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SORTING OUT MOSS FROGS: mtDNA DATA ON TAXONOMIC DIVERSITY AND PHYLOGENETIC RELATIONSHIPS OF THE INDOCHINESE SPECIES OF THE GENUS *Theloderma* (ANURA, RHACOPHORIDAE)

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We discuss phylogenetic relationships and taxonomic diversity of the rhacophorid frogs of the genus *Theloderma* in sight of the novel phylogenetic data obtained from the Bayesian analysis of the up to 1987 bp length fragment of mtDNA (12S rRNA, tRNA^{val}, and 16S rRNA) from the 90 specimens of the 21 nominal species of *Theloderma* and 3 species of *Nyctixalus*. Our data suggest monophyly of the tribe Nyctixalini, including *Th. moloch*, and indicate deep divergence between the three major clades: *Th. horridum* + *Th. stellatum* group, *Nyctixalus* and the rest of the *Theloderma* species (*Theloderma sensu stricto*). We establish new subgenus *Stelladerma* subgen. nov. for *Th. horridum* + *Th. stellatum* group and discuss provisional taxonomy of Nyctixalini. We also indicate that the taxonomic status of the certain Indochinese *Theloderma* requires reassessment. In particular, our data suggest deep divergence between Malayan and Indochinese taxa of *Th. asperum* group and indicate non-monophyly of *Th. asperum sensu lato*; we resurrect the name *Th. albopunctatum* (Liu et Hu, 1962) for the Indochinese species. We provide molecular evidence for syninomization of *Th. chuyangsinense* Orlov et al., 2012 with *Th. palliatum* Rowley et al., 2011; as well as morphological and genetic evidence for syninomization of *Th. bambusicola* Orlov et al., 2012 with *Th. laeve* (Smith, 1924). We indicate a deep morphological and genetic differentiation within the *Th. truongsonense* (Orlov et Ho, 2005) complex. Finally, we report on the deep divergence within *Th. stellatum* Taylor, 1962 from eastern Thailand, southern Cambodia, and Vietnam, and describe a new species, *Theloderma vietnamense* sp. nov., based on morphological, acoustic and genetic lines of evidence.

Keywords: mitochondrial DNA; molecular phylogeny; sequence divergence; morphology; morphometrics; advertisement call; cryptic species; Vietnam.

INTRODUCTION

The family Rhacophoridae is one of the most diverse and speciose amphibian groups in the world, consisting of 388 currently recognized species in 17 genera and representing almost 6% of all known anurans (AmphibiaWeb, 2015; Frost, 2015). This largely arboreal group of frogs is distributed throughout sub-Saharan Africa, China, Southern and Southeast Asia, Japan, Taiwan, the Philippines, and the Greater Sunda Islands (Frost, 2015).

Among the rhacophorid genera, the taxonomy of *Theloderma* Tschudi, 1838 has been revised several times and has been a subject of recent intensive phylogenetic studies (e.g., Rowley et al., 2011; Dever et al., 2015; Nguyen et al., 2015). To date, 23 recognized species of *Theloderma* are distributed throughout Southeast

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Asia from Assam in northeastern India to Myanmar, southern China and Indochina, to Malay peninsula, Sumatra and Borneo of the Greater Sundas, but new species in the genus continue to be discovered with 11 species have been described in the last 15 years (Frost, 2015).

The frogs of the genus *Theloderma* (see Fig. 1) are small (*Th. andersoni* SVL up to 20 mm; *Th. bambusicola* SVL up to 26 mm) to medium (*Th. horridum* SVL up to 45 mm, Fig. 1*a*) and large sized (*Th. ryabovi* SVL up to 65 mm, Fig. 1*i*, *j*; *Th. corticale* SVL up to 75 mm, Fig. 1*l*) strictly arboreal species, which are supposed to be distinguished from other Rhacophoridae by the following combination of morphological attributes: (1) having some degree of tuberculate skin with sometimes calcified warts on the dorsum [though skin is totally smooth in *Th. bambusicola* (Fig. 1*t*), and almost smooth in *Th. laeve* (Fig. 1*v*), *Th. lateriticum* (Fig. 1*o*) and *Th. licin* (Fig. 1*e*)], (2) two slips of M. extensor digitorum communis longus (but only shown for *Th. gordoni* and *Th. stellatum* by Liem, 1970), (3) Y-shaped terminal phalanges (vs. simple or bifurcate in *Philautus*), (4) a distinct tympanum, (5) rounded canthus rostralis (vs. sharp in *Nyctixalus* Boulenger, 1882; Fig. 1*d*), (6) absence of bony ridges from canthus rostralis to occiput (vs. present in *Nyctixalus*), (7) skin on head not co-ossified with skull (vs. co-ossified in *Nyctixalus*), and (8) reproductive behavior of depositing eggs in water-filled tree hollows, karst crevices or man-made ponds (this feature shared with closely-related genus *Nyctixalus* and more remote *Kurixalus*) (Taylor, 1962; Liem, 1970; Manthey and Grossmann, 1997; Orlov et al., 2006, 2010, 2012; McLeod and Norhayati, 2007; Rowley et al., 2011; Dever et al., 2015; Nguyen et al., 2015).

However, none of these characteristics forms a morphological synapomorphy for *Theloderma* with all of them being convergent characters found in other Rhacophoridae members, though their combination appears to be unique for *Theloderma* (Liem, 1970; Dever et al., 2015). Therefore, because no morphological synapomorphy is known for the genus *Theloderma*, the monophyly of the group has been put into question (Wilkinson and Drewes, 2000; Wilkinson et al., 2002; McLeod and Norhayati, 2007; Yu et al., 2007, 2008; Bain et al., 2009; Li et al., 2008, 2009, 2013; Rowley et al., 2011; Nguyen et al., 2015; Dever et al., 2015). Furthermore, from the results of recent extensive fieldwork and molecular analyses, some species with smooth skin or unwebbed fingers, which were once placed in other Rhacophoridae genera such as *Philautus*, *Chirixalus*, and *Aquixalus*, have been transferred to this genus (e.g., Yu et al., 2007; Rowley et al., 2011; Orlov et al., 2006, 2012; Nguyen et al., 2014, 2015).

Traditional works on phylogenetic relationships of Rhacophoridae are scarce and include few members of *Theloderma*. The most extensive work by Liem (1970) suggested close affinities between *Theloderma* and *Nyctixalus* based mostly on similarities in reproductive biology; though the phylogenetic analysis implemented in this work placed these genera distantly from each other. Later, Channing (1989) suggested sister relationships between *Theloderma* and *Nyctixalus* based on morphological data. Recently, Dubois (2005) assigned both *Theloderma* and *Nyctixalus* to the tribe Philautini (including also *Aquixalus*, *Kurixalus*, and *Philautus*), whereas more recently Grosjean et al. (2008) proposed separation of *Theloderma* and *Nyctixalus* in the new tribe Nyctixalini.

This assignment and distant phylogenetic position of *Theloderma* and *Nyctixalus* in respect to other members of the subfamily Rhacophorinae was also supported by subsequent phylogenetic analyses (Li et al., 2008, 2009, 2013; Pyron and Wiens, 2011). Based on the analysis of mtDNA genetic markers, Li et al. (2008) showed sister clade relationships between *Nyctixalus* (*N. pictus* and *N. spinosus*) and *Theloderma* (*Th. corticale*, *Th. rhododiscum*, and *Th. asperum*) and were first to report the distant phylogenetic position of an enigmatic rhacophorid specimen identified as *Th. moloch*, not forming a monophyly with *Theloderma* + *Nyctixalus* clade.

Yu et al. (2008) based on the analysis of mtDNA genetic markers, suggested sister clade relationships of *Theloderma* and *Nyctixalus* and showed that *Philautus albopunctatus* from China should be assigned to the genus *Theloderma* and appears to be a junior synonym of *Th. asperum*. This result was also confirmed by Rowley et al. (2011) who performed a DNA-barcoding study based on short-length fragments of the 16S rRNA mtDNA gene and obtained a phylogenetic tree, suggesting paraphyly of *Theloderma* with respect to the genus *Nyctixalus*, but poorly resolving phylogenetic relationships among nine species of *Theloderma* (*Th. rhododiscum*, *Th. palliatum*, *Th. bicolor*, *Th. corticale*, *Th. gordoni*, *Th. nebulosum*, *Th. truongsonense*, *Th. asperum*, *Th. stellatum*) and one species of *Nyctixalus* (*N. pictus*) studied. The study by Rowley et al. (2011) also illustrated that *Philautus truongsonensis* should be shifted to the genus *Theloderma*, based on mtDNA genetic data.

