

Phylogenetic relationships and generic taxonomy of the tribe Paini (Amphibia, Anura, Ranidae, Dicroglossinae), with diagnoses of two new genera

Annemarie OHLER
Alain DUBOIS

Muséum national d'Histoire naturelle, Département Systématique et Évolution,
Reptiles et Amphibiens, USM 0602,
case postale 30, 25 rue Cuvier, F-75231 Paris cedex 05 (France)
ohler@mnhn.fr

Ohler A. & Dubois A. 2006. — Phylogenetic relationships and generic taxonomy of the tribe Paini (Amphibia, Anura, Ranidae, Dicroglossinae), with diagnoses of two new genera. *Zoosystema* 28 (3): 769-784.

ABSTRACT

KEY WORDS
Amphibia,
Anura,
Ranidae,
Dicroglossinae,
Paini,
morphology,
cladistic relationships,
new genera.

A preliminary cladistic analysis of the relationships between 26 frog species of the tribe Paini (Ranidae, Dicroglossinae) was carried out on the basis of 31 morphological characters, mainly from external morphology of adults. Combined with the results of a molecular analysis published elsewhere, these data 1) confirm that, after exclusion of the species *Rana delacouri* Angel, 1928, the Paini are a homophyletic group, and 2) allow to redefine the genera of this tribe, which are now six in number, including two new ones described herein.

RÉSUMÉ

MOTS CLÉS
Amphibia,
Anura,
Ranidae,
Dicroglossinae,
Paini,
morphologie,
analyse cladistique,
genres nouveaux.

Relations phylogénétiques et taxonomie générique de la tribu Paini (Amphibia, Anura, Ranidae, Dicroglossinae), avec diagnoses de deux nouveaux genres.

Une analyse cladistique préliminaire des relations entre 26 espèces de grenouilles de la tribu des Paini (Ranidae, Dicroglossinae) a été menée en utilisant 31 caractères morphologiques, principalement de la morphologie externe des adultes. Combinées avec les résultats d'une analyse moléculaire publiée ailleurs, ces données 1) confirment qu'après exclusion de l'espèce *Rana delacouri* Angel, 1928, les Paini constituent un groupe homophylétique, et 2) permettent de redéfinir les genres de cette tribu, qui sont maintenant au nombre de six, dont deux genres nouveaux décrits ici.

INTRODUCTION

We recently (Dubois & Ohler 2005) described the male secondary sex characters of *Chaparana aenea* (Smith, 1922), which had remained unknown since the discovery of the species. These observations suggest that the provisional taxonomy proposed by Dubois (1992) for this frog and related species (distributed in two genera, *Chaparana* Bourret, 1939 and *Paa* Dubois, 1975, grouped in a tribe Paini) cannot be maintained, and lead us to suggest some changes in this scheme. The discovery of the sexual secondary characters of this species implies taxonomic changes for the whole group where it belongs. We provide below a first tentative cladistic analysis of this group of frogs based on external morphological characters. Following the results of the work of Jiang & Zhou (2005), the genus *Nanorana* Günther, 1896 was included in this analysis, and the tribe Dicroglossini (as defined by Dubois 2003) was considered the sister-taxon of the Paini, in the subfamily Dicroglossinae of the family Ranidae. Combined with the results of molecular studies published elsewhere (Jiang *et al.* 2005), these results allow to propose a new taxonomy for this tribe, with diagnoses of two new genera.

MATERIAL AND METHODS

MATERIAL

For this analysis, the ingroup was composed of 25 species of the genera *Chaparana* and *Paa* as defined by Dubois (1992) and one species of the genus *Nanorana*. For the outgroup, given the results of the studies of Jiang & Zhou (2005) and Jiang *et al.* (2005), we used four species of the dicroglossine genera *Euphlyctis* Fitzinger, 1843, *Fejervarya* Bolkay, 1915, *Hoplobatrachus* Peters, 1863 and *Limnonectes* Fitzinger, 1843, as defined by Dubois (1992, 2003). Specimens studied are from the following collections: American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Chengdu Institute of Biology, Academia Sinica, Chengdu, Sichuan (CIB); Malcolm A. Smith collection (MAS), now housed in the BMNH col-

lection; Museum of Comparative Zoology, Harvard (MCZ); Muséum national d'Histoire naturelle, Paris (MNHN); Naturhistorisches Museum, Wien (NMW); Senckenberg Museum, Frankfurt (SMF); Zoological Museum Kobenhavn (ZMK). Appendix presents a list of the specimens examined for this analysis with their localities. In the text below, in Figure 1 and Table 1, we use the specific names of the species studied "naked", without generic names, pending the taxonomic proposals of our conclusion.

Specimens were sexed either according to their external characters (in the case of adult breeding males) or through a slight lateral incision in order to examine the gonad: the state of development of the latter and its ducts allowed to distinguish two developmental stages, juvenile (including subadult) and adult, as explained in detail by Dubois (1976: 31-33). A specimen was radiographed using a Hewlett-Packard 43805N X-Ray System apparatus (Faxitron Series).

CHARACTERS AND CHARACTER STATES

In order to be able to use as many species as possible, including rare ones or species for which we had access to a single or a few specimens, we mainly studied characters of the external morphology, that can be scored without damaging the specimens. We scored 0 the characters states as observed in the outgroups but no polarity of character states was given prior to analysis. Table 1 gives the distribution of character states in the species studied, according to the following definitions of character states:

(C01) Warts on mid-dorsal skin: [0] absent or indistinct; [1] present.

(C02) Aspects of warts on mid-dorsal skin: [0] rounded or slightly elongate, but if elongate not regularly arranged on back; [1] longitudinally elongate, regularly arranged on back.

(C03) Latero-dorsal folds: [0] absent; [1] discontinuous or replaced by warts more or less in line; [2] narrow and continuous all along back.

(C04) Tympanum: [0] distinct; [1] indistinct in external examination.

(C05) Relative length of fingers I and II: [0] finger I longer than II; [1] finger I shorter than or as long as II.

- (C06) Tips of toes: [0] pointed or blunt; [1] enlarged.
- (C07) Proximal subarticular tubercles of fingers: [0] small or medium; [1] large.
- (C08) Leg length: [0] shorter than half of snout-vent length; [1] longer than half of snout-vent length.
- (C09) Webbing: [0] very incurved between extremities of adjacent toes; [1] slightly incurved between extremities of adjacent toes; [2] complete, not incurved between extremities of adjacent toes.
- (C10) Flap of skin along toe V: [0] from tip of toe to level of first subarticular tubercle of toe V; [1] from tip of toe to between subarticular tubercle of toe V and base of metatarsus; [2] from tip of toe to base of metatarsus of toe V or nearly so.
- (C11) Tarsal fold: [0] present, well developed; [1] very weak or absent.
- (C12) Mid-dorsal chevron: [0] always absent; [1] may be present.
- (C13) Mid-dorsal line: [0] always absent; [1] may be present.
- (C14) Vocal sacs in adult male: [0] present; [1] absent.
- (C15) Forearm in adult male in breeding condition: [0] not enlarged; [1] enlarged.
- (C16) Nuptial spines on prepollex and finger I of adult male in breeding condition: [0] present; [1] absent.
- (C17) Nuptial spines on finger II of adult male in breeding condition: [0] always absent; [1] may be present.
- (C18) Nuptial spines on finger III of adult male in breeding condition: [0] always absent; [1] may be present.
- (C19) Nuptial spines on arm and forearm of adult male in breeding condition: [0] always absent; [1] may be present.
- (C20) Nuptial spines on anterior part of throat of adult male in breeding condition: [0] always absent; [1] may be present.
- (C21) Nuptial spines on breast of adult male in breeding condition: [0] always absent; [1] may be present.
- (C22) Nuptial spines on belly of adult male in breeding condition: [0] always absent; [1] may be present.
- (C23) Aspect of nuptial spines on fingers (and chest

if applicable) of adult male in breeding condition: [0] small, indistinct, uncountable; [1] large, distinct, countable.

(C24) Colour of nuptial spines on fingers and breast of adult male in breeding condition: [0] black or brownish; [1] translucent or creamy.

(C25) Patches of nuptial spines on breast of adult male in breeding condition: [0] two well delimited patches of densely packed spines; [1] two separated patches of unequally spaced spines; [2] two confluent patches or a single patch covering both sides of chest.

(C26) Arrangement of spines on arms, breast and belly of adult male in breeding condition: [0] isolated; [1] in clusters.

(C27) Vent of adult male in breeding condition: [0] without morphological differentiation; [1] with a square dermal flap; [2] with spines around and inside vent.

