.9018. Juvenile female (SVL 38.8 mm) from Pu Hoat (1300 m; 19°25′N, 104°37′E), Nghe An Province, Vietnam. This specimen was collected much further south, in the Annamite mountain range. In general morphology and coloration it resembles the topotypes from Fan Si Pan.

Specimen from China

MNHN 2001.0277. Juvenile male (SVL 39.2 mm) from Luchun Xian (altitude about 2050 m; 23°01′N, 104°21′E), Huang Lian Shan Nature Reserve, Yunnan, China. This specimen, the only one of this species known from China, is very similar in aspect and coloration to the Vietnamese specimens. It has a very conspicuous chevron on the anterior part of the back.

Morphometric comparisons

Intraspecific comparisons within Chaparana aenea *(Smith, 1922)*

Despite the low number of specimens referable to the species *Chaparana aenea* available, we tried to carry out comparisons between them. As mentioned above, in their overall aspects and colours these 13 specimens are very similar. Part of the variation observed is related to age (size) and sex (especially in breeding adult males). However, the shapes and proportions of these specimens, as studied through 32 measurements (Table II), do not show any clear geographical trend, as shown in Figure 5 which presents the distribution of the 13 specimens according to the first two regression factor scores provided by the PCA. Before and after application of Bonferroni correction, Mann–Whitney *U* tests based on the first three regression factor scores of PCA (Table III) do not show significant differences between subgroups of these 13 specimens, based either on sex (males versus females) or on main geographic origin (mountains of northern Vietnam and southern Yunnan versus mountains of northern Thailand). However, prior to Bonferroni correction, when ontogenetic stages (juveniles versus adults) are considered, the first regression factor scores of juveniles are statistically different from those of adults. After Bonferroni correction the value is slightly too high for significance. The existence of significant differences between different ontogenetic stages is meaningful as it points to allometric growth in this species, as is usual in frogs, and especially in this group of torrent frogs (Dubois 1976). From these limited available data, we conclude that, for the time being, no significant difference is documented between populations from Thailand, Vietnam and China referred to this species, and we consider the name *Rana fansipani* Bourret, 1939 as a junior subjective synonym of *Rana aenea* Smith, 1922. Further data, based on more specimens and using additional information (molecular data, bioacoustics, tadpole morphology) will be necessary to confirm or refute this conclusion.

Comparisons between Chaparana aenea *(Smith, 1922) and* Chaparana unculuanus *(Liu, Hu and Yang, 1960)*

Besides *Chaparana aenea* (Smith, 1922) and its synonym *Chaparana fansipani* (Bourret, 1939), Dubois (1992) included a third nominotypical species in his subgenus *Chaparana (Chaparana)*, namely *Chaparana unculuanus* (Liu, Hu and Yang, 1960). The latter (Figure 4d–f) is indeed very similar to *Chaparana aenea* in general morphology, and both