One of the most extensive studies performed recently is the work of Nguyen et al. (2015) who included 17 out of 23 *Theloderma* species and all the three recognized *Nyctixalus* species in their analysis, based on 2412 bp sequences of the mitochondrial DNA genes of 12S rRNA, tRNA^{val}, and 16S rRNA. Their study clarified preliminary phylogenetic relationships within the genus and assumed sister clade relationships between *Theloderma* and *Nyctixalus*. According to their data *Theloderma mo-*

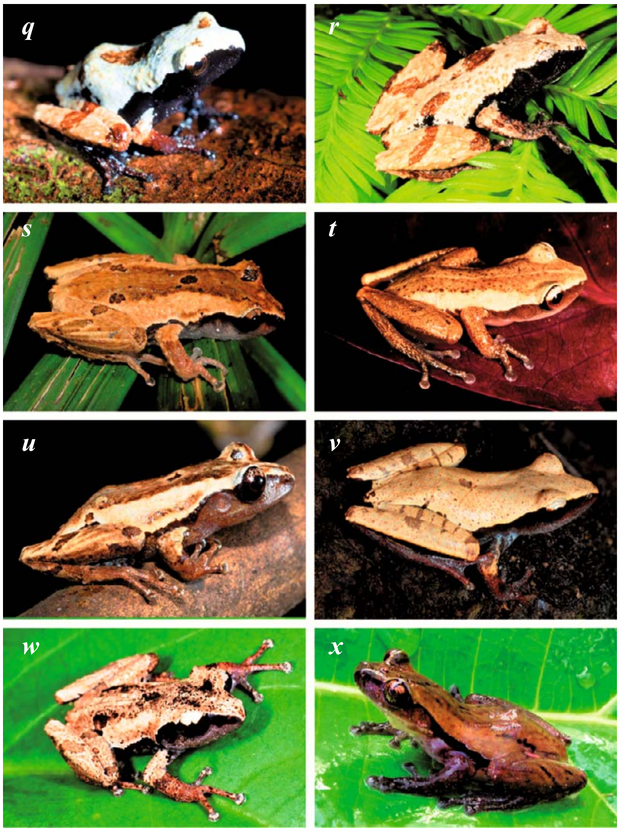

Fig. 1. *Theloderma* species of Indochina and Thailand. ***a***, *Th. horridum* (Thailand, Satun Province, Tha Le Ban N. P., photo N. A. Poyarkov); ***b***, *Th. stellatum* (Thailand, Uthai Thani Province, Hauy Kha Khaeng W. S.; photo P. Pawangkhanant); ***c***, *Th.* cf. *stellatum* [described below as *Th. vietnamense* sp. nov.] (Vietnam, Kon Tum Province, Kon Plong); ***d***, *Th. pictum* (Thailand, Satun Province, Tha Le Ban N. P.; photo P. Pawangkhanant); ***e***, *Th. licin* (Thailand, Satun Province, Tha Le Ban N. P., photo P. Pawangkhanant); ***f***, *Th.* cf. *asperum*, northern population (Vietnam, Vinh Phuc Province, Tam Dao; photo N. L. Orlov); ***g***, *Th.* cf. *asperum*, southern population (Vietnam, Kon Tum Province, Kon Plong; photo N. L. Orlov); ***h***, *Th. asperum* (Thailand, Kamphaeng Phet Province, photo P. Pawangkhanant); ***i***, *Th. ryabovi*, male (Vietnam, Kon Tum Province, Kon Plong; photo N. L. Orlov); ***j***, *Th. ryabovi*, female (Vietnam, Kon Tum Province, Kon Plong; photo N. L. Orlov); ***k***, *Th. bicolor* (Vietnam, Lao Cai, Fan Si Pan Mt.; photo N. L. Orlov); ***l***, *Th. corticale* (Vietnam, Quang Tri Province, Ban Cup; photo N. L. Orlov); ***m***, *Th. gordoni*, northern population (Vietnam, Lao Cai, Sa Pa; photo N. L. Orlov); ***n***, *Th. gordoni*, southern population (Vietnam, Kon Tum Province, Kon Plong; photo N. L. Orlov); ***o***, *Th. lateriticum* (Vietnam, Bac Giang; photo Nguyen Thien Tao); ***p***, *Th. rhododiscum* (China, Yunnan; photo N. L. Orlov); ***q***, *Th. palliatum* (Vietnam, Lam Dong Province, Bi Doup; photo E. A. Galoyan); ***r***, *Th. chuyangsinense* (Vietnam, Dak Lak Province, Chu Yang Sin; photo N. A. Poyarkov); ***s***, *Th. truongsonense* (Vietnam, Quang Tri Province, Ban Cup; photo N. L. Orlov); ***t***, *Th. bambusicola* (Vietnam, Lam Dong Province, Cat Loc; photo N. A. Poyarkov); ***u***, *Th.* cf. *nebulosum* (Vietnam, Kon Tum Province; photo N. L. Orlov); ***v***, *Th.* cf. *truongsonense* (Vietnam, Kon Tum Province, Kon Plong; photo N. L. Orlov); ***w***, (Vietnam, Khanh Hoa Province, Hon Ba; photo A. B. Vassilieva); ***x***, *Th. petilum* (Vietnam, Dien Bien Province, Muong Nhe; photo Le Trung Dung).

loch is phylogenetically outside *Theloderma* and *Nyctixalus* clade and closer to *Chiromantis*, *Feihyla*, *Gracixalus*, *Kurixalus*, *Philautus*, *Polypedates*, *Raorchestes*, and *Rhacophorus*.

However, these results contradict the recent results by Li et al. (2013) based on the large dataset of 2041 bp of mtDNA and 3225 bp of five nuclear DNA genes for all rhacophorid genera. Although this study included a more limited sampling of *Theloderma* (*Th. rhododiscum*, *Th. corticale*, *Th. asperum*, *Th.* cf. *horridum*, and *Th. moloch*) and *Nyctixalus* (*N. pictus* and *N. spinosus*), it confirmed Nyctixalini as the most basal split within Rhacophorinae with exception for *Liuixalus*, indicated paraphyly of *Theloderma* in respect with *Nyctixalus*, with *Th. horridum* forming the most basal split within Nyctixalini, and nested *Th. moloch* within *Theloderma* + *Nyctixalus* clade. Li et al. (2013) estimated the basal split in Nyctixalini as ca. 29 mya, whereas the basal split of *Theloderma sensu stricto* (excluding *Nyctixalus* and *Th. horridum*) was estimated as 26.1 – 16.4 mya.

Within Southeast Asia, the Indochinese peninsula is renowned for its high diversity of amphibian species (Orlov and Ananjeva, 2007; Bain and Hurley, 2012 and references therein). The southern part of Indochina is comparatively poorly investigated area with many new species of amphibians and reptiles having been discovered from this region during the last several years, both from highland areas of the southern Annamite, or Truong Son Mountains (Nazarov et al., 2008, 2012; Rowley et al., 2010, 2011; Ngo and Chan, 2010; Stuart et al., 2011; Orlov et al., 2012; Vassilieva et al., 2014; Poyarkov et al., 2014, 2015), and from lowland areas of southern Vietnam (Stuart et al., 2006; Ngo and Bauer, 2008; Geissler et al., 2009, 2014; Orlov et al., 2009, 2012; Rowley et al., 2012; Chan et al., 2013; Hartmann et al., 2013; Ngo, 2013; Vassilieva et al., 2013; Poyarkov et al., 2014).

In recent years, the Indochinese peninsula was the center of discovery of new *Theloderma* species, with 14 species of *Theloderma* and 1 species of *Nyctixalus* being reported from its territory (see Fig. 1); 9 of these species were discovered and described within a decade (Orlov and Ananjeva, 2007; Nguyen et al., 2009; Orlov et al., 2010, 2012; Rowley et al., 2011; Frost, 2015). Some newly discovered small-sized species are morphologically conserved, mainly differentiated by coloration and their taxonomic relationships remain unclear, whereas the others were transferred to *Theloderma* from other rhacophorid genera (Rowley et al., 2011; Orlov et al., 2012; Nguyen et al., 2014). Though the work of Nguyen et al. (2015) had elucidated the phylogenetic relationships within the genus, some of them remain controversial and contradictory to the results by Li et al. (2013), and the taxon sampling for Indochina remains limited.

Therefore, the present paper is focused on scrutinizing diversity of *Theloderma* frogs of Indochina by molecular phylogenetic analysis of 1987 bp 12S rRNA – 16S rRNA mtDNA fragment for 90 specimens of 21 nominal species of *Theloderma* and 3 species of *Nyctixalus*. We also discuss genus-level taxonomy of Nyctixalini and update data on distribution and systematics of Indochinese taxa. Finally, we describe a new species of *Theloderma* frogs from southern and central Vietnam based on genetic, morphological and acoustic lines of evidence.