(C28) Intersexuality (adult females with nuptial spines on finger I): [0] always absent; [1] may be present.

(C29) Colour of eggs: [0] with coloured animal pole; [1] entirely whitish or creamy.

(C30) Number of ridges bearing keratodont rows on upper lip of tadpoles: [0] 1-3 rows, median value in species ranges from 1.5 to 2 rows; [1] 2-5 rows, median value in species ranges from 3 to 3.5 rows; [2] 4-8 rows, median value in species ranges from 4.5 to 7 rows; [3] 7-9 rows, median value in species ranges from 8 to 8.5 rows; [4] 0-1 row, median value in species 0.5 row.

(C31) Number of ridges bearing keratodont rows on lower lip of tadpoles: [0] 2-3 rows, median value in species ranges from 2.5 to 3 rows; [1] 0-3 rows, median value in species ranges from 1.5 to 2 rows; [2] 3-5 rows, median value in species 4 rows.

CLADISTIC METHODOLOGY

We carried out a cladistic analysis based on the 31 characters above in 30 species (Table 1), using PAUP, version 4.0b10 (Swofford 2001). We conducted heuristic searches with initial trees obtained from random addition sequence using 100 replicates, followed by branch swapping using the TBR (trees bisection-reconnection) routine implemented in PAUP.

Since the present study did not include all species referable to the tribe Paini as defined here, some

TABLE 1. — Matrix of character states in the groups of Ranidae studied. In this table, in Table 2 and in Figure 1, species are designated by their specific names given “naked”, without generic names, pending the taxonomic conclusions given at the end of this paper. The complete ►

	C01	C02	C03	C04	C05	C06	C07	C08	C09	C10	C11	C12	C13	C14	C15	C16
<i>cyanophlyctis</i>	1	0	0	0	0	0	0	0	2	2	1	0	0	0	0	0
<i>chinensis</i>	1	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0
<i>blythii</i>	1	0	1	0	0	0	1	1	1	2	0	1	1	1	0	1
<i>delacouri</i>	1	1	0	0	0	1	1	1	2	2	0	0	0	1	0	1
<i>limnocharis</i>	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>aenea</i>	0	?	2	1	0	0	0	1	0	0	1	1	0	1	1	0
<i>liebigii</i>	1	0	1	1	1	0	0	1	1	0	1	1	0	1	1	0
<i>minica</i>	1	0	1	0	1	1	0	1	0	0	1	1	0	0	0	0
<i>annandalii</i>	1	0	1	1	1	0	0	1	0	0	1	0	0	0	1	0
<i>polunini</i>	0	?	1	1	1	0	0	1	0	0	1	0	0	0	1	0
<i>blanfordii</i>	1	0	1	1	1	0	0	1	0	0	1	0	0	0	1	0
<i>vicina</i>	1	0	1	1	1	0	0	1	2	0	1	0	0	1	0	1
<i>quadranus</i>	1	0	1	0	1	0	0	1	2	1	1	1	0	1	0	1
<i>gammii</i>	0	?	2	0	1	0	0	1	2	0	1	1	0	0	0	1
<i>unculuanus</i>	0	?	2	1	1	0	0	1	0	0	1	0	0	1	0	1
<i>rostandi</i>	1	0	1	1	1	0	0	1	1	0	1	0	0	0	1	0
<i>ercepeae</i>	1	0	1	1	1	0	0	1	2	0	1	0	0	0	1	0
<i>chayuensis</i>	1	0	0	1	1	0	0	1	2	0	1	0	0	0	1	0
<i>maculosa</i>	1	0	0	1	1	0	1	1	2	0	1	0	0	0	1	0
<i>parkeri</i>	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	0
<i>sternosignata</i>	1	0	0	0	1	0	0	0	2	1	0	0	0	0	1	0
<i>fasciculispina</i>	1	1	0	1	0	1	1	1	2	2	0	0	0	1	1	0
<i>boulengeri</i>	1	1	0	1	0	0	0	1	1	2	0	0	0	0	1	0
<i>robertingeri</i>	1	1	0	1	0	0	0	1	2	2	0	0	0	0	1	0
<i>shini</i>	1	1	0	1	0	1	0	1	1	2	0	0	1	0	1	0
<i>spinosa</i>	1	0	0	1	0	1	0	1	1	2	0	1	1	0	1	0
<i>exilispinosa</i>	1	0	0	0	0	1	0	1	0	2	0	0	0	0	1	0
<i>yunnanensis</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0
<i>bourreti</i>	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
<i>hazarensis</i>	1	0	0	0	0	0	0	0	2	1	0	1	0	0	1	0

species remain that cannot be allocated with certainty to clades or groups as defined below. Therefore our data cannot allow to define unambiguously groups that could be termed “monophyletic” (Hennig 1950) or “holophyletic” (Ashlock 1971), as such groups would have to be clearly both non-polyphyletic and complete (see Delorme *et al.* 2004). Therefore, in the discussion below, we used the term “homophyletic” (Dubois 1986, 1988) to designate a group that is non-polyphyletic but whose completeness is not ascertained. We used the following terms with the following definitions: 1) *homophyletic* for a group that includes the last common ancestor of all its members, irrespective of the fact that it includes, or not, all the descendants of this ancestor; 2) *holophyletic* for a group including an ancestor and all its descendants; 3) *paraphyletic* for a group including an ancestor and *part only* of its descendants; 4)

polyphyletic for a group that does not include the last common ancestor of all its members.

Pending the final allocation of species to new provisional taxa at the end of the discussion below, species will be designated by their specific names (epithets) only, unassociated with any generic names.

RESULTS

Despite the low number of characters (31) in comparison to the number of taxa included in the study (30), a relatively well resolved tree was obtained (67 trees, 107 steps, CI 0.374, RI 0.668) (Fig. 1), but its robustness is very low as most of the branchings have a Bremer’s index of 1 only. Table 2 gives the list of clades found by this analysis and of their synapomorphies, and their scientific names when

combinations following these conclusions are given in the Appendix with the list of specimens examined. **0, 1, 2, 3, 4**, character state in the species; **9**, character irrelevant for the species; **?**, character state unknown in the species; **C01-C31**, characters used in analysis, see text.

	C17	C18	C19	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	C31
<i>cyanophlyctis</i>	0	0	0	0	0	0	0	1	9	9	0	0	0	4	1
<i>chinensis</i>	0	0	0	0	0	0	0	1	9	9	0	0	0	1	2
<i>blythii</i>	0	0	0	0	0	0	9	9	9	9	0	0	0	0	1
<i>delacouri</i>	0	0	0	0	0	0	9	9	9	9	2	0	0	?	?
<i>limnocharis</i>	0	0	0	0	0	0	0	1	9	9	0	0	0	0	1
<i>aenea</i>	1	1	0	1	1	0	1	0	0	0	0	0	?	?	?
<i>liebigii</i>	1	1	1	0	1	0	1	0	1	0	0	0	0	2	0
<i>minica</i>	1	1	0	0	1	0	1	1	1	0	0	0	1	2	0
<i>annandalii</i>	1	1	1	0	1	0	1	0	1	0	0	0	0	2	0
<i>polunini</i>	1	1	1	0	1	0	1	0	1	0	0	0	0	2	0
<i>blanfordii</i>	1	1	0	0	1	0	1	0	1	0	0	0	0	2	0
<i>vicina</i>	0	0	0	0	0	0	9	9	9	9	0	0	0	2	0
<i>quadranus</i>	0	0	0	0	0	0	9	9	9	9	1	0	0	3	0
<i>gammii</i>	0	0	0	0	0	0	9	9	9	9	2	0	0	3	0
<i>unculuanus</i>	0	0	0	0	0	0	9	9	9	9	2	0	0	2	0
<i>rostandi</i>	1	0	1	0	0	0	1	0	9	0	0	0	0	2	0
<i>ercepeae</i>	1	0	0	0	0	0	1	0	9	9	0	0	0	?	?
<i>chayuensis</i>	1	1	0	0	1	0	1	0	1	0	0	0	0	2	0
<i>maculosa</i>	1	1	0	0	1	0	1	0	1	0	0	0	0	2	0
<i>parkeri</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
<i>sternosignata</i>	1	0	0	0	1	1	1	0	0	0	0	1	0	2	0
<i>fasciculispina</i>	1	1	1	0	1	1	1	0	2	1	0	0	0	?	?
<i>boulengeri</i>	1	1	0	0	1	1	1	0	2	0	0	0	0	2	0
<i>robertingeri</i>	1	1	0	1	1	1	1	0	2	0	0	0	0	2	0
<i>shini</i>	1	1	0	0	1	1	1	0	2	0	0	0	0	2	0
<i>spinosa</i>	1	1	0	0	1	0	1	0	2	0	0	0	0	2	0
<i>exilispinosa</i>	1	1	0	0	1	0	1	0	2	0	0	0	0	2	0
<i>yunnanensis</i>	1	1	0	0	1	0	1	0	1	0	0	1	0	2	0
<i>bourreti</i>	1	1	0	1	1	0	1	0	1	0	0	1	0	?	?
<i>hazarensis</i>	0	0	0	0	0	0	1	0	9	9	0	0	0	2	0

such names are available. The numbers of these clades appear on the branches in Figure 1.