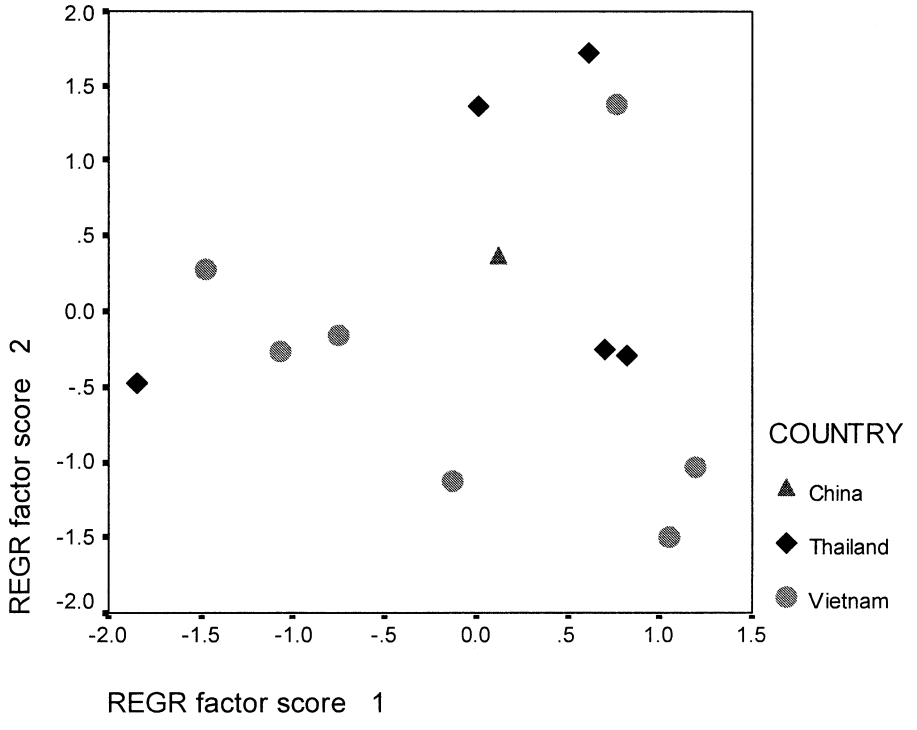

Figure 5. Plots of factors 1 and 2 of principal component analysis based on varimax rotated coefficients for log-transposed characters (32 measurements) for 13 specimens of *Chaparana aenea* (Smith, 1922) from China, Thailand and Vietnam (see Table II).

species occur in southern Yunnan, although in different areas (Figure 2). However, these two species differ markedly in their male secondary sex characters: as discussed above, breeding males of *Chaparana aenea* have enlarged forelimbs and black cornified spines on the fingers and chest, but no spines around the vent. In contrast, breeding males of *Chaparana unculuanus* are devoid of spines on fingers and chest and their forelimbs are not enlarged, but the skin around their vent is distended and bears spines. We examined and measured two adult males and four adult females of *Chaparana unculuanus* from Jingdong Xian (Yunnan, China) (Table IV). Univariate comparisons by Mann–Whitney *U* tests of measurements (expressed as ratios of SVL, except for SVL itself) between the four adult specimens of *Chaparana aenea* listed in Table II and the six adult specimens of *Chaparana unculuanus* listed in Table IV show that the two samples differ statistically in seven measurements out of 27 (HL, FLL, TFL, TL, IN, TYE, IMT). If these 10 specimens are included in a PCA, the two samples appear as two well-separated groups (Figure 6) and the second regression factor scores for the two samples are significantly different (Table V). These data confirm the morphological distinctness of the two samples, independently from their male secondary sex characters, and they support the interpretation that the two samples represent different biological species. This is consistent with the result of the analysis of partial sequences of mitochondrial 12S and 16S rRNA genes provided elsewhere (Jiang et al. forthcoming), which confirms that the two species have distinct, although closely similar, sequences.

Table III. Comparison by Mann–Whitney *U* test of the first three regression factor scores (RFS) generated by principal component analysis based on 32 measurements between subsamples of a sample of 13 specimens of *Chaparana aenea* (Smith, 1922) (see Table II).

Subsamples compared	Regression factor score	First subsample	Second subsample	Mann–Whitney *U* test	BBC $\alpha=0.05$	ABC $\alpha'=0.0167$
Geographic origin	RFS 1	G1 ($n=5$) −1.852–0.818	G2 ($n=8$) −1.473–1.191	$U=20.0$ $P=1.00$	ns	ns
Geographic origin	RFS 2	G1 ($n=5$) −0.482–1.727	G2 ($n=8$) −1.497–1.378	$U=15.0$ $P=0.52$	ns	ns
Geographic origin	RFS 3	G1 ($n=5$) −1.033–2.182	G2 ($n=8$) −1.281–0.727	$U=13.0$ $P=0.354$	ns	ns
Sex	RFS 1	S1 ($n=9$) −1.852–1.049	S2 ($n=2$) 0.700–1.191	$U=2.0$ $P=0.15$	ns	ns
Sex	RFS 2	S1 ($n=9$) −1.497–1.378	S2 ($n=2$) −1.029–−0.248	$U=6.0$ $P=0.58$	ns	ns
Sex	RFS 3	S1 ($n=9$) −1.281–0.968	S2 ($n=2$) 0.208–0.083	$U=6.0$ $P=0.58$	ns	ns
Ontogenetic stage	RFS 1	D1 ($n=9$) −1.473–1.191	D2 ($n=4$) −1.852–−0.125	$U=3.0$ $P=0.02$	*	ns
Ontogenetic stage	RFS 2	D1 ($n=9$) −1.497–1.727	D2 ($n=4$) −1.129–−0.159	$U=10.0$ $P=0.26$	ns	ns
Ontogenetic stage	RFS 3	D1 ($n=9$) −1.033–2.182	D2 ($n=4$) −1.281–0.968	$U=11.0$ $P=0.33$	ns	ns