MATERIAL AND METHODS

Sample collection. All specimens were collected during fieldwork in Vietnam and Thailand between 2007 and 2014. The geographic position of the surveyed localities and samples included in the molecular analyses is given in Table 1. The distribution of *Theloderma stellatum* Taylor, 1962 in southern Indochina (eastern Thailand, southern Cambodia and Vietnam) is shown in Fig. 5, surveyed localities are marked with filled icons. Geographic coordinates and altitude were obtained using a Garmin GPSMAP 60CSx GPS receiver and recorded in datum WGS 84. The newly collected specimens were deposited in the herpetological collection of the Zoological Museum of Moscow State University (ZMMU) in Moscow, Russia, the Zoological Institute RAS (ZISP) in St. Petersburg, Russia, and the Vietnam National Museum of Nature (VNMN) in Hanoi, Vietnam. Comparative materials examined are stored in herpetological collections of ZMMU, ZISP, and National Science Museum of Thailand (NHMT) in Bangkok, Thailand.

Morphological analysis. Examined specimens are listed in *Appendix 1*. Specimens were photographed in life, and tissue samples for genetic analysis were taken prior to preservation and stored in 96% ethanol. Specimens were preserved in 72 – 75% ethanol. Sex was determined by direct observation of calling in life, and by examining for the presence of nuptial pads in males and/or gonadal inspection by dissection.

Adults. We recorded morphological data from adult specimens fixed and stored in 75% ethanol. All measurements were taken using digital caliper under the light dissecting microscope to the nearest 0.1 mm; morphometrics follow Orlov et al. (2012) and Milto et al. (2013) and includes the following 27 measurements: SVL, snout-vent length; A-G, axilla to groin, measured as distance from posterior base of forelimb at its emergence from body to anterior base of hind limb at its emergence from body; HW, head width at the greatest cranial width; HL, head length measured from the rear of the lower jaw to the tip of the snout; HD, head depth, measured as the greatest transverse depth of head, taken beyond interorbital region; UEW, upper eyelid width measured as the greatest width of upper eyelids; IOD, interorbital distance; IND, internarial distance measured as distance between nostrils; ED, horizontal diameter of eye; TD, horizontal diameter of tympanum; ESL, tip of snout – eye distance; TED, tympanum – eye distance measured from anterior edge of tympanum to posterior corner of the eye; END, eye to nostril distance measured as distance from anterior corner of eye to nostril; FLL, length of forelimb measured from the tip of disk of finger III to axilla; FFL, first finger length; TFL, third finger length; FTD, maximal diameter of disc of finger III; NPL, nuptial pad length, measured for males only; MKTe, length of external metacarpal tubercle; HLL, length of hindlimb measured from the tip of disk of toe IV to groin; FL, femur length; TL, tibia length; FOT, length of hindlimb measured from the tip of disk of toe IV to posterior edge of tibia; FTL, first toe length; FFTL, fourth toe length; HTD, diameter of the fourth toe tip measured as the greatest diameter of disc on fourth toe; MTTi, length of internal metatarsal tubercle. Skin texture, dorsal coloration, ventral coloration, and presence of supratympanic folds, circummarginal grooves, dorsolateral folds, vomerine teeth, hind limb and forelimb webbing, dorsal, lateral and ventral coloration were recorded. The webbing formula followed Savage and Heyer (1997).

Larval stages. Morphological description of larval stages included the following 16 measurements: TL, total length; BL, body length; TaL, tail length; BW, maximal body width; BH, maximal body height; TH, maximal tail height; SVL, snout-vent length; SSp, snout-spiracle length; UF, maximal upper tail fin height; LF, maximal lower fin height; IN, internarial distance; IP, interpupilar distance; RN, rostro-narial distance; NP, naro-pupilar distance; ED, eye diameter; ODW, oral disk width. LTRF (labial tooth row formula) was recorded following Wassersug et al. (1981). Tadpoles were staged after Gosner (1960); morphometrics followed Grosjean (2001).

The diagnosis of the genus *Theloderma* and morphological characters chosen for comparison were taken from Wolf (1936); Taylor (1962); Inger (1966); Liem (1970); Zhao and Adler (1993); Orlov (1997, 2007); Orlov et al. (2006, 2010, 2012); McLeod and Norhayati (2007); Rowley et al. (2011).

We obtained comparative morphological data from museum specimens of *Theloderma* and allied taxa and from photographs of these specimens in life and from the following literature: *Theloderma andersoni* (Anderson, 1879; Ahl, 1927, 1931; Bourret, 1942; Fei et al., 1990, 2009, 2010; Mathew and Sen, 2010); *Th. asperum* (Fig. 1*f* – *h*; Boulenger, 1886; Smith, 1930; Taylor, 1962; Liu and Hu, 1962; Fei et al., 1990, 2009, 2010; Li et al., 2011); *Th. baibengense* (Jiang et al. in Fei et al., 2009; Fei et al., 2010); *Th. bambusicolum* (Fig. 1*t*; Orlov et al., 2012); *Th. bicolor* (Fig. 1*k*; Bourret, 1937; Orlov et al., 2010); *Th. chuyangsinense* (Fig. 1*r*; Orlov et al., 2012); *Th. corticale* (Fig. 1*l*; Boulenger, 1903; Orlov et al., 2010); *Th. gordoni* (Fig. 1*m*, *n*; Taylor, 1962; Chan-ard, 2003; Orlov et al., 2010); *Th. horridum* (Fig. 1*a*; Boulenger, 1903; Smith, 1926, 1930; Taylor, 1962; Manthey and Grossmann, 1997; Das, 2007); *Th. kwangsiense* (Liu and Hu, 1962; Fei et al., 1990, 2009, 2010; Orlov et al., 2010; Li et al., 2011); *Th. laeve* (Fig. 1*t*, V; Smith, 1924; Orlov and Ananjeva, 2007; Orlov et al., 2012); *Th. lateriticum* (Fig. 1*o*; Bain et al., 2009); *Th. leporosum* (Tschudi, 1838; Manthey and Grossmann, 1997; Chan and Norhayati, 2009); *Th. licin* (Fig. 1*e*; McLeod and Norhayati, 2007; Das et al., 2013); *Th. moloch* (Annandale, 1912; Liem, 1970; Fei et al., 1990, 2009, 2010; Mathew and Sen, 2010; Orlov et al., 2010); *Th. nagalandense* (Orlov et al., 2006); *Th. nebulosum* (Fig. 1*u*; Rowley et al., 2011); *Th. palliatum* (Fig. 1*q*; Rowley et al., 2011; Orlov et al., 2012); *Th. petilum* (Fig. 1*x*; Stuart and Heatwole, 2004; Nguyen et al., 2014); *Th. phrynoderma* (Boulenger, 1893; Ahl, 1927; Manthey and Grossmann, 1997; Dever et al., 2015); *Th. rhododiscum* (Fig. 1*p*; Liu and Hu, 1962; Fei et al., 1990, 2009, 2010; Orlov et al., 2010; Li et al., 2011); *Th. ryabovi* (Fig. 1*i*, *j*; Orlov et al., 2006, 2010; Orlov, 2007); *Th. stellatum* (Fig. 1*b*, *c*; Taylor, 1962; Chan-ard, 2003; Orlov and Ananjeva, 2007; Orlov et al., 2010); *Th. truongsonense* (Fig. 1*s*, *w*; Orlov and Ho, 2005; Rowley et al., 2011; Orlov et al., 2012); *Nyctixalus margaritifer* (Boulenger, 1882; Smith, 1931; Inger, 1966; Manthey and Grossmann, 1997); *N. pictus* (Fig. 1*d*; Peters, 1871; Taylor, 1962; Inger, 1966; Liem, 1970; Manthey and Grossmann, 1997; Das, 2007); and *N. spinosus* (Taylor, 1920; Inger, 1954). Due to the high undiagnosed diversity within the genus, where available, we relied on examination of type specimens, topotypic material and/or original species descriptions.

Statistical analyses. The morphological data of *Theloderma* sp. nov. and *Theloderma stellatum* was analyzed by using software STATISTICA 10 (StatSoft, 2010). Subadult and juvenile specimens were excluded from the statistical morphological analyses. We performed an analysis of variance (ANOVA) of morphological characters to identify characters showing significant differences between the two OTUs (sexes were analyzed together). Those characters that showed no significant differences ($p > 0.05$), were excluded from the concluding principal component analysis (PCA).