The morphological data support the Paini as a homophyletic group. They are characterized by six states of characters: (C10.1) presence of a flap of skin along toe V from tip of toe to between first subarticular tubercle of toe V and base of metatarsus; (C15.1) forearm enlarged in breeding male; (C23.1, C24.0) large, distinct, black or brownish nuptial spines on fingers and breast of breeding male; (C30.2, C31.0) in tadpoles, 4-8 rows (median value in species ranging from 4.5 to 7 rows) of ridges bearing keratodont rows on upper lip and 2-3 rows (median value in species ranging from 2.5 to 3 rows) such ridges on lower lip.

The cladogram shown in Figure 1 sorts the species previously referred to the tribe Paini into four groups:

(1) the species *delacouri*, the only species referred by Dubois (1992) to the subgenus *Chaparana* (*Annandia*), which has a unique combination of character states, is clearly excluded from the Paini and appears as the sister-group of the genus *Limnonectes*, represented by *Limnonectes blythii* (Boulenger, 1920);

(2) all other 25 species, referable to the genera *Chaparana*, *Nanorana* and *Paa* under the taxonomy of Dubois (1992), form a homophyletic clade, but their distribution within this group is not consistent with the generic and subgeneric taxonomy then proposed. This clade consists of three major groups, two of which are composed of members of several of the taxa of Dubois (1992): (A) a single species, also with a unique combination of character states, namely *hazarensis* (previously referred to the subgenus *Paa* of the genus *Paa*), appears as the sister-group of

all other Paini; (B) among the latter, a first group of eight species includes previous members of the subgenera *Eripaa*, *Gynandropaa* and *Quasipaa* of the genus *Paa*; and (C) a second group of 16 species includes species previously referred to the genera *Chaparana* (subgenera *Chaparana*, *Feirana* and *Ombrana*), *Nanorana* and *Paa* (subgenera *Gynandropaa* and *Paa*). The details of these groupings are discussed at more length below.

DISCUSSION

CRITERIA FOR THE TAXONOMIC INTERPRETATION OF THE PHYLOGENETIC DATA

A striking feature of the group Paini is the importance, conspicuousness and variability of male secondary sex characters, such as spines on the fingers, arms, breast or around the vent. We interpret the presence of these spines as an adaptation to breeding in swiftly running water, allowing better grasping of the female by the male. This interpretation is supported by the fact that similar spines on the fingers, arms and chest are also found in other groups of torrent-breeding frogs, either in the same geographic region (e.g., megophryid frogs of the genera *Scutigera* Theobald, 1868 and *Oreolalax* Myers & Leviton, 1962; see e.g., Fei 1999) or in other regions (e.g., in the South American leptodactylid genus *Alsodes* Bell, 1843 or in the Central American ranid species *Rana sierramadrensis* Taylor, 1939; see respectively e.g., Cei 1980 and Webb 1978).

Therefore, not surprisingly, among the 31 characters used in our analysis, 14 (i.e. 45.2%) are male secondary sex characters. Such characters can be particularly useful taxonomic tools, not only at specific (see e.g., Dubois 1976), but also at generic level. They are no doubt informative on the cladistic relationships among species, at least between species that share particular distributions of spines on some parts of body. However, they must be used with caution: whereas the fact that several species share the *presence* of such characters can be strong evidence that they are closely related, the same does not hold for the *absence* of such characters, as these can be “easily” lost in speciation. In some cases, it is quite clear that closely related species

may differ mostly by loss of spines in some parts of body (e.g., *vicina* vs. *liebigii*; see Dubois 1980) or loss of vocal sacs (e.g., *sikimensis* vs. *liebigii*; see Dubois & Ohler in prep. a). Therefore, whereas the positive information provided by *shared presence* of such characters may be phylogenetically informative, the *mere absence* of such characters may be uninformative or misleading. Due to the low number of external morphological characters available, we used this information, but bearing in mind these limitations.

The data obtained in the present study are usefully compared with those of the molecular work of Jiang *et al.* (2005) (see Fig. 2), although unfortunately the species sampling of both studies is in part different. Particularly significant is the fact that some groups appear as homophyletic in both analyses, which supports their recognition as taxa. On the other hand, some important discrepancies exist between both trees, which are likely to be at least in part caused by the artifacts introduced by the over-emphasis put on male secondary sex characters in the morphological analysis: in such cases we tended to place more confidence in the molecular tree, although its results clearly need to be strengthened by further works dealing with additional genes, including nuclear ones.

As already stated in Jiang *et al.* (2005), the present data do not allow the establishment of a robust taxonomic scheme for this whole group of frogs. However, to go on with their works, taxonomists and biologists cannot afford to wait for a “final phylogeny and taxonomy” of organisms, and need provisional “working taxonomies” (Dubois 1999). In the absence of a consensual genus concept in zoology (Dubois 1988) and particularly in amphibians (Dubois 1987), we support the recognition of genera in frogs for well defined groups that are homophyletic, especially if they include species that are liable to produce viable adult hybrids and/or that share a similar developmental mode (for more details, see Dubois 2004). In the Paini, no hybridizable pairs of species are known, and all species whose developmental mode is known have free tadpoles, so that the only usable criterion here is that of homophyly. Under such guidelines, the present data allow to build up a provisional