Criteria of construction of subsamples: (G) geographic origin: Thailand (G1) versus Vietnam + China (G2); (S) sex: males (S1) versus females (S2); (D) ontogenetic stage: juveniles (D1) versus adults (D2). The sex of two juveniles is unknown, hence the total sample of 11 instead of 13 for the criterion "sex". For each criterion of comparison, minimum and maximum values of RFS given for subsamples are those obtained by PCA for the first (RFS 1), second (RFS 2) and third (RFS 3) regression factor scores. Significance levels before Bonferroni correction (BBC): ns, not significant, $P>0.05$; $*P\leqslant 0.05$; significance levels after Bonferroni correction (ABC): ns, not significant, $P>0.0167$; $*P\leqslant 0.0167$.

Taxonomic consequences of these observations at the generic level

Beside the synonymization of *Rana aenea* and *Rana fansipani*, the observations presented above have taxonomic consequences at the generic level. The nominotypical species *Rana fansipani* being the type-species of *Chaparana* Bourret, 1939, the status of the latter name needs to be re-evaluated. Dubois (1992) recognized two genera in the tribe Paini Dubois, 1992 of the subfamily Raninae Rafinesque-Schmaltz, 1814: *Chaparana* Bourret, 1939 (with four subgenera) and *Paa* Dubois, 1975 (with four subgenera). Based on unpublished molecular data, this tribe was transferred to the subfamily Dicroglossinae of the Ranidae Anderson, 1871 by Dubois et al. (2001), a taxonomy followed by Dubois (2003) and Roelants et al. (2004). Furthermore, following the results of the work of Jiang and Zhou (2003), the genus *Nanorana* Günther, 1896, placed by Dubois (1992) in the Ranini, must be included in the tribe Paini.

In Dubois's (1992) taxonomic arrangement, breeding males of all species of the genus *Chaparana* were stated to be devoid of breeding spines both on the forelimbs and on the breast, whereas most (but not all) species of *Paa* had such spines, at least on the first finger. Besides, breeding males of several species referred to *Chaparana* were known to have a specialized zone of skin, either swollen or bearing spines, around the vent. It is now known that the type-species of *Chaparana* is devoid of this latter character but has spines on the fingers and chest, thus fitting with the genus *Paa* as understood by Dubois (1992). This

Table IV. Measurements (in mm) of six specimens from Jingdong (Yunnan, China) of the species *Chaparana (Chaparana) unculuanus* (Liu, Hu and Yang, 1960).

	Ad. female CIB 581270	Ad. female CIB 581267	Ad. male CIB 581597	Ad. male CIB 581664	Ad. female CIB 581666	Ad. female MNHN 2001.0280
SVL	77.6	78.4	77.0	69.0	80.0	72.9
HW	29.6	30.2	27.5	25.9	29.3	27.9
HL	27.5	28.0	25.5	24.5	27.6	25.9
MN	22.8	23.3	21.0	20.0	22.3	22.1
MFE	18.5	19.0	16.4	16.1	18.1	19.1
MBE	11.7	11.7	9.5	9.8	11.4	12.5
IFE	11.7	12.0	10.5	11.3	12.2	11.5
IBE	19.5	19.5	17.8	17.3	20.0	19.3
IN	8.4	7.2	7.0	6.5	7.8	6.8
NS	nm	nm	nm	nm	nm	7.5
EN	4.7	4.4	3.9	4.2	4.5	4.3
EL	6.8	7.6	7.3	7.1	7.6	9.0
TYD	2.9	2.7	2.7	2.5	3.0	3.3
TYE	3.8	4.5	4.1	2.7	3.4	4.0
IUE	4.5	4.6	4.3	3.9	4.0	5.0
UEW	5.6	5.7	6.1	5.4	5.8	6.1
SL	nm	nm	nm	nm	nm	10.7
FLL	16.3	17.1	17.3	15.4	16.9	15.4
HAL	19.0	19.1	18.2	17.7	19.1	17.8
TFL	9.9	9.7	9.5	9.3	10.4	10.3
TL	44.9	45.5	43.1	40.0	45.5	42.6
TW	nm	nm	nm	nm	nm	15.7
FL	nm	nm	nm	nm	nm	39.6
TFOL	nm	nm	nm	nm	nm	52.2
FOL	43.6	41.4	41.8	38.3	42.0	40.5
FTL	24.2	23.1	22.1	21.6	24.0	23.6
IMT	4.1	4.5	4.1	3.9	5.0	4.7
ITL	9.6	9.5	9.2	8.5	9.3	10.4
WTF	9.9	9.0	9.2	9.0	10.4	11.8
WFF	8.8	8.6	8.0	7.8	7.8	9.3
WI	9.0	8.7	7.5	7.7	9.6	9.9
WII	7.5	7.1	6.0	6.1	7.7	6.6
MTTF	nm	nm	nm	nm	nm	22.1
MTFF	nm	nm	nm	nm	nm	22.1
TFTF	nm	nm	nm	nm	nm	14.2
FFTF	nm	nm	nm	nm	nm	17.1