DNA isolation, PCR and sequencing. The full list of samples included in the molecular analyses is given in Table 1. For molecular analysis, total genomic DNA was extracted from ethanol-preserved muscle or liver tissues

TABLE 1. Specimens and Genbank Sequences of *Theloderma* used in Molecular Analyses and the Newly Proposed Taxonomy

No.	Taxon	Specimen ID	Genbank AN	Country	Locality	Reference	Proposed taxonomy
1	*Rana kukunoris*	KIZ 0152	KC465786	China	Qinghai	Li et al., 2013	—
2	*Mantella aurantiaca*	UMMZ 201411	DQ283035	Madagascar	Toamasina: Moramanga	Frost et al., 2006	—
3	*Buergeria buergeri*	TTU-R-11759	AF458122	Japan	—	Wilkinson et al., 2002	—
4	*Buergeria japonica*	UMFS 5821	DQ283055	China	Taiwan: Yilan	Frost et al., 2006	—
5	*Buergeria oxycephala*	SCUM 050267YJ	EU215524	China	Hainan	Li et al., 2008	—
6	*Buergeria robusta*	TTU-R-11761	AF458125	China	Taiwan	Wilkinson et al., 2002	—
7	*Chiromantis doriae*	SN 030051	EU215527	China	Hainan	Li et al., 2008	—
8	*Chiromantis xerampelina*	CAS; no number	AF458132	—	—	Wilkinson et al., 2002	—
9	*Feihyla vittata*	KIZ 0001rao	GQ285684	China	Yunnan	Li et al., 2009	—
10	*Feihyla kajau*	FMNH 269090	KC465789	Malaysia	Sarawak: Bintulu Div.	Li et al., 2013	—
11	*Feihyla palpebralis*	Vietnam 712	GQ285681	Vietnam	Lam Dong	Li et al., 2009	—
12	*Gracixalus gracilipes*	KIZ 060821196Rao	GQ285668	China	Yunnan: Daweishan	Li et al., 2009	—
13	*Kurixalus banaensis*	ROM 32986	GQ285667	Vietnam	Gia Lai: Krong Pa	Li et al., 2009	—
14	*Kurixalus bisacculus*	200602010	KC465801	China	Yunnan: Wenshan	Li et al., 2013	—
15	*Kurixalus idiootocus*	SCUM 061107L	EU215547	China	Taiwan: Lianhuachi	Li et al., 2008	—
16	*Kurixalus verrucosus*	CAS HERP 224381	KC465822	Myanmar	Kachin: Putao	Li et al., 2013	—
17	*Liuixalus hainanus*	LJT V15	KC465826	China	Hainan: Diaoluoshan	Li et al., 2013	—
18	*Philautus abditus*	ROM 33145	GQ285673	Vietnam	Gia Lai: Krong Pa	Li et al., 2009	—
19	*Polypedates* cf. *leucomystax*	ROM 29908	KC465833	Vietnam	Gia Lai: Tram Lap	Li et al., 2013	—
20	*Polypedates* cf. *megacephalus*	HN 0806103	KC465830	China	Hainan: Jianfengling	Li et al., 2013	—
21	*Polypedates megacephalus*	6212RAO	KC465834	China	Xizang: Motuo	Li et al., 2013	—
22	*Raorchestes* sp.	ROM 38828	KC465838	Vietnam	Tuyen Quang: Pac Ban	Li et al., 2013	—
23	*Rhacophorus annamensis*	KIZ 64	JX219448	Vietnam	Binh Phuoc: Bu Gia Map	Li et al., 2012	—
24	*Rhacophorus dennysi*	Li06	JX219433	China	Hunan	Li et al., 2012	—
25	*Rhacophorus kio*	SCUM 37941C	EU215532	China	Yunnan: Xishuangbanna	Li et al., 2008	—
26	*Rhacophorus maximus*	Rao6241	JX219411	China	Xizang: Motuo	Li et al., 2012	—
27	*Rhacophorus schlegelii*	—	NC007178	Japan	Hiroshima	Sano et al., 2005	—
28	*Nyctixalus margaritifer*	TNHCJAM 3030	EU178087	Indonesia	Java	Biju et al., 2008	*Th. margaritifer*
29	*Nyctixalus pictus*	FMNH 231095	DQ283133	Malaysia	Sabah: Lahad Datu	Frost et al., 2006	*Th. pictum*
30	*Nyctixalus pictus*	FMNH 231094	GQ204777; GQ204726	Malaysia	—	Meegaskumbura et al., 2010	*Th. pictum*
31	*Nyctixalus pictus*	—	AF215349	Malaysia	—	Vences 2000, unpubl.	*Th. pictum*
32	*Nyctixalus pictus*	NMBE 1056413	JN705355; JN377342	Malaysia	Sarawak: Batang Ai	Hertwig et al., 2013	*Th. pictum*
33	*Nyctixalus pictus*	MVZ 239460	GQ204783; GQ204732	Indonesia	—	Meegaskumbura et al., 2010	*Th. pictum*
34	*Nyctixalus pictus*	FMNH 231094 – 2	AF458135	Malaysia	—	Wilkinson et al., 2002	*Th. pictum*
35	*Nyctixalus pictus*	—	AF268255	Malaysia	—	Richards 2000, unpubl.	*Th. pictum*
36	*Nyctixalus pictus*	AH07001	GU154888	Malaysia	Sarawak: Gunung Mulu	Das and Haas 2010	*Th. pictum*
37	*Nyctixalus spinosus*	pet trade	KT461916	Philippines	Mindanao	this study	*Th. spinosum*
38	*Nyctixalus spinosus*	ACD 1043	DQ283114	Philippines	Mindanao	Frost et al., 2006	*Th. spinosum*
39	“*Theloderma*” *moloch*	6255Rao	GQ285679	China	Xizang: Motuo	Li et al., 2009	*Th. moloch*

TABLE 1 (continued)