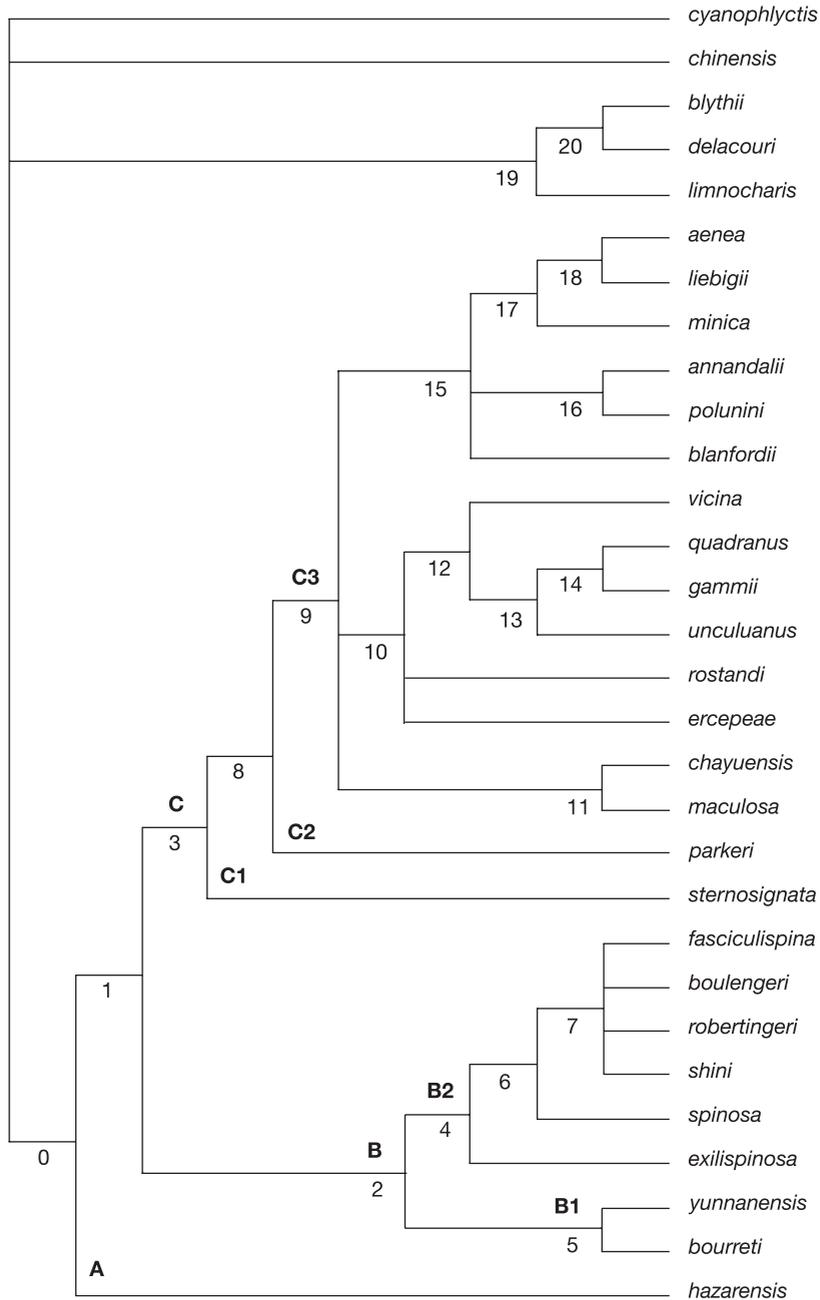


FIG. 1. — Strict consensus of 16 trees (107 steps, CI 0.364, RI 0.653) based on 30 species of the tribe Painsi and 31 morphological characters obtained by simple stepwise addition, followed by branch swapping using the TBR (trees bisection-reconnection) routine implemented in PAUP 4. Numbers of the stems below the horizontal lines on this tree are those used in Table 2 which presents the results of the heuristic analysis, whereas letters above some horizontal lines (**A**, **B**, **B1**, **B2**, **C**, **C1**, **C2**, **C3**) are those of the groups discussed in our taxonomic analysis and which are the basis for our recognition of taxa. Bremer indices were 1 for almost all numbered stems but larger than 1 for the four following stems: 0, 1, 12, 20.

taxonomy of the Paini, that will have to be tested by further morphological, anatomical, cytogenetic and molecular studies.

TAXONOMIC INTERPRETATION OF THE DATA

According to the results presented above, the Paini appear as a homophyletic group within the Dicroglossinae. Our molecular results, presented elsewhere (Jiang *et al.* 2005), confirm the existence of this clade. In contrast, concerning the relationships between taxa within the Paini, the situation is more complex than previously proposed (Dubois 1987, 1992). Some of the previously recognized groups (*Paa*, *Gynandropaa*, *Quasipaa* and *Nanorana*) are confirmed, unchanged or almost unchanged, by this cladistic analysis, but a number of species cannot be allocated to these groups. Let us consider successively the groups outlined here in Figure 1.

(1) *Rana delacouri* was described by Angel (1928) on the basis of two syntype specimens from Bac-Kan (Tonkin, Vietnam). The name *Rana delacouri* was considered a synonym of *Rana spinosa* David, 1875 by Pope & Boring (1940: 13), a synonymy accepted by Bourret (1942). Consequently, when he collected again two specimens of the Bac-Kan frog in Chapa (Vietnam), the latter author (Bourret 1937: 30-31; 1942: 291-293) redescribed this frog as *Rana microlineata*. Dubois (1975: 1098; 1987: 48-49) pointed to the distinctness of this species, and to its valid name being *delacouri*. This species has not been collected recently from Vietnam nor from adjacent China, and could not be included in the molecular study of Jiang *et al.* (2005). Our analysis clearly indicates that it is not a member of the Paini but a form closely related to *Limnonectes blythii*, with which it shares three synapomorphies (stem 20 in Fig. 1 and Table 2): (C08.1) leg longer than half of snout-vent length; (C14.1) absence of vocal sacs and (C16.1) of nuptial spines on prepollex and finger I of breeding adult male. The validity of the genus-group name *Annandia* Dubois, 1992 (type species by original designation *Rana delacouri* Angel, 1928) is in need of re-evaluation (Delorme *et al.* 2004), but the three characters originally used to define this taxon (tips of toes enlarged; absence of mid-dorsal line; presence of spines around and inside vent of breeding male) lead us to tentatively

keep it as a distinct genus of the tribe Limnonectini of the subfamily Dicroglossinae. Male secondary characters so far known in this tribe include tooth-like projections on lower jaw (in some members of the nominotypical subgenus of the genus *Limnonectes*) (see Dubois & Ohler 2001) and flap-like skin structures on top of head (in most members of the subgenus *Elachyglossa* of *Limnonectes*) (Ohler & Dubois 1999), but no spines in the vent region have been described for any species of this tribe so far. Interestingly, a radiograph of the lectotype of *Rana microlineata* (MNHN 1948.0130) allowed us to see that its omosternum is strongly forked, a character that fits with the Limnonectini but not with the Paini, which show an entire omosternum (Dubois 1975, 1992).

(2) All other species surveyed belong in a single clade (stem 0 in Fig. 1 and Table 2), whose validity is supported both in our morphological study and in the molecular study of Jiang *et al.* (2005), and which we recognize taxonomically as the tribe Paini of the subfamily Dicroglossinae of the family Ranidae. As shortly presented above, this clade consists of three distinct groups (A), (B) and (C), that we will survey successively.

(A) The first interesting species occurs in northern Pakistan. It was originally described as *Rana (Paa) hazarensis* by Dubois & Khan (1980), and again under the name *Rana (Paa) barmoachensis* by Khan & Tasnim (1989), a name placed in the synonymy of the former, after study of the holotype, by Dubois (1992: 339). On the basis of our morphological data, this species, which could not be included in the molecular study of Jiang *et al.* (2005), appears as the sister-group of all the remaining species of Paini surveyed here. It displays a unique combination of characters, already briefly pointed out (Dubois 1992: 320), in particular a high number (10-20) of papillae at the commissure of larval lips. These data require erection of a new genus (see below) as its keeping in the subgenus *Paa* (as redefined below) would make the latter polyphyletic and its inclusion in the genus *Quasipaa* (see below) would make the latter paraphyletic. In biogeographical terms, erection of this genus makes sense, as its distribution is disjunct from that of all other Paini being West of most of the latter, and North of that

TABLE 2. — Result of heuristic analysis. Stem numbers refer to numbered internal stems or to terminal taxa shown in Figure 1. In square brackets, letters and numbers designate the groups discussed in our taxonomic conclusion. In brackets available names for supraspecific taxa, when available, are given. Species (terminal taxa) are designated by their specific names only (see text and Appendix).

Branch	Character state
Stem 0 (Paini)	C10.1, C15.1, C23.1, C24.0, C30.2, C31.0
[A] <i>hazarensis</i>	C12.1
Stem 1	C17.1, C21.1
[B] Stem 2	C09.1, C18.1, C25.1
[C] Stem 3	C05.1
[B2] Stem 4 (<i>Quasipaa</i>)	C06.1, C08.1, C10.2, C25.2
[B1] Stem 5 (<i>Gynandropaa</i>)	C28.1
<i>bourreti</i>	C20.1
Stem 6	C04.1
Stem 7	C02.1, C22.1
<i>fasciculispina</i>	C07.1, C09.2, C14.1, C19.1, C26.1
<i>boulengeri</i>	C06.0
<i>robertingeri</i>	C06.0, C09.2, C20.1
<i>shini</i>	C13.1
<i>spinosa</i>	C12.1, C13.1
<i>exilispinosa</i>	C09.0
Stem 8	C04.1, C10.0, C11.1
[C3] Stem 9 (<i>Chaparana</i>)	C03.1, C08.1, C18.1, C25.1
Stem 10	C18.0, C21.0
Stem 11	C03.0, C07.1
Stem 12	C14.1, C15.0, C16.1, C17.0
Stem 13	C01.0, C03.2, C27.2
Stem 14	C04.0, C12.1, C30.3
<i>quadranus</i>	C01.1, C03.1, C10.1, C27.1
<i>gammii</i>	C14.0
<i>unculuanus</i>	C09.0
<i>rostandi</i>	C09.1, C19.1
Stem 15	C09.0
Stem 16	C18.1
<i>polunini</i>	C01.0
Stem 17	C12.1
Stem 18	C14.1
<i>aenea</i>	C01.0, C03.2, C05.0, C20.1, C25.0
<i>liebigii</i>	C09.1, C19.1
<i>minica</i>	C04.0, C06.1, C15.0, C24.1, C29.1
[C2] <i>parkeri</i>	C02.1, C09.0, C13.1, C14.1, C23.0, C30.1
[C1] <i>sternosignata</i>	C22.1, C28.1
Stem 19	C02.1, C07.1, C13.1
Stem 20	C08.1, C14.1, C16.1
<i>blythii</i>	C02.0, C03.1, C09.1, C12.1
<i>delacouri</i>	C06.1, C13.0, C27.2
<i>limnocharis</i>	C09.0, C10.0
<i>cyanophlyctis</i>	C12.1, C30.4
<i>chinensis</i>	C02.1, C15.1, C30.1, C31.2

of the species *sternosignata* (see below). Obtention of molecular data for this group appears very necessary: quite possibly it might prove not to be a member of the Painsi but of the Dicroglossini.