Ad., adult (as defined in Dubois 1976, p 31–33); nm, measurement not taken on this specimen. Of the 36 measurements, only 27 are available for all six specimens and were used for the principal component analysis of Figure 6 and Table V.

species, but this species alone, must be removed from the group called *Chaparana* by Dubois (1992), and placed in the group called *Paa* by this author. The name *Chaparana* has priority to designate this genus.

However, two significant differences remain between *Chaparana aenea* and all species referred by Dubois (1992) to the subgenus *Paa (Paa)*: (1) whereas, in breeding males of the former, both sides of the chest are covered by a well-delimited patch of densely packed spines, whose general shape recalls that of a bean or kidney (Figure 7), in breeding males of those species of *Paa* that have breast spines (i.e. only a part of the species of this group), the two patches are composed of unequally spaced spines and have variable limits, so that these

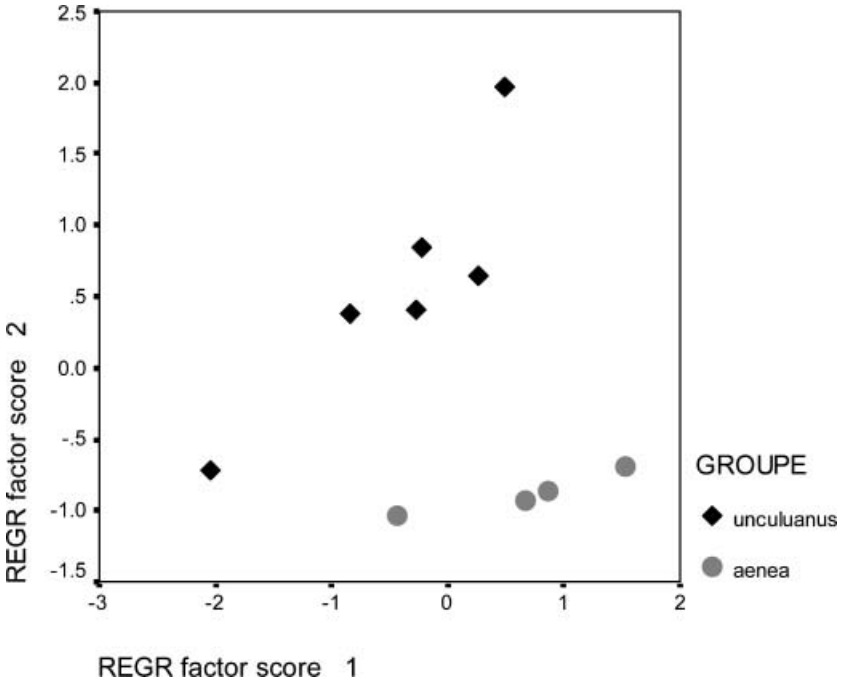

Figure 6. Plots of factors 1 and 2 of principal component analysis based on varimax rotated coefficients for log-transposed characters (25 measurements) for four adult specimens of *Chaparana aenea* (Smith, 1922) (see Table II) and six adult specimens of *Chaparana unculuanus* (Liu, Hu and Yang, 1960) (see Table IV).