No.	Taxon	Specimen ID	Genbank AN	Country	Locality	Reference	Proposed taxonomy
40	*Theloderma asperum*	KIZ 060821217	EF564522	China	Guangxi: Jinxiu	Yu et al., 2008	*Th. albopunctatum*
41	*Theloderma asperum*	KIZ 060821201	EF564521	China	Yunnan: Jinping	Yu et al., 2008	*Th. albopunctatum*
42	*Theloderma asperum*	VNMN J2916	KJ802913	Vietnam	Vinh Phuc	Nguyen et al., 2014	*Th. albopunctatum*
43	*Theloderma asperum*	VNMN 3540	KJ802914	Vietnam	Lao Cai	Nguyen et al., 2014	*Th. albopunctatum*
44	*Theloderma asperum*	060821203Rao	GQ285677	China	Yunnan: Jinping	Li et al., 2009	*Th. albopunctatum*
45	*Theloderma asperum*	ZRC 1.1. 9321	GQ204725; GQ204776	Malaysia	—	Meegaskumbura et al., 2010	*Th. asperum*
46	*Theloderma asperum*	pet trade	KT461929	Malaysia	Perak	this study	*Th. asperum*
47	*Theloderma asperum*	asperum-1	KT461884	Vietnam	Kon Tum: Kon Plong	this study	*Th. albopunctatum*
48	*Theloderma asperum*	asperum-2	KT461908	Vietnam	Kon Tum: Kon Plong	this study	*Th. albopunctatum*
49	*Theloderma asperum*	asperum-3	KT461909	Vietnam	Kon Tum: Kon Plong	this study	*Th. albopunctatum*
50	*Theloderma asperum*	ZMMU NAP-03557	KT461910	Vietnam	Hai Phong: Cat Ba	this study	*Th. albopunctatum*
51	*Theloderma asperum*	ZMMU NAP-03566	KT461911	Vietnam	Hai Phong: Cat Ba	this study	*Th. albopunctatum*
52	*Theloderma asperum*	ZMMU NAP-03575	KT461912	Vietnam	Hai Phong: Cat Ba	this study	*Th. albopunctatum*
53	*Theloderma asperum*	HN0806100	GQ285678	China	Hainan: Yinggeling	Li et al., 2009	*Th. albopunctatum*
54	*Theloderma bambusicolum*	ZMMU NAP-01640	KT461928	Vietnam	Lam Dong: Cat Loc	this study	*Th. laeve*
55	*Theloderma bambusicolum*	ZMMU NAP-01644	KT461907	Vietnam	Lam Dong: Cat Loc	this study	*Th. laeve*
56	*Theloderma bambusicolum*	ZMMU NAP-01645	KT461913	Vietnam	Lam Dong: Cat Loc	this study	*Th. laeve*
57	*Theloderma bambusicolum*	ZMMU NAP-02906	KT461883	Vietnam	Binh Phuoc: Bu Gia Map	this study	*Th. laeve*
58	*Theloderma bambusicolum*	ZMMU NAP-02907	KT461905	Vietnam	Binh Phuoc: Bu Gia Map	this study	*Th. laeve*
59	*Theloderma bambusicolum*	ZMMU NAP-02908	KT461906	Vietnam	Binh Phuoc: Bu Gia Map	this study	*Th. laeve*
60	*Theloderma bambusicolum*	ZMMU NAP-03383	KT461892; KT461900	Vietnam	Lam Dong: Bao Loc	this study	*Th. laeve*
61	*Theloderma bambusicolum*	ZMMU NAP-03408	KT461897; KT461898	Vietnam	Lam Dong: Bao Loc	this study	*Th. laeve*
62	*Theloderma bambusicolum*	ZMMU NAP-03409	KT461920	Vietnam	Lam Dong: Bao Loc	this study	*Th. laeve*
63	*Theloderma bicolor*	VNMN 1394	JX046475	Vietnam	Lao Cai: Sa Pa	Gawor et al., 2012	*Th. bicolor*
64	*Theloderma bicolor*	bicolor-2	KT461923	Vietnam	Ninh Binh: Cuc Phuong	this study	*Th. bicolor*
65	*Theloderma bicolor*	bicolor-3	KT461891; KT461899	Vietnam	Ninh Binh: Cuc Phuong	this study	*Th. bicolor*
66	*Theloderma bicolor*	IEBR A. 2011.4	JX046474	Vietnam	Lao Cai: Sa Pa	Gawor et al., 2012	*Th. bicolor*
67	*Theloderma bicolor*	VNMN 3536	KJ802915	Vietnam	Lao Cai	Nguyen et al., 2014	*Th. bicolor*
68	*Theloderma chuyangsinense*	ZMMU NAP-02757	KT461896; KT461904	Vietnam	Dak Lak: Chu Yang Sin	this study	*Th. palliatum*
69	*Theloderma chuyangsinense*	ZMMU NAP-02756	KT461930	Vietnam	Dak Lak: Chu Yang Sin	this study	*Th. palliatum*
70	*Theloderma chuyangsinense*	ZMMU NAP-02735	KT461926	Vietnam	Dak Lak: Chu Yang Sin	this study	*Th. palliatum*
71	*Theloderma chuyangsinense*	ZMMU NAP-02736	KT461927	Vietnam	Dak Lak: Chu Yang Sin	this study	*Th. palliatum*
72	*Theloderma corticale*	AMNH A161499	DQ283050	Vietnam	Vinh Phuc: Tam Dao	Frost et al., 2006	*Th. corticale*
73	*Theloderma corticale*	IEBR 3267	JX046477	Vietnam	Vinh Phuc: Tam Dao	Gawor et al., 2012	*Th. corticale*
74	*Theloderma corticale*	corticale-1	KT461885	Vietnam	Ninh Binh: Cuc Phuong	this study	*Th. corticale*
75	*Theloderma corticale*	corticale-2	KT461886	Vietnam	Ninh Binh: Cuc Phuong	this study	*Th. corticale*
76	*Theloderma corticale*	IEBR E193.15	JX046476	Vietnam	Vinh Phuc: Tam Dao	Gawor et al., 2012	*Th. corticale*
77	*Theloderma corticale*	VNMN J2892	KJ802916	Vietnam	Tuyen Quang	Nguyen et al., 2014	*Th. corticale*
78	*Theloderma corticale*	VNMN J2932	KJ802917	Vietnam	Vinh Phuc: Tam Dao	Nguyen et al., 2014	*Th. corticale*
79	*Theloderma gordoni*	VNMN 03013	JN688167	Vietnam	Nghe An	Rowley et al., 2011	*Th. gordoni*
80	*Theloderma gordoni*	VNMN PAE217	KJ802918	Vietnam	Son La	Nguyen et al., 2014	*Th. gordoni*

TABLE 1 (continued)

No.	Taxon	Specimen ID	Genbank AN	Country	Locality	Reference	Proposed taxonomy
81	*Theloderma gordoni*	KUHE 32447	KJ802919	Laos	Houaphan	Nguyen et al., 2014	*Th. gordoni*
82	*Theloderma horridum*	LJT W44	KC465843	Malaysia	—	Li et al., 2013	*Th. horridum*
83	*Theloderma horridum*	LJT W45	KC465842	Malaysia	—	Li et al., 2013	*Th. horridum*
84	*Theloderma horridum*	ZMMU NAP-04015	KT461890	Thailand	Satun	this study	*Th. horridum*
85	*Theloderma leporosum*	LJT W46	KC465841	Malaysia	—	Li et al., 2013	*Th. leporosum*
86	*Theloderma leporosum*	leporosum-1	KT461922	Malaysia	Selangor	this study	*Th. leporosum*
87	*Theloderma leporosum*	KUHE 52581	AB847128	Malaysia	Negeri Sembilan	Nguyen et al., 2014	*Th. leporosum*
88	*Theloderma licin*	KUHE 52599	KJ802920	Malaysia	Selangor	Nguyen et al., 2014	*Th. licin*
89	*Theloderma nebulosum*	ROM 39588	KT461887	Vietnam	Kon Tum: Ngoc Linh	this study	*Th. nebulosum*
90	*Theloderma nebulosum*	AMS R 173409	JN688168	Vietnam	Kon Tum: Ngoc Linh	Rowley et al., 2011	*Th. nebulosum*
91	*Theloderma nebulosum*	AMS R 173877/UNS00141	JN688169	Vietnam	Kon Tum: Ngoc Linh	Rowley et al., 2011	*Th. nebulosum*
92	*Theloderma palliatum*	AMS R 173130	JN688172	Vietnam	Lam Dong: Bi Doup — Nui Ba	Rowley et al., 2011	*Th. palliatum*
93	*Theloderma palliatum*	ZMMU NAP-01846	KT461893; KT461901	Vietnam	Lam Dong: Bi Doup — Nui Ba	this study	*Th. palliatum*
94	*Theloderma palliatum*	ZMMU NAP-02511	KT461894; KT461902	Vietnam	Lam Dong: Bi Doup — Nui Ba	this study	*Th. palliatum*
95	*Theloderma palliatum*	ZMMU NAP-02516	KT461895; KT461903	Vietnam	Lam Dong: Bi Doup — Nui Ba	this study	*Th. palliatum*
96	*Theloderma petilum*	HNUE MNA.2012.0001	KJ802925	Vietnam	Dien Bien: Muong Nhe	Nguyen et al., 2014	*Th. petilum*
97	*Theloderma rhododiscum*	AMNH A163892; A163893	DQ283392; DQ283393	Vietnam	Ha Giang: Tay Con Linh	Frost et al., 2006	*Th. rhododiscum*
98	*Theloderma rhododiscum*	KIZ060821063	EF564533	China	Guangxi: Jinxiu	Yu et al., 2008	*Th. rhododiscum*
99	*Theloderma rhododiscum*	KIZ060821170	EF564534	China	Guangxi: Jinxiu	Yu et al., 2008	*Th. rhododiscum*
100	*Theloderma rhododiscum*	SCUM 061102L	EU215530	China	Guangxi: Dayaoshan	Li et al., 2008	*Th. rhododiscum*
101	*Theloderma rhododiscum*	CIB GX200807048	KJ802921	China	Guangxi	Nguyen et al., 2014	*Th. rhododiscum*
102	*Theloderma ryabovi*	ryabovi-1	KT461914	Vietnam	Kon Tum: Kon Plong: Mang Canh	this study	*Th. ryabovi*
103	*Theloderma ryabovi*	ryabovi-2	KT461915	Vietnam	Kon Tum: Kon Plong: Mang Canh	this study	*Th. ryabovi*
104	*Theloderma stellatum*	stellatum-1	KT461918	Thailand	Chanthaburi: Phliu	this study	*Th. stellatum*
105	*Theloderma stellatum*	ZMMU NAP-03961	KT461917	Thailand	Nakhon Nayok: Nang Rong	this study	*Th. stellatum*
106	*Theloderma stellatum*	VNMN 3686	KJ802922	Vietnam	Phu Yen	Nguyen et al., 2014	*Th. vietnamense* sp. nov.
107	*Theloderma stellatum*	VNMN 3687	KJ802923	Vietnam	Phu Yen	Nguyen et al., 2014	*Th. vietnamense* sp. nov.
108	*Theloderma stellatum*	ZMMU NAP-00707	KT461889	Vietnam	Dong Nai: Nam Cat Tien	this study	*Th. vietnamense* sp. nov.
109	*Theloderma stellatum*	ZMMU NAP-03680	KT461921	Vietnam	Tay Ninh: Lo Go – Xa Mat	this study	*Th. vietnamense* sp. nov.
110	*Theloderma stellatum*	ZMMU NAP-03723	KT461919	Vietnam	Kien Giang: Phu Quoc	this study	*Th. vietnamense* sp. nov.
111	*Theloderma stellatum*	ZMMU NAP-03724	KT461888	Vietnam	Kien Giang: Phu Quoc	this study	*Th. vietnamense* sp. nov.
112	*Theloderma stellatum*	AMS R 173283	JN688170	Vietnam	Binh Thuan	Rowley et al., 2011	*Th. vietnamense* sp. nov.
113	*Theloderma stellatum*	AMS R 174047	JN688171	Cambodia	Mondol Kiri	Rowley et al., 2011	*Th. vietnamense* sp. nov.
114	*Theloderma truongsonense*	ROM 39363	KT461925	Vietnam	Quang Binh: Phong Nha — — Ke Bang	this study	*Th. truongsonense*
115	*Theloderma* sp.	ZMMU ABV-00301	KT461882	Vietnam	Khanh Hoa: Hon Ba	this study	*Theloderma* sp.
116	*Theloderma* sp.	ZMMU ABV-00319	KT461924	Vietnam	Khanh Hoa: Hon Ba	this study	*Theloderma* sp.
117	*Theloderma* cf. *truongsonense*	AMS R 171510	JN688174	Vietnam	Quang Nam	Rowley et al., 2011	*Th.* cf. *truongsonense*