(B) The second group of the Painsi (stem 2 in Fig. 1 and Table 2) is well characterised by several

morphological synapomorphies: (C09.1) webbing slightly incurved between extremities of toes; (C18.1, C25.1) breeding adult males with nuptial spines on finger III and on breast as two separated patches of unequally spaced spines. This group consists of two distinct subgroups also well characterized

morphologically (Table 1), which we propose to recognize as two distinct genera, (B1) *Gynandropaa* and (B2) *Quasipaa*.

(B1) The species *yunnanensis* and *bourreti* form a homophyletic group (stem 5 in Fig. 1 and Table 2) characterised by a peculiar apomorphy: (C28.1) intersexuality present in some specimens. According to Dubois (1992: 319), this character may be related to the very unusual polyploid caryotype (64 micro-chromosomes) documented at least in one species of this group, namely *yunnanensis* (Wu & Zhao 1984). This clade is also firmly supported in the molecular tree (bootstrap 99; Fig. 2). These results support upgrading the subgenus *Gynandropaa* to the generic rank. On the other hand, the relationships of this group with other groups of Painei are not congruent in both analyses. In the morphological analysis, this group appears as the sister-group of the genus (B2) *Quasipaa*, whereas in the molecular tree it appears as nested in the clade that also contains the groups *Chaparana*, *Feirana*, *Nanorana* and *Paa*, i.e. the group (C) of the present analysis (see below). The status of the taxon *Feirana* is unclear. In the molecular tree of Figure 2, its type species *quadrans* appears as the sister-group of *Gynandropaa* with a bootstrap support of 53. In other molecular trees, its relationships with the other taxa of group (C) is unresolved (see Jiang *et al.* 2005). In contrast, in the morphological tree of Figure 1 the species *quadrans* appears grouped with the species *gammii*, *unculuuanus* and *vicina*. However, it is striking that the latter group only consists of species of the males of which are devoid of spines on the fingers, arms and chest, unlike most other Painei, so we consider this grouping as an artifact. To avoid the multiplication of monotypic genera, we propose to treat provisionally *Feirana* as a subgenus of *Gynandropaa*. The priority of *Gynandropaa* over *Feirana* was fixed by the first-reviser action of Dubois (1999: 91). Finally, as concerns the species *sternosignata*, which unfortunately could not be included in the molecular analysis, the morphological tree clearly suggests that it should be removed from *Gynandropaa* to be placed in a group of its own (see below).

(B2) The group recognized by Dubois (1992) as a subgenus *Paa* (*Quasipaa*) appears as homophyletic in both the morphological and molecular trees, with

a bootstrap support of 94 in the molecular tree. As suggested by Jiang *et al.* (2005), this supports the recognition of *Quasipaa* as a distinct genus (group II in Fig. 2), which is characterised by four morphological apomorphies (stem 4 in Fig. 1 and Table 2): (C06.1) tips of toes enlarged; (C08.1) leg longer than half of snout-vent length; (C10.2) flap of skin along toe V extending to base of metatarsal or nearly so; (C25.2) patches of nuptial spines on breast of breeding adult male in two confluent patches or a single patch covering both sides of breast. Although both analyses support the close relationships of *spinosa* and *exilispinosa* on one hand (bootstrap 100 in the molecular tree), and of *boulengeri* and *robertingeri* on the other (bootstrap 100), the cladistic relationships between the other species of this genus are not congruent between the two analyses, so that for the time being it seems premature to recognize subgenera or species-groups within this genus. In the morphological tree, the species *fasciculispina*, placed by Dubois (1992) in a monotypic subgenus *Paa* (*Eripaa*), appears nested within the genus *Quasipaa*. Unfortunately this species could not be included in the molecular study. For the time being, and pending further data, we propose to treat *Eripaa* Dubois, 1992 as a synonym of *Quasipaa* Dubois, 1992. The priority of *Quasipaa* over *Eripaa* was fixed by the first-reviser action of Dubois (1999: 91).

(C) A third group within the Painei (stem 3 in Fig. 1 and Table 2) includes the 16 remaining species surveyed in our morphological study. This group is equivalent to group I of our molecular study (Fig. 2). Morphologically, this group is diagnosed by a single apomorphy: (C05.1) finger I shorter than or subequal to II. This group consists of three distinct subgroups (C1), (C2) and (C3), which we propose to treat taxonomically as genera.

(C1), (C2) In the morphological tree (Fig. 1 and Table 2), the characters of the species *sternosignata* (not included in the molecular study) exclude it from the major group (C3) including the type species of *Chaparana* and *Paa*, and this is also the case of the species *parkeri*. In the molecular tree this latter species and its sister-species *pleskei* appear as nested in the group (C3) but the bootstrap support for this grouping is very low so that the phylogenetic

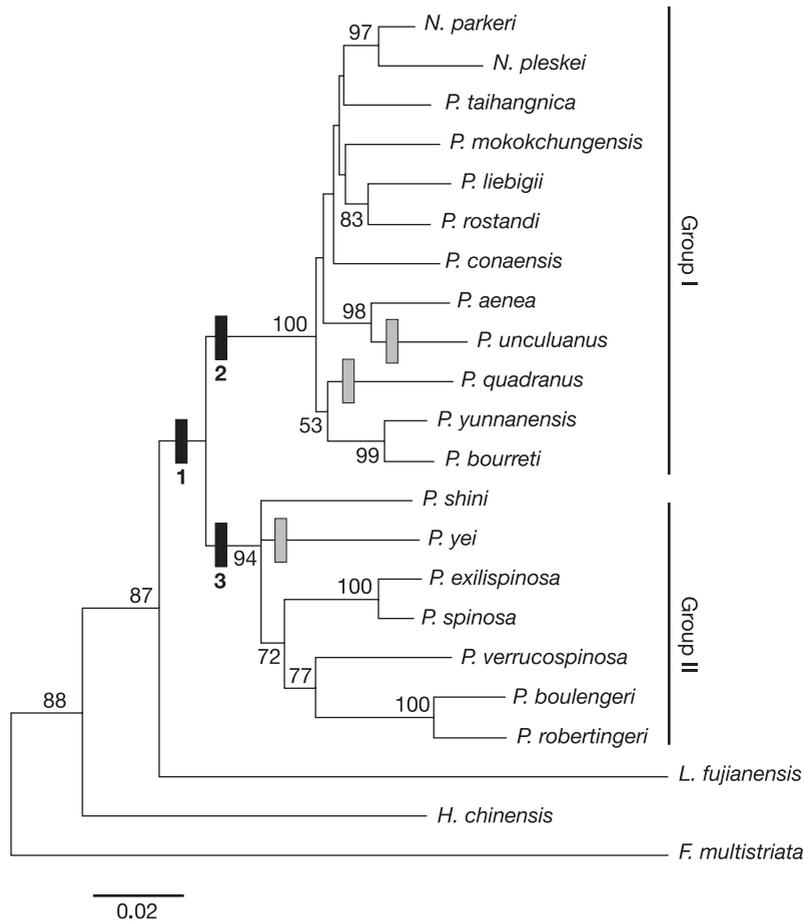


FIG. 2. — Result of neighbour-joining analysis of phylogenetic analysis of 19 species of the tribe Painsi based on partial sequences of mitochondrial 12S and 16S rRNA genes (Jiang *et al.* 2005). Black bars indicate presence of large sized horny spines: **1**, presence of such spines; **2**, two separated patches of spines on breast; **3**, a single patch of spines covering breast and parts of belly. Grey bars indicate loss of horny spines on breast and belly of adult males.

relationships of these species must be considered unresolved. Pending further convincing results, we adopt a conservative approach in keeping *Nanorana* as a valid genus (C2), but this leads us to erect a new genus (C1) for the species *sternosignata*. The unique characters of this species had retained our attention long ago because of its unusual shape of head with a canthal region largely flared, its peculiar skin, male secondary characters and mode of life. The genus (C1) is cladistically defined by two apomorphies: (C22.1) nuptial spines on belly of breeding adult male; (C28.1) intersexuality present in some specimens.