patches do not have a common general shape (see e.g. Dubois 1976, p 52, 89, 105, 121); (2) in *Chaparana*, the first finger is usually longer than the second (both fingers may be subequal in some juveniles), whereas in *Paa* the first finger is usually shorter than the second (in some large adults, both fingers may be subequal, or the first one may be exceptionally longer in the species *Paa liebigii* (Günther, 1860): see Dubois 1976, p 65): in this character, *Chaparana aenea* is similar to the frogs placed by Dubois (1992) in the subgenus *Paa (Quasipaa)*. This suggests that the relationships between *Chaparana* and *Paa*

Table V. Comparison by Mann–Whitney *U* test of first three regression factor scores (RFS) generated by principal component analysis based on 27 measurements between a sample of four adult specimens of *Chaparana aenea* (Smith, 1922) (see Table II) and six adult specimens of *Chaparana unculuanus* (Liu, Hu and Yang, 1960) (see Table IV).

Regression factor score	*Chaparana aenea* (n=4)	*Chaparana unculuanus* (n=6)	Mann–Whitney *U* test
RFS 1	−0.428–1.522	−2.046–0.494	U=4.0 P=0.114 ns
RFS 2	−1.030–−0.698	−0.720–1.971	U=1.0 P=0.019⋆
RFS 3	−1.107–1.773	−1.018–1.364	U=9.0 P=0.610 ns

For each criterion of comparison, minimum and maximum values of RFS given for samples are those obtained by PCA for the first (RFS 1), second (RFS 2) and third (RFS 3) regression factor scores. Significance levels: ns, not significant, $P>0.05$; ⋆$P\leqslant 0.05$.

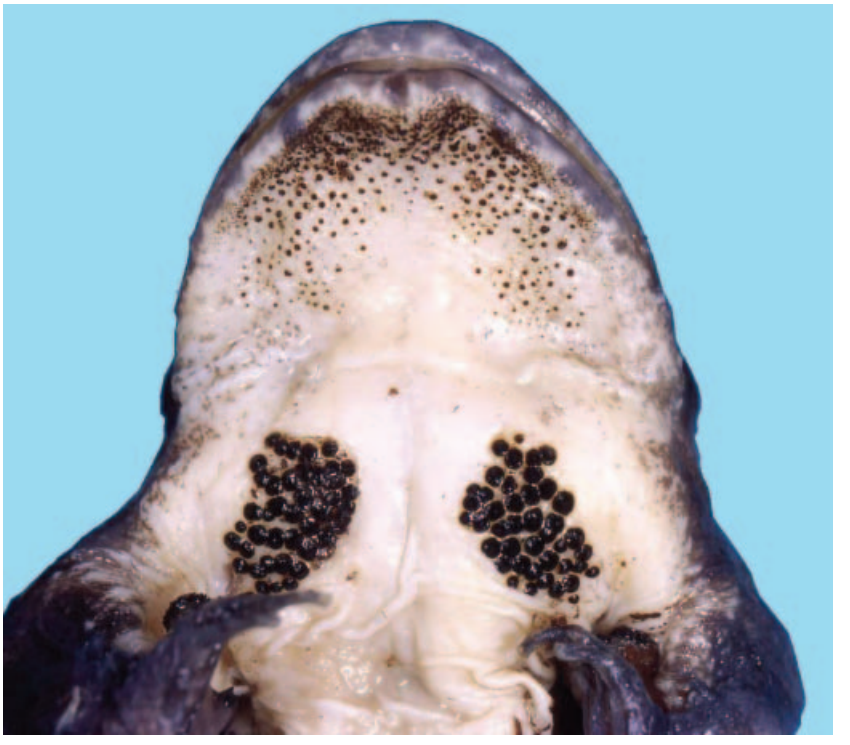

Figure 7. *Chaparana aenea* (Smith, 1922), MNHN 1999.5821, topotype of *Rana (Chaparana) fansipani* Bourret, 1939, adult male from Fan Si Pan, Vietnam: ventral view of chest and throat showing shape of patch of nuptial spines.

should be explored further. As for the other groups referred by Dubois (1992) to several other subgenera of *Chaparana* and *Paa*, their taxonomy and nomenclature will also have to be modified as a result of a re-evaluation of the significance of some characters following the results presented above. To start clarifying this matter, we recently proposed a preliminary cladistic analysis of the Paini based on partial sequences of mitochondrial 12S and 16S rRNA genes of 17 species of the clade (Jiang et al. forthcoming), but this analysis only provides partial information. Therefore we explored the phylogenetic relationships in this clade on the basis of external morphological characters of adults and of a few other characters as available. These results and their implications will be presented elsewhere.