Notes. AN, Accession number. Numbers of specimens (No. 1 – 117) correspond to those in Figs. 2 and 3.

using standard phenol-chloroform extraction procedures (Hillis et al., 1996) followed with isopropanol precipitation. The isolated total genomic DNA was visualized in agarose electrophoresis in presence of ethidium bromide. Concentration of the total DNA was measured in 1 μl using NanoDrop 2000 (Thermo Scientific), and consequently adjusted to ca. 100 ng DNA/μl.

We amplified mtDNA fragments of 12S rRNA, tRNA^{val}, and 16S rRNA mtDNA genes, to obtain a fragment with length up to 1987 bp. DNA barcoding techniques (e.g., Vences et al., 2005a, 2005b; Smith et al., 2008; Jiang et al., 2013; Murphy et al., 2013) have greatly facilitated the assessment of cryptic taxonomic diversity in amphibians. 16S rRNA is a molecular marker widely applied for biodiversity surveys in amphibians (Vences et al., 2005a; 2005b; Vieites et al., 2009), and was also proven to be useful in studies of Rhacophoridae diversity (Wilkinson and Drewes, 2000; Wilkinson et al., 2002; Bain et al., 2009; Li et al., 2008, 2009, 2013; Meegaskumbura et al., 2015), including the genus *Theloderma* (Yu et al., 2007, 2008; Rowley et al., 2011; Nguyen et al., 2014, 2015; Dever et al., 2015; and references therein). Amplification was performed in 25 μl reactions using ca. 50 ng genomic DNA, 10 nmol of each primer, 15 nmol of each dNTP, 50 nmol additional $MgCl_2$, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM $MgCl_2$ and 0.01% gelatin) and 1 U of Taq DNA polymerase.

Primers used in PCR and sequencing were obtained from the previous studies (Hedges, 1994; Wilkinson et al., 2002; Li et al., 2008, 2009) and were as follows: forward primers: F0001 (5'-AGATACCCCACTATGCCTA CCC-3'); F0483 (5'-GAAGAGGCAAGTCGTAACATG G-3'); F0937 (5'-TGGGATGATTTTCAAGTAG-3'); F1624 (5'-GTATCAACGGCATCACGAGGG-3'); 16S-L-1 (5'-CTGACCGTGCAAAGGTAGCGTAATCACT-3'); 16S-L2021 (5'-CCTACCGAGCTTAGTAATAGCT GGTT-3'); reverse primers: R0483 (5'-CCATGTTACG ACTTGCCTCTTC-3'); R1169 (5'-GTGGCTGCTTTTA GGCCCACT-3'); R1624 (5'-CCCTCGTGATGCCGTT GATAC-3'); Rend (5'-GACCTGGATTACTCCGGTCT GA-3'); 16S-H-1 (5'-CTCCGGTCTGAACTCAGATCA CGTAGG-3'); 16S-H2715 (5'-AAGCTCCATAGGGTC TTCTCGTC-3'). The PCR conditions for amplification of 16S rRNA fragments included an initial denaturation step of 5 min at 94°C and 33 cycles of denaturation for 30 sec at 94°C, primer annealing for 30 sec at 48°C, and extension step for 1 min 30 sec at 72°C, followed with a final extension step for 10 min at 72°C. The PCR conditions for amplification of 12S rRNA fragments included an initial denaturation step of 5 min at 94°C and 35 cycles of denaturation for 1 min at 94°C, primer annealing for 1 min at 55°C, and extension step for 1 min at 72°C, followed with a final extension step for 10 min at 72°C.

PCR products were visualized in 1% agarose gels stained with Ethidium bromide in a Dark reader trans-illuminator. If distinct bands were produced, products were purified using 2 μl from a 1:4 dilution of ExoSapIt (Amersham), per 5 μl of PCR product prior to cycle sequencing. A 10 μl sequencing reaction included 2 μl of template, 2.5 μl of sequencing buffer, 0.8 μl of 10 pmol primer, 0.4 μl of BigDye Terminator version 3.1 Sequencing Standard (Applied Biosystems) and 4.2 μl of water. The cycle-sequencing reaction was 35 cycles of 10 sec at 96°C, 10 sec at 50°C and 4 min at 60°C. Cycle sequencing products were purified by ethanol precipitation. Sequence data collection and visualization were performed on an ABI 3730xl automated sequencer (Applied Biosystems). The obtained sequences are deposited in GenBank under the accession numbers KT461882-KT461930 (see Table 1).

Phylogenetic analysis. 12S rRNA – 16S rRNA fragment sequences of 117 specimens (90 representatives of *Theloderma*, 25 sequences of outgroup members of Rhacophoridae (genera *Rhacophorus*, *Raorchestes*, *Polypedates*, *Philautus*, *Liuixalus*, *Kurixalus*, *Gracixalus*, *Feihyla*, *Chiromantis*, *Buergeria*) and 2 outgroup sequences of *Rana kukunoris* (Ranidae, KC465786) and *Mantella aurantiaca* (Mantellidae, DQ283035), the data on voucher specimens and GenBank sequences used in phylogenetic analyses are summarized in Table 1) with a total length of up to 1987 bp were included in the final alignment and subjected to phylogenetic analyses. Sequences were also submitted to a BLAST search in GenBank to confirm that the intended sequences had been amplified. The forward and reverse sequences were checked visually in Chromas Pro software (Technelysium Pty Ltd., Tewntin, Australia) and a consensus sequence was compiled with BioEdit 5.0.9 (Hall, 1999). Nucleotide sequences were initially aligned using ClustalX 1.81 (Thompson et al., 1997) with default parameters, and then checked by eye in BioEdit 7.0.5.2 (Hall, 1999) and MEGA 6.0 (Tamura et al., 2013) and slightly adjusted.

The dataset was first divided into three partitions, 12S rRNA, tRNA^{val}, and 16S rRNA. MODELTEST v. 3.06 (Posada and Crandall, 1998) was used to estimate the optimal evolutionary models for partitions to be used for the data set analysis. The best-fitting model as suggested by the Akaike Information Criterion (AIC) for 12S rRNA and 16S rRNA partitions was the general time-reversible (GTR) model with a gamma shape parameter (G); for tRNA^{val} partition the Kimura 2-parameter model (+G+I) was selected as the best fit.

Phylogenetic analyses were conducted in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) software. Transitions and transversions were equally weighted, and gaps were treated as missing data. Confidence in tree topology was tested by posterior probability (PP) for Bayesian inference (BI) in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001). Two independent runs of four Markov Chains for 10,000,000 generations were summarized by the BI, with the tree sampled every 100 generations with a consensus topology calculated for 70,000 trees (burn-in = 3,000,000).

We a priori regarded the tree nodes with posterior probabilities values over 0.95 as sufficiently resolved, those between 0.95 and 0.90 were regarded as tendencies, those below 0.90 were considered to be non-resolved (Huelsenbeck and Hillis, 1993). Mean uncorrected genetic distances (*p*-distances) between sequences were determined with MEGA 6.0 (Tamura et al., 2013).