(C3) The last group pointed out by the morphological cladistic analysis (stem 9 in Fig. 1 and Table 2) is defined by four characters: (C03.1) presence of discontinuous latero-dorsal folds; (C08.1) leg longer than half of snout-vent length; (C18.1, C25.1) nuptial spines present on finger III and as two separated patches of unequally spaced spines on breast of breeding adult male. This group is largely supported by the molecular analysis (Fig. 2), except for the inclusion within it of two species traditionally placed in the genus *Nanorana* (see above). In the present state of information, we

recognize this group (C3) as a genus. It includes the type species of both *Chaparana* (namely *Rana aenea*) and *Paa* (namely *Rana liebigii*), so that the name *Chaparana* has priority to designate this genus. The possible recognition of several taxa (subgenera or species-groups) within this genus is open to question.

A particular problem is posed by the presence in this group of a subgroup composed of four species (*quadrans*, *gammii*, *unculuanus* and *vicina*) that share the following male secondary sex characters: (C14.1) vocal sacs absent, (C15.0) forearms not enlarged, (C16.1, C17.0) nuptial spines absent on fingers. These shared characters can all be interpreted as consequences of loss, and are therefore of questionable cladistic significance. On the other hand, these four species, which had been placed by Dubois (1992) in four distinct subgenera, do not share any clearly common derived character. Therefore we consider this subgroup, which is not supported by the molecular data (Fig. 2), as an artifact, and we do not recognize it as a taxon.

For reasons already presented elsewhere (Dubois & Ohler 2005), however, we propose to recognize two distinct subgenera, *Chaparana* and *Paa*, within this genus. According to the molecular data (Fig. 2), beside the clade treated above as a distinct genus *Nanorana*, two subgroups have high bootstrap supports: the group *aenea-unculuanus* (bootstrap 98), and the group *liebigii-rostandi* (bootstrap 83). Neither of these subgroups appears homophyletic in the morphological analysis (Fig. 1), which has nothing surprising as the subgroups in group (C3) outlined by this analysis are mostly based on male secondary sex characters, so we largely come back to the problem just discussed. In the molecular tree of Figure 2, the subgroup *aenea-unculuanus* appears of the sister-group of a subgroup including all other species of group (C3), as well as the genus *Nanorana*. Pending more robust results, we adopt a conservative attitude and we recognize a subgenus *Chaparana* (*Chaparana*) for the subgroup *aenea-unculuanus*, and a subgenus *Chaparana* (*Paa*) for all other species of group (C3) of Figure 1. This latter subgenus is probably in part artificial and may have to be dismantled when more information is available.

CONCLUSION

As a result of the analysis above, we provide below names and diagnoses for two new genera of Paini, and a new working taxonomy of the tribe Paini.

TWO NEW GENERA OF PAINI

Allopaa n. gen.

TYPE SPECIES. — *Rana* (*Paa*) *hazarensis* Dubois & Khan, 1980: 403.

DIAGNOSIS. — Genus distinguished from all other genera of Paini by the following combination of characters: 1) first finger slightly longer than second; 2) extremities of fingers and toes blunt; 3) hind legs short, tibia slightly shorter than half of snout-vent length, without significant sex dimorphism in length; 4) a feeble tarsal fold present; 5) webbing complete; 6) flap of skin along external side of toe V extending proximally beyond first subarticular tubercle of toe but not reaching basis of metatarsus; 7) mid-dorsal chevron present in some specimens; 8) breeding males with slightly enlarged forearm, with black nuptial spines scattered on dorsal part of metacarpal tubercle and finger I alone, with internal vocal sacs; 9) intersexuality not known to exist; and 10) tadpoles with a keratodont formula of 6-8/3.

INCLUDED SPECIES. — *Allopaa hazarensis* (Dubois & Khan, 1980) n. comb. Synonym: *Rana* (*Paa*) *barmoachensis* Khan & Tasnim, 1989.

DISTRIBUTION. — Northern Pakistan.

ETYMOLOGY OF GENERIC NAME. — From the Greek *allos*, “other, different”, and from the generic name *Paa* Dubois, 1975 (from the Tamang name *paa*, “frog”). This name refers to the unusual combination of characters of this taxon as compared to the other genera of Paini.

Chrysopaa n. gen.

TYPE SPECIES. — *Rana sternosignata* Murray, 1885: 120.

DIAGNOSIS. — Genus distinguished from all other genera of Paini by the following combination of characters: 1) first finger as long as second; 2) extremities of fingers and toes blunt; 3) hind legs short, tibia shorter than half of snout-vent length; 4) a feeble tarsal fold present; 5) webbing complete; 6) flap of skin along external side of toe V extending proximally beyond first subarticular tubercle of toe but not reaching basis of metatarsus;

7) mid-dorsal chevron absent; 8) breeding males with enlarged forearm, with black nuptial spines scattered on dorsal part of prepollex and fingers I and II, with a plate of very small sized black spines on each side of breast, with internal vocal sacs; 9) intersexuality rather frequent (adult females with blackish spines on prepollex and fingers I and II); and 10) tadpoles with a keratodont formula of 7/3.

INCLUDED SPECIES. — *Chrysopaa sternosignata* (Murray, 1885) n. comb.

DISTRIBUTION. — Afghanistan and Pakistan.

ETYMOLOGY OF GENERIC NAME. — From the Greek *chrysos*, “gold”, and from the generic name *Paa* Dubois, 1975 (from the Tamang name *paa*, “frog”). This name refers to the presence of golden flacks on the body of numerous specimens of this species in life.

A NEW WORKING TAXONOMY FOR THE PAINI

For the reasons discussed above, we here propose to exclude the Vietnamese species *Annandia delacouri* (Angel, 1928) (synonym: *Rana microlineata* Bourret, 1937) from the tribe Paini, and to refer it to the tribe Limnionectini Dubois, 1992 of the subfamily Dicroglossinae Anderson, 1871. On the other hand, we follow Jiang & Zhou (2005) to include the genus *Nanorana* in the Paini. As a result, the new working taxonomy of the tribe Paini is as follows. Some of the specific names in the list below (i.e. *Rana sikimensis* Jerdon, 1870; *R. gammii* Anderson, 1871; *R. courtoisi* Angel, 1922; *R. tibetana* Boulenger, 1917) will be discussed in more details elsewhere (Dubois & Ohler in prep. a-c). For all other species, information is available in various published works (e.g., Dubois 1992, 2002; Wu & Zhao 1995; Fei 1999; Inger *et al.* 1999; Ohler *et al.* 2000; Dubois & Ohler 2001; Chen & Jiang 2002; Chen *et al.* 2002).

Family RANIDAE Rafinesque-Schmaltz, 1814

Subfamily DICROGLOSSINAE Anderson, 1871

Tribe PAINI Dubois, 1992

Genus *Allopaa* n. gen.

Species: *Allopaa hazarensis* (Dubois & Khan, 1979) n. comb.

Genus *Chaparana* Bourret, 1939

Subgenus *Chaparana* Bourret, 1939

Species: *Chaparana (Chaparana) aenea* (Smith, 1922); *Chaparana (Chaparana) gammii* (Anderson, 1871); *Chaparana (Chaparana)*

unculuuanus (Liu, Hu & Yang, 1960)

Subgenus *Paa* Dubois, 1975

Species: *Chaparana (Paa) annandalii* (Boulenger, 1920); *Chaparana (Paa) arnoldi* (Dubois, 1976); *Chaparana (Paa) blanfordii* (Boulenger, 1882); *Chaparana (Paa) chayuensis* (Ye, 1977); *Chaparana (Paa) conaensis* (Fei & Huang, 1981); *Chaparana (Paa) ercepeae* (Dubois, 1974); *Chaparana (Paa) liebighii* (Günther, 1860); *Chaparana (Paa) maculosa* (Liu, Hu & Yang, 1960); *Chaparana (Paa) medogensis* (Fei & Ye, 1999); *Chaparana (Paa) minica* (Dubois, 1976); *Chaparana (Paa) mokokchungensis* (Das & Chanda, 2000); *Chaparana (Paa) polunini* (Smith, 1951); *Chaparana (Paa) rarica* (Dubois, Matsui & Ohler, 2001); *Chaparana (Paa) rostandi* (Dubois, 1974); *Chaparana (Paa) sikimensis* (Jerdon, 1870); *Chaparana (Paa) taihangnica* (Chen & Jiang, 2002); *Chaparana (Paa) vicina* (Stoliczka, 1872)

Genus *Chrysopaa* n. gen.

Species: *Chrysopaa sternosignata* (Murray, 1885) n. comb.