Acknowledgements

We are very grateful to the following colleagues, without the help of whom this study would not have been possible: Steven Swan, Andrew Tordoff and other members of the Frontier field staff (Hanoi, Vietnam), for collecting on Fan Si Pan the two crucial adult breeding males of the species and presenting them to us for study; Jarujin Nabhitabhata (Bangkok, Thailand) for depositing in the MNHN collection three specimens of this species recently collected in Thailand; Nick Arnold and Barry Clarke (London, UK) for allowing us to examine specimens in their care in the BMNH collection; Fei Liang and Ye Changyuan (Chengdu, Sichuan, China) for doing the same in the CIB collection. Thierry Deuve once again provided us with very useful specimens from Asian mountains.

References

Bossuyt F, Dubois A. 2001. A review of the frog genus *Philautus* Gistel, 1848 (Amphibia, Anura, Ranidae, Rhacophorinae). Zeylanica 6(1):1–112.

Bourret R. 1939. Notes herpétologiques sur l'Indochine française. XVII. Reptiles et Batraciens reçus au Laboratoire des Sciences Naturelles de l'Université au cours de l'année 1938. Descriptions de trois espèces nouvelles. Annexe du Bulletin Général de l'Instruction Publique 6:13–34, 1 plate.

Bourret R. 1942. Les Batraciens de l'Indochine. Hanoi: Institut océanographique de l'Indochine. 547 p, 4 plates.

Delorme M, Dubois A. 2001. Une nouvelle espèce de *Scutiger* du Bhutan, et quelques remarques sur la classification subgénérique du genre *Scutiger* (Megophryidae, Leptobrachiinae). Alytes 19(2–4):53–79.

Dubois A. 1975. Un nouveau sous-genre (*Paa*) et trois nouvelles espèces du genre *Rana*. Remarques sur la phylogénie des Ranidés (Amphibiens, Anoures). Bulletin du Muséum National d'Histoire Naturelle, Série 3 324(Zoologie 231):1093–1115.

Dubois A. 1976. Les grenouilles du sous-genre *Paa* du Népal (famille Ranidae, genre *Rana*). Cahiers népalais—Documents 6. Paris: CNRS. 275 p.

Dubois A. 1977. Morphologie et statut systématique de *Rana fansipani* Bourret, 1939 (Amphibiens, Anoures). Bulletin du Muséum National d'Histoire Naturelle, Série 3 480(Zoologie 337):981–992.

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. 2003. True frogs (Ranidae). In: Hutchins M, Duellman WE, Schlager N, editors. Grzimek's animal life encyclopedia. 2nd ed. Volume 6, Amphibians, Farmington Hill (MI): Gale Group. p 245–264.

Dubois A, Matsui M. 1983. A new species of frog (genus *Rana*, subgenus *Paa*) from western Nepal (Amphibia: Anura). Copeia 1983:895–901.

Dubois A, Ohler A. 1998. A new species of *Leptobrachium (Vibrissaphora)* from northern Vietnam, with a review of the taxonomy of the genus *Leptobrachium* (Pelobatidae, Megophryinae). Dumerilia (Paris) 4(1):1–32.

Dubois A, Ohler A. 1999. Asian and Oriental toads of the *Bufo melanostictus*, *Bufo scaber* and *Bufo stejnegeri* groups (Amphibia, Anura): a list of available and valid names and redescription of some name-bearing types. Journal of South Asian Natural History 4(2):133–180.

Dubois A, Ohler A. 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.

Dubois A, Ohler A. 2001. A new genus for an aquatic ranid (Amphibia, Anura) from Sri Lanka. Alytes 19(2–4):81–106.