Acoustic analysis. Advertisement calls of the *Theloderma* cf. *stellatum* were recorded in situ in the natural habitat in Cat Tien National Park, Dong Nai Province, Vietnam, on 5th April, 2012, at 18:48 at temperature 25.5°C (the temperature was measured at the calling site immediately after recording with a digital thermometer KTJ TA218A Digital LCD Thermometer-Hydrometer), using a Nikon D7000 digital SLR camera (Nikon Corporation, Japan) in video mode with default sound settings (16 bit, 48 kHz, linear PCM audio format and auto sound level control); in total, 16 advertisement calls from a single male individual were recorded. The total duration of the recording was 54.25 sec.

For comparison we also analyzed the advertisement calls of the *Theloderma stellatum* recorded in captivity from a male individual, collected from environs of Khao Yai National Park, Nakhon Nayok Province, Thailand. The calls were recorded at temperature 25.0°C; in total, 32 advertisement calls from a single male individual were recorded. The total duration of the recording was 32.30 sec. The both audio tracks were removed from original recording using Avisoft SASLab Pro software v. 5.2.05 (Avisoft Bioacoustics, Germany) with a 22.05 kHz sampling frequency and 16-bit precision.

Calls were analyzed using Avisoft SASLab Pro software v. 5.2.05; the temporal parameters were measured with the standard marker cursor in the main window of Avisoft and the frequency parameters were measured using the reticule cursor in the spectrogram window of Avisoft. Spectrograms for analysis were created using Hamming window, FFT-length 1024 points, frame 75%, and overlap 93.75%. Figure spectrograms were created using Hamming window, FFT-length 512 points, frame 100%, and overlap 75%. We reduced the low-frequency noise using the low-pass filter (up to 500 Hz). In total we measured 16 calls of *Theloderma* cf. *stellatum* from Vietnam and 32 calls of *Theloderma stellatum* from Thailand.

We measured two temporal parameters: the duration of each call, the interval between successive calls and five frequency parameters: the initial and final fundamental frequency, the minimum and maximum of fundamental frequency and the frequency of maximum amplitude. All numeral parameters are given as mean ± SE, the minimum and maximum values are given in parentheses (min – max).

RESULTS

Molecular differentiation

Sequence and statistics. Of 1987 nucleotide sites of the studied mtDNA fragment, 909 sites were conserved and 1067 sites were variable, of which 904 were found to be parsimony-informative. The transition-transversion bias (R) was estimated as 3.621 (all data given for ingroup only). Nucleotide frequencies were 30.61% (A), 21.31% (T/U), 24.46% (C), and 23.62%.

Sequence divergence. The uncorrected *p*-distances among and within the studied 1987 bp. mtDNA fragment of the *Theloderma sensu lato* taxa are shown in Table 2 (data given for the ingroup only). Values of the uncorrected genetic *p*-distances in ingroup and outgroup comparisons notably overlapped.

Preliminary phylogenetic relationships of Indochinese *Theloderma*. Results of the phylogenetic analysis of the studied mtDNA fragment are presented in Fig. 2 (position of the genus *Theloderma* within Rhacophoridae) and Fig. 3 (relationships within the ingroup). Phylogenetic relationships between the accessed taxa of *Theloderma* and *Nyctixalus* are well resolved with the exception for several nodes within the group level having low values of support (BPP < 0.95). At the same time, monophyly of subgeneric and species-level groups and species complexes is significantly supported (BPP ≤ ≤ 0.95). Monophyly of Rhacophoridae, Buergeriinae, Rhacophorinae is strongly supported (BPP = 1.0) (see Fig. 2). Monophyly of all Rhacophorinae with the exception for *Liuixalus* is also strongly supported, though the relationships within the former clade are not resolved (see Fig. 2). Monophyly of Nyctixalini — the clade, comprising *Theloderma sensu stricto*, *Nyctixalus* and *Theloderma moloch* is strongly supported (1.0) (Fig. 2) well in concordance with the results obtained in a large-scale phylogeny by Li et al. (2013). Hereafter we indicate this clade as *Theloderma sensu lato*.

The Bayesian tree (Fig. 3) infers the following set of phylogenetic relationships among studied Nyctixalini

TABLE 2. Uncorrected *p*-Distance (%) between 16S rRNA Sequences of *Theloderma* Species Included in Phylogenetic Analyses (below the diagonal) and Standard Error Estimates (above the diagonal)

Clade	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 — *Th. moloch*	—	2.20	2.44	2.13	1.60	1.89	1.47	2.17	1.65	2.12	1.99	1.88	1.86	1.98	1.91	1.86	1.93	1.72	1.77	1.90	1.93	1.61	2.07	1.90
2 — *Th. horridum*	19.26	**0.45**	1.22	1.49	1.81	1.77	2.07	2.00	1.93	1.88	1.87	1.88	1.57	1.49	1.79	1.74	1.71	1.82	1.67	1.95	1.77	1.63	1.64	1.56
3 — *Th. stellatum*	19.59	8.45	**0.00**	1.65	2.01	2.03	2.06	2.25	2.10	2.27	1.93	2.03	1.75	1.91	1.87	1.91	2.13	2.21	1.92	2.06	2.06	1.99	1.99	1.83
4 — *Th. vietnamense* sp. nov.	19.10	10.28	9.38	**1.9**	1.97	2.00	1.91	2.05	1.90	2.13	1.89	1.89	1.51	1.63	2.00	1.95	1.89	1.91	1.83	2.05	1.96	1.73	1.72	1.72
5 — *Th. pictum*	14.64	19.00	19.91	18.17	**5.66**	1.46	1.53	1.85	1.60	1.76	1.89	1.69	1.76	1.80	1.64	1.62	1.82	1.59	1.75	1.76	1.82	1.70	1.77	1.67
6 — *Th. spinosum*	14.86	15.77	15.88	13.65	11.36	**0.00**	1.44	1.85	1.59	1.83	1.85	1.63	1.73	1.73	1.71	1.67	1.94	1.84	1.75	2.09	1.96	1.99	1.96	2.04
7 — *Th. margaritifer*	6.90	13.65	11.64	11.91	7.46	6.03	—	1.91	1.58	2.10	1.62	1.59	1.86	1.93	1.98	1.94	1.77	1.64	2.10	1.94	1.78	1.71	1.89	1.75
8 — *Th. ryabovi*	18.64	19.89	22.37	19.63	15.04	15.59	12.07	**0.00**	1.77	1.93	2.04	1.91	1.76	1.93	1.96	1.98	2.06	1.84	1.91	2.05	2.09	2.02	2.15	2.07
9 — *Th. albopunctatum*	15.39	17.52	17.86	17.58	14.20	12.79	7.43	14.66	**3.16**	1.66	1.69	1.54	1.87	1.68	1.59	1.57	1.69	1.76	1.85	1.68	1.82	1.59	1.73	1.58
10 — *Th. petilum*	17.23	16.10	16.89	17.15	15.51	14.86	10.78	15.25	9.25	—	1.74	1.94	1.92	1.80	1.80	1.82	1.79	2.05	1.93	1.71	2.01	1.77	1.72	1.65
11 — *Th. licin*	16.89	17.79	18.58	17.87	15.28	16.22	8.19	15.59	11.00	12.16	—	1.86	2.01	1.63	1.85	1.83	1.97	2.02	1.86	1.82	1.83	1.99	2.00	1.95
12 — *Th. asperum*	15.88	18.58	19.59	19.01	15.98	16.22	7.33	16.61	12.24	13.85	13.18	—	1.76	1.71	1.78	1.74	1.77	1.69	1.76	1.76	1.77	1.78	1.96	1.70
13 — *Th. corticale*	16.64	15.34	15.63	12.90	15.39	12.19	8.68	14.85	15.00	16.01	15.04	14.17	**1.62**	1.30	1.70	1.67	1.70	1.72	1.65	2.08	1.60	1.95	1.80	1.85
14 — *Th. bicolor*	14.53	13.31	14.32	12.64	14.54	11.62	8.36	15.05	12.43	12.97	12.30	12.97	6.09	**0.27**	1.49	1.41	1.57	1.76	1.56	1.96	1.58	1.85	1.68	1.79
15 — *Th. rhododiscum* Vietnam	15.20	15.09	15.20	15.93	15.42	14.53	11.21	14.24	12.66	13.51	13.18	13.51	11.27	8.58	—	0.82	1.84	1.71	1.72	1.77	1.87	1.99	2.00	1.76
16 — *Th. rhododiscum* China	14.57	14.12	14.92	14.75	14.83	13.98	10.78	13.52	13.24	13.30	13.81	13.47	11.63	8.61	2.29	**0.51**	1.81	1.76	1.70	1.78	1.80	1.91	1.88	1.64
17 — *Th. leporosum*	13.98	15.30	17.25	15.10	14.58	13.98	8.19	14.82	13.34	13.64	15.33	14.21	10.20	8.03	10.94	10.43	**0.68**	1.67	1.82	2.02	1.67	1.80	1.79	1.82
18 — *Th. gordoni*	13.49	15.58	18.29	15.49	13.31	13.94	8.43	14.22	14.37	14.86	15.88	14.06	10.59	8.93	10.86	9.83	8.53	**2.33**	1.74	2.01	1.94	1.91	2.09	1.95
19 — *Th. palliatum*	16.19	16.71	17.36	16.74	15.96	14.90	9.78	17.09	14.14	15.42	15.76	15.21	11.55	8.34	10.92	11.75	11.53	12.60	**0.65**	2.00	1.90	1.99	2.09	1.88
20 — *Th. laeve*	19.49	21.13	22.28	20.19	17.37	16.92	13.21	13.67	13.75	14.52	17.59	16.88	17.59	17.18	15.58	15.33	15.92	16.84	17.27	**0.92**	1.73	1.81	1.84	1.73
21 — *Th. nebulosum*	15.88	17.57	17.91	16.27	15.35	13.85	7.76	14.92	14.95	15.20	14.19	13.51	10.16	9.12	13.85	12.88	10.26	12.00	14.79	13.14	**0.00**	1.75	1.84	1.72
22 — *Th. truongsonense*	13.90	18.31	17.63	16.41	15.50	16.27	8.19	14.63	14.55	14.92	16.61	13.90	14.22	12.54	14.58	13.69	12.33	14.33	14.96	13.11	9.49	—	1.22	1.34
23 — *Th.* cf. *truongsonense*	16.61	18.41	17.69	16.21	16.94	16.25	9.39	17.03	16.89	16.61	16.61	16.97	13.75	11.91	15.16	14.22	13.37	15.26	18.02	13.93	9.75	4.35	—	1.25
24 — *Theloderma* sp.	16.22	17.23	17.23	15.42	15.82	16.55	9.05	16.61	15.15	15.54	16.55	14.19	12.72	11.82	13.51	12.62	12.51	15.08	15.30	12.83	9.46	6.10	5.78	**0.00**

Notes. The ingroup mean uncorrected *p*-distances are shown on the diagonal and shaded with gray. Clade numbers correspond to those at Fig. 3.

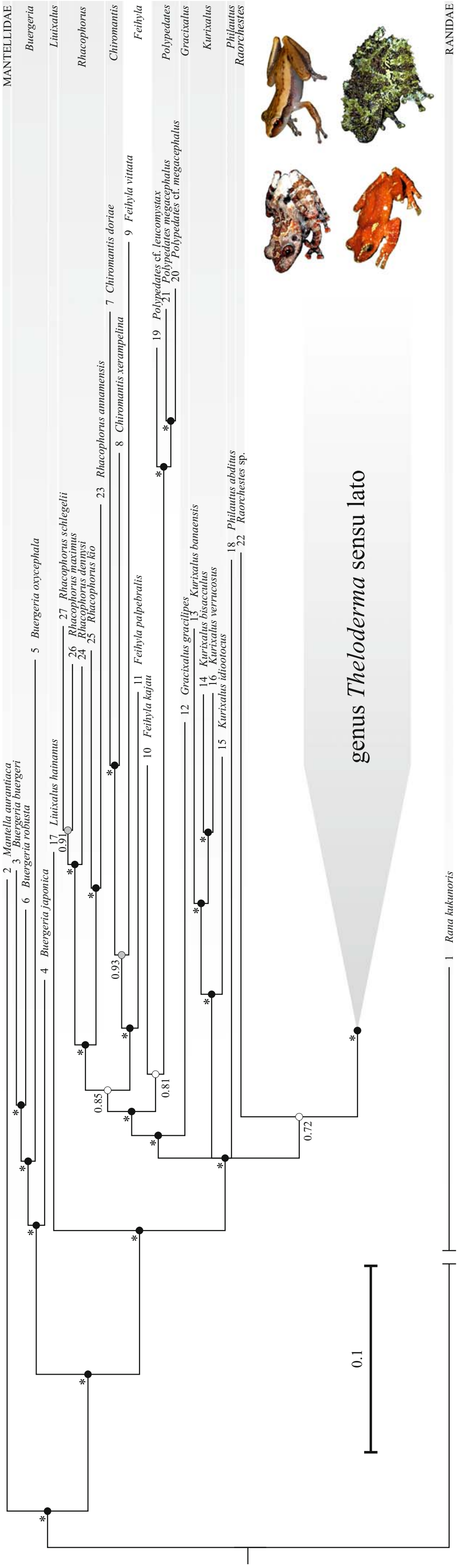

Fig. 2. Bayesian inference dendrogram of Rhacophoridae derived from the analysis of 1987 bp of 12SrRNA – 16S rRNA mtDNA gene fragment, showing position of the genus *Theloderma sensu lato* within the Rhacophoridae. Voucher specimen IDs and Genbank accession numbers are given in Table 1. *Rana kukunoris* used as an outgroup. Color of node correspond to the support value (black — highly supported; gray — moderate support; white — no significant support). Star near the node indicate significant value of PP node support (PP > 0.95). Numbers near branches represent posterior probability (PP) for poorly supported nodes. Numbers of specimens (No. 1 – 117) correspond to those in Table 1.

(*Theloderma sensu lato*) species. *Theloderma moloch* (Fig. 3, clade 1) is recovered as a sister clade to all other Nyctixalini with strong support (BPP = 1.0). Monophyly of the clade comprising *Theloderma* other than *Th. moloch* + *Nyctixalus* is also strongly supported (BPP = 1.0).

General topology of the Bayesian tree suggests that within Nyctixalini other than *Th. moloch*, the most basal split separates *Th. horridum* from Malayan Peninsula (Fig. 3, clade 2), *Th. stellatum sensu stricto* from Thailand (clade 3) and *Th.* cf. *stellatum* from Vietnam (clade 4); monophyly of this clade receives strong support (BPP = 1.0). This topology with *Nyctixalus* being nested within *Theloderma*, and *Th. horridum* forming a more basal split, was also recovered in the study by Li et al. (2013). However, monophyly of the group, joining *Nyctixalus* (Fig. 3, clades 5 – 7) and the rest of *Theloderma* species (Fig. 3, clades 8 – 24) got poor support (BPP = = 0.86). Within the *Th. stellatum* — *Th. horridum* group, *Th. stellatum sensu lato* is clearly paraphyletic with respect to *Th. horridum* (Fig. 3, clade 2), the latter species form a well-supported clade (BPP = 0.96) with *Th. stellatum* from Thailand (clade 3), whereas *Th.* cf. *stellatum* from Vietnam forms a distantly related clade 4 (*p*-distance = 9.38 – 10.28%, see Table 2). Certain variation is observed between populations of *Th.* cf. *stellatum* from southern (samples 108 – 111, Table 1, Fig. 3) and central (samples 106 – 107) Vietnam (*p* = 1.90%).

Monophyly of *Nyctixalus* got high support (BPP = = 1.0) (Fig. 3, clades 5 – 7), but relationships within the group are not sufficiently resolved; there is a tendency for *N. margaritifer* (clade 7) from Java to form a basal split. We report a high divergence between different lineages of *N. pictus* (samples 29 – 36; *p* = 5.66%): 4 subclades are revealed within this species; taxonomy of *N. pictus* complex appears to be insufficiently studied.

Monophyly of the clade, comprising Nyctixalini members with exception for *Th. moloch*, *Th. horridum* group and *Nyctixalus* (= *Theloderma sensu stricto*; clades 8 – 24, Fig. 3), is strongly supported (BPP = 1.0). General topology of the tree correspond well to the results of Nguyen et al. (2015) and suggests that *Theloderma sensu stricto* is divided into the two major groups: the first group joins *Th. ryabovi*, *Th. asperum sensu lato*, *Th. petilum* and *Th. licin* (these species we indicate as members of *Th. asperum* group; see Fig. 3, clades 8 – – 12), while the second group (clades 13 – 24) comprises all other *Theloderma* taxa from both Sundaland and the mainland Southeast Asia including *Th. leporosum* (the type species of *Theloderma* Tschudi, 1838).

Within the *Th. asperum* group, *Th. ryabovi* from Kon Tum Province in central Vietnam (clade 8) forms the most distant lineage (*p*-distance 14.66 – 16.61%; Table 2), sister to other *Th. asperum* group taxa. The rest