Genus *Gynandropaa* Dubois, 1992

Subgenus *Feirana* Dubois, 1992

Species: *Gynandropaa (Feirana) quadranus* (Liu, Hu & Yang, 1960)

Subgenus *Gynandropaa* Dubois, 1992

Species: *Gynandropaa (Gynandropaa) bourreti* (Dubois, 1987); *Gynandropaa (Gynandropaa) feae* (Boulenger, 1887); *Gynandropaa (Gynandropaa) liui* (Dubois, 1987); *Gynandropaa (Gynandropaa) sichuanensis* (Dubois, 1987); *Gynandropaa (Gynandropaa) yunnanensis* (Anderson, 1878)

Genus *Nanorana* Günther, 1896

Subgenus *Altirana* Stejneger, 1927

Species: *Nanorana (Altirana) parkeri* (Stejneger, 1927)

Subgenus *Nanorana* Günther, 1896

Species: *Nanorana (Nanorana) pleskei* Günther, 1896; *Nanorana (Nanorana) ventripunctata* Fei & Huang, 1985

Genus *Quasipaa* Dubois, 1992

Species: *Quasipaa boulengeri* (Günther, 1889); *Quasipaa courtoisi* (Angel, 1922); *Quasipaa exilispinosa* (Liu & Hu, 1975); *Quasipaa fasciculispina* (Inger, 1970); *Quasipaa jiu-longensis* (Huang & Liu, 1985); *Quasipaa robertingeri* (Wu & Zhao, 1995); *Quasipaa shini* (Ahl, 1930); *Quasipaa spinosa* (David, 1875); *Quasipaa tibetana* (Boulenger, 1917); *Quasipaa verrucospinosa* (Bourret, 1937); *Quasipaa yei* (Chen, Qu & Jiang, 2002)

Acknowledgements

We are very grateful to Nick Arnold and Barry Clarke (BMNH), to Prof. Fei Liang, Prof. Ye Changyuan and Prof. Jiang Jianping (CIB), and to HR Dr Franz Tiedemann and Dr Heinz Grillitsch (NMW), for allowing us to examine specimens in their care. Many thanks also to Stéphane Grosjean (MNHN) for his help in the cladistic analysis.

REFERENCES

- ANGEL M. F. 1928. — Sur une espèce nouvelle de grenouille du Tonkin, appartenant au genre *Rana*. *Bulletin du Muséum national d'Histoire naturelle* 34: 319-320.
- ASHLOCK P. D. 1971. — Monophyly and associated terms. *Systematic Zoology* 20: 63-69.
- BOURRET R. 1937. — Notes herpétologiques sur l'Indochine française. XIV. Les Batraciens de la collection du Laboratoire des Sciences naturelles de l'Université. Descriptions de quinze espèces ou variétés nouvelles. *Annexe du Bulletin général de l'Instruction publique* 4: 5-56.
- BOURRET R. 1942. — *Les Batraciens de l'Indochine*. Institut océanographique de l'Indochine, Hanoi, x + 547 p., 4 pls.
- CEI J. M. 1980. — Amphibians of Argentina. *Monitore zoologico italiano* (n.s.), Monografia 2: i-xii + 1-609.
- CHEN X.-H. & JIANG J.-P. 2002. — A new species of the genus *Paa* from China. *Herpetologica sinica* 9: 231.
- CHEN X.-H., QU W.-Y. & JIANG J.-P. 2002. — A new species of the subgenus *Paa* (*Feirana*) from China. *Herpetologica sinica* 9: 230.
- DELORME M., DUBOIS A., KOSUCH J. & VENCES M. 2004. — Molecular phylogenetic relationships of *Lankanectes corrugatus* from Sri Lanka: endemism of South Asian frogs and the concept of monophyly in phylogenetic studies. *Alytes* 22 (1-2): 53-64.
- 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*, 3^e sér., 324, Zoologie 231: 1093-1115.
- DUBOIS A. 1976. — Les grenouilles du sous-genre *Paa* du Népal (famille Ranidae, genre *Rana*). *Cahiers népalais – Documents*, Paris, CNRS 6: i-vi + 1-275.
- DUBOIS A. 1980. — L'influence de l'homme sur la répartition des Amphibiens dans l'Himalaya central et occidental. *Comptes-Rendus de la Société de Biogéographie* 55: 155-178.
- DUBOIS A. 1986. — À propos de l'emploi controversé du terme « monophylétique » : nouvelles propositions. *Bulletin mensuel de la Société linnéenne de Lyon* 55: 248-254.
- DUBOIS A. 1987. — Miscellanea taxinomica batrachologica (I). *Alytes* 5 (1-2): 7-95.
- DUBOIS A. 1988. — The genus in zoology: a contribution to the theory of evolutionary systematics. *Mémoires du Muséum national d'Histoire naturelle* (A) 140: 1-123.
- 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. 1999. — Miscellanea nomenclatorica batrachologica. 19. Notes on the nomenclature of Ranidae and related groups. *Alytes* 17 (1-2): 81-100.
- DUBOIS A. 2002. — The taxonomic status of *Scutigera mokochungensis* Das & Chanda, 2000 (Amphibia, Anura). *Amphibia-Reptilia* 22 (1): 499-506.
- DUBOIS A. 2003. — True frogs (Ranidae), in HUTCHINS M., DUELLMAN W. E. & SCHLAGER N. (eds), *Grzimek's Animal Life Encyclopedia*, 2nd edition, volume 6, *Amphibians*. Gale Group, Farmington Hill, Michigan: 245-264.
- DUBOIS A. 2004. — Developmental pathway, speciation and supraspecific taxonomy in amphibians. 2. Developmental pathway, hybridizability and generic taxonomy. *Alytes* 22 (1-2): 38-52.
- DUBOIS A. & KHAN M. S. 1980. — A new species of frog (genus *Rana*, subgenus *Paa*) from Northern Pakistan (Amphibia, Anura). *Journal of Herpetology* 13 (4): 403-410 (dated 1979, published 1980).
- 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. 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.
- DUBOIS A. & OHLER A. in prep. a. — Taxonomic notes on the Asian frogs of the tribe Paini (Ranidae, Dicroglossinae). 2. Sibling species distinguished from *Chaparana liebigii* (Günther, 1860).
- DUBOIS A. & OHLER A. in prep. b. — Taxonomic notes on the Asian frogs of the tribe Paini (Ranidae, Dicroglossinae). 3. The status of *Chaparana gammii* (Anderson, 1871).
- DUBOIS A. & OHLER A. in prep. c. — Taxonomic notes on the Asian frogs of the tribe Paini (Ranidae, Dicroglossinae). 4. Sibling species distinguished from *Quasipaa spinosa* (David, 1875).
- DUBOIS A., OHLER A. & BIJU S. D. 2001. — A new genus and species of Ranidae (Amphibia, Anura) from south-western India. *Alytes* 19 (2-4): 53-79.
- FEI L. (ed.) 1999. — *Atlas of Amphibians of China*. Henan Press of Science and Technology, Zhengzhou, [ii] +

- 432 p. (in Chinese).
- HENNIG W. 1950. — *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin, 370 p.
- INGER R. F., ORLOV N. & DAREVSKY I. 1999. — Frogs of Vietnam: a report on new collections. *Fieldiana: Zoology* (n.s.) 92: i-iv + 1-46.
- JIANG J. & ZHOU K. 2005. — Phylogenetic relationships among Chinese ranids inferred from sequence data set of 12s and 16s rDNA. *Herpetological Journal* 15: 1-8.
- JIANG J., DUBOIS A., OHLER A., TILLIER A., CHEN X., XIE F. & STÖCK M. 2005. — Phylogenetic relationships of the tribe Painsi (Amphibia, Anura, Ranidae) based on partial sequences of mitochondrial 12s and 16s rRNA genes. *Zoological Science* 22: 353-362.
- KHAN M. S. & TASNIM R. 1989. — A new frog of the genus *Rana*, subgenus *Paa*, from Southwestern Azad Kashmir. *Journal of Herpetology* 23: 419-423.
- MURRAY J. A. 1885. — A new frog (*Rana sternosignata*) from Sind. *Annals and Magazine of Natural History* (5) 16: 120-121.
- 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.
- POPE C. H. & BORING A. M. 1940. — A survey of Chinese Amphibia. *Peking natural History Bulletin* 15: 13-86, 1 map.
- SWOFFORD D. L. 2001. — *PAUP**, *Phylogenetic Analysis Using Parsimony (* and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts (software).
- 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.
- WEBB R. G. 1978. — A systematic review of the Mexican frog *Rana sierramadrensis* Taylor. *Contributions in Science of the Natural History Museum of Los Angeles County* 300: 1-13.
- WU G. & ZHAO E. 1984. — A rare karyotype of anurans, the karyotype of *Rana phrynoides*. *Acta herpetologica sinica* 3: 29-32, pl. 3 (in Chinese).
- WU G.-F. & ZHAO E.-M. 1995. — A new ranid species of the *spinosa* group from Sichuan, in ZHAO E.-M. (ed.), Amphibian zoogeographic division of China. *Herpetological Series* 8: 52-55.