Dubois A, Ohler A, Biju SD. 2001. A new genus and species of Ranidae (Amphibia, Anura) from south-western India. Alytes 19(2–4):53–79.

Jiang J, Dubois A, Ohler A, Tillier A, Chen X, Xie F, Stöck M. The phylogenetic relationships of the tribe Paini (Amphibia, Anura, Ranidae) based on partial sequences of mitochondrial 12S and 16S rRNA genes. Zoological Science (Tokyo). Forthcoming.

Jiang JP, Zhou KY. Phylogenetic relationships among Chinese ranids inferred from sequence data set of 12S and 16S rDNA. Herpetological Journal. Forthcoming.

Myers CW, Duellman WE. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. American Museum Novitates 2752:1–25.

Ohler A, Dubois A. 1999. The identity of *Elachyglossa gyldenstolpei* Andersson, 1916 (Amphibia, Ranidae), with comments on some aspects of statistical support to taxonomy. Zoologica Scripta 28(3/4):269–279.

Ohler A, Marquis O, Swan S, Grosjean S. 2000. Amphibian biodiversity of Hoang Lien Nature Reserve (Lao Cai Province, northern Vietnam) with description of two new species. Herpetozoa 13(1/2):71–87.

Ohler A, Swan SR, Daltry JC. 2002. A recent survey of the amphibian fauna of the Cardamom mountains, southwest Cambodia with descriptions of three new species. Raffles Bulletin of Natural History 50(2):465–482.

Perneger TV. 1998. What's wrong with Bonferroni adjustments. British Medical Journal 316:1236–1238.

Roelants K, Jiang J, Bossuyt F. 2004. Endemic ranid (Amphibia: Anura) genera in southern mountain ranges of the Indian subcontinent represent ancient frog lineages: evidence from molecular data. Molecular Phylogenetics and Evolution 31:730–740.

Smith MA. 1922. Notes on Reptiles and Batrachians from Siam and Indo-China (No. 1). Journal of the Federal Natural History Society of Siam 4(4):203–214, Plate 8.

Sneath PHA, Sokal RR. 1973. Numerical taxonomy. San Francisco: Freeman. 573 p.

SPSS Inc, 1999. SPSS advanced models 9.0. Chicago: SPSS Inc. 497 p.

Veith M, Kosuch J, Ohler A, Dubois A. 2001. Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 2. Morphological and molecular variation in frogs from the Greater Sunda Islands (Sumatra, Java, Borneo) with the definition of two species. Alytes 19(1):5–28.
Zar JH. 1984. Biostatistical analysis. 2nd ed. Englewood Cliffs (NJ): Prentice-Hall. 718 p.

Appendix

Measurements taken on specimens

Body. SVL, snout–vent length.

Head. EL, eye length; EN, distance from anterior corner of eye to nostril; HL, head length (from posterior corner of mandible to tip of snout); HW, head width, at the angle of jaws; IBE, distance between posterior corner of eyes; IFE, distance between anterior corner of eyes; IN, internarial distance; IUE, minimum distance between upper eyelids; MBE, distance from posterior corner of mandible to posterior corner of eye; MFE, distance from posterior corner of mandible to anterior corner of eye; MN, distance from posterior corner of mandible to nostril; NS, distance from nostril to tip of snout; SL, distance from anterior corner of eye to tip of snout; TYD, maximum tympanum diameter; TYE, distance between tympanum and posterior corner of eye; UEW, maximum width of upper eyelid.

Forelimb. FLL, forelimb length (from elbow to base of outer palmar tubercle); HAL, hand length (from base of outer palmar tubercle to tip of third finger); TFL, third finger length (from base of first subarticular tubercle).

Hindlimb. FFTF, distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe, toes being spread; FL, femur length (from vent to knee); FOL, foot length (from base of inner metatarsal tubercle to tip of fourth toe); FTL, fourth toe length (from base of first subarticular tubercle); IMT, length of inner metatarsal tubercle; ITL, inner toe length; MTFF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between fourth and fifth toe, toes being spread; MTTF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between third and fourth toe, toes being spread; TFOL, length of tarsus and foot (from base of tarsus to tip of fourth toe); TFTF, distance from maximum incurvation of web between third and fourth toe to tip of fourth toe, toes being spread; TL, tibia length; TW, maximum tibia width.