Submitted on 26 January 2005;
accepted on 11 July 2005.

APPENDIX

Species and specimens used in the morphological cladistic analysis presented here. The specific names in the first column are those that appear in the cladogram of Figure 1 and in Tables 1 and 2. The binomen of species (generic name combined with the specific name) in the second column are those as derived from the analysis presented in this paper. The specimens are kept in the following collections: American Museum of Natural History, New York (AMNH); National History Museum, London (BMNH); Museum of Comparative Zoology, Harvard (MCZ); Muséum national d'Histoire naturelle, Paris (MNHN); Naturhistorisches Museum Wien (NMW); Naturalis, National Museum of Natural History, Leiden (RMNH); Senckenberg Museum, Frankfurt (SMF); United States National Museum, Smithsonian Institution, Washington D.C. (USNM); Zoological Museum Kobenhavn (ZMK); Zoological Survey of India, Kolkata (ZSI).

Specific name	Binomen of species	Tribe	Collection localities and specimen numbers
<i>aenea</i>	<i>Chaparana aenea</i> (Smith, 1922)	Paini	See list in Dubois & Ohler (2005)
<i>annandalii</i>	<i>Chaparana annandalii</i> (Boulenger, 1920)	Paini	See list in Dubois (1976)
<i>blanfordii</i>	<i>Chaparana blanfordii</i> (Boulenger, 1882)	Paini	See list in Dubois (1976)
<i>blythii</i>	<i>Limnionectes blythii</i> (Boulenger, 1920)	Limnionectini	See list in Dubois & Ohler (2001)
<i>boulengeri</i>	<i>Quasipaa boulengeri</i> (Günther, 1889)	Paini	China, <i>Guizhou</i> (MNHN 1912.0356); Leishan (MNHN 2001.0290); Yijiang (MNHN 2001.0288, 0289); <i>Sichuan</i> , Tianguan (MNHN 2001.0283)
<i>bourreti</i>	<i>Gynandropaa bourreti</i> (Dubois, 1987)	Paini	See list in Ohler <i>et al.</i> (2000)
<i>chayuensis</i>	<i>Chaparana chayuiensis</i> (Ye, 1977)	Paini	China, <i>Xizang</i> , Chayu (MNHN 2001.0287)
<i>chinensis</i>	<i>Hoplobatrachus chinensis</i> (Osbeck, 1765)	Dicroglossini	See list in Dubois <i>et al.</i> (2001)
<i>cyanophlyctis</i>	<i>Euphylyctis cyanophlyctis</i> (Schneider, 1799)	Dicroglossini	See list in Dubois <i>et al.</i> (2001)
<i>delacouri</i>	<i>Annandia delacouri</i> (Angel, 1928)	Limnionectini	See list in Dubois (1987)
<i>ercepeae</i>	<i>Chaparana ercepeae</i> (Dubois, 1974)	Paini	See list in Dubois (1976)
<i>exilispinosa</i>	<i>Quasipaa exilispinosa</i> (Liu & Hu, 1975)	Paini	China, <i>Hong Kong</i> , The Peak (MNHN 1988.7891-7893; MNHN 2003.0003)
<i>fasciculispina</i>	<i>Quasipaa fasciculispina</i> (Inger, 1970)	Paini	Thailand, <i>Changwat Cahntaburi</i> , Kao Soi Dao (MNHN 1989.0706-0710); and list in Ohler <i>et al.</i> (2002)
<i>gammii</i>	<i>Chaparana gammii</i> (Anderson, 1871)	Paini	See list under the name <i>Rana sikimensis</i> in Dubois (1976)
<i>hazarensis</i>	<i>Allopaa hazarensis</i> (Dubois & Khan, 1979) n. comb.	Paini	Pakistan, Barmoch (USNM 257534, holotype of <i>Rana barmochensis</i> Khan & Taksim, 1989; AMNH A102457); and list in Dubois & Khan (1980)
<i>liebigii</i>	<i>Chaparana liebigii</i> (Günther, 1860)	Paini	See list in Dubois (1976)
<i>limnocharis</i>	<i>Fejervarya limnocharis</i> (Gravenhorst, 1829)	Dicroglossini	See lists in Dubois <i>et al.</i> (2001); Ohler <i>et al.</i> (2000); Veith <i>et al.</i> (2001)
<i>maculosa</i>	<i>Chaparana maculosa</i> (Liu, Hu & Yang, 1960)	Paini	China, <i>Yunnan</i> , Jingdong (MNHN 2001.0281)
<i>minica</i>	<i>Chaparana minica</i> (Dubois, 1975)	Paini	See list in Dubois (1976)
<i>parkeri</i>	<i>Nanorana parkeri</i> (Stejneger, 1927)	Paini	China, <i>Xizang</i> (MNHN 1988.7907-7910); Kampa (MNHN 2003.0004); Lhasa (MNHN 1982.1079-1094)
<i>polunini</i>	<i>Chaparana polunini</i> (Smith, 1951)	Paini	See list in Dubois (1976)
<i>quadranus</i>	<i>Gynandropaa quadranus</i> (Liu, Hu & Yang, 1960)	Paini	China, <i>Sichuan</i> , Wushan (MNHN 2001.0286)
<i>robertingeri</i>	<i>Quasipaa robertingeri</i> (Wu & Zhao, 1995)	Paini	China, <i>Sichuan</i> , Hejiang (MNHN 2001.0285)
<i>rostandi</i>	<i>Chaparana rostandi</i> (Dubois, 1974)	Paini	See list in Dubois (1976)
<i>shini</i>	<i>Quasipaa shini</i> (Ahl, 1930)	Paini	China, <i>Guizhou</i> , Leishan (MNHN 2001.0284; MCZ 17651)
<i>spinosa</i>	<i>Quasipaa spinosa</i> (David, 1875)	Paini	China, <i>Fujian</i> , Choangan (MNHN 2001.0292; <i>Guangxi</i> , Jinxiu (MNHN 2001.0291)
<i>sternosignata</i>	<i>Chrysopaa sternosignata</i> (Murray, 1885) n. comb.	Paini	Afghanistan, Arbarp (BMNH 1940.3.1.6-9); Ganz (SMF 67971, 67972); Hokak (NMW 19602.1-3); Kabul (SMF 68292; ZMK R.07294-07311); Kaikaj (ZMK R.07312, 07313); Karokh (NMW 18608); Mukur (ZMK R.07288); Sinjiri (MNHN 1994.4505) Pakistan, Baleli (AMNH 68382-68385); Bruwery Nala (SMF 47764); Dhobi Ghat (SMF 62833-62834); Hanna valley (SMF 62837); near Mastung (AMNH 75190-75193); near Pishin (AMNH 75198-75202.A-D, AMNH 68386-68389, AMNH 75195-75197); near Quetta (AMNH 75194; AMNH 57971-57976; BMNH 1891.4.14.21-22; BMNH 1947.2.1.21-22; SMF 62835-62836; SMF 65888); Yaseen (SMF 47763)
<i>unculuanus</i>	<i>Chaparana unculuanus</i> (Liu, Hu & Yang, 1960)	Paini	See list in Dubois & Ohler (2005)
<i>vicina</i>	<i>Chaparana vicina</i> (Stoliczka, 1872)	Paini	India, <i>Himachal Pradesh</i> , Khoti (MNHN 1985.1108-1123); Kotegurh (NMW 13429); Manali (MNHN 1985.1076-1107); Mussoorie (BMNH 1905.10.27.9-10); Simla (BMNH 1909.7.12.40; NMW 2548.1-2; RMNH 4158); <i>Jammu and Kashmir</i> , Patnitop (MNHN 1985.1046-1050); Sanasar (MNHN 1985.1051-1075) Pakistan, Murree (ZSI 9147)
<i>yunnanensis</i>	<i>Gynandropaa yunnanensis</i> (Anderson, 1879)	Paini	China (MNHN 1907.0013, 1907.0208); <i>Yunnan</i> , Dongchuan Shi ("Tongchuan Fu"; 26°10'N, 103°02'E) (BMNH 1947.2.3.76); and list in Dubois (1987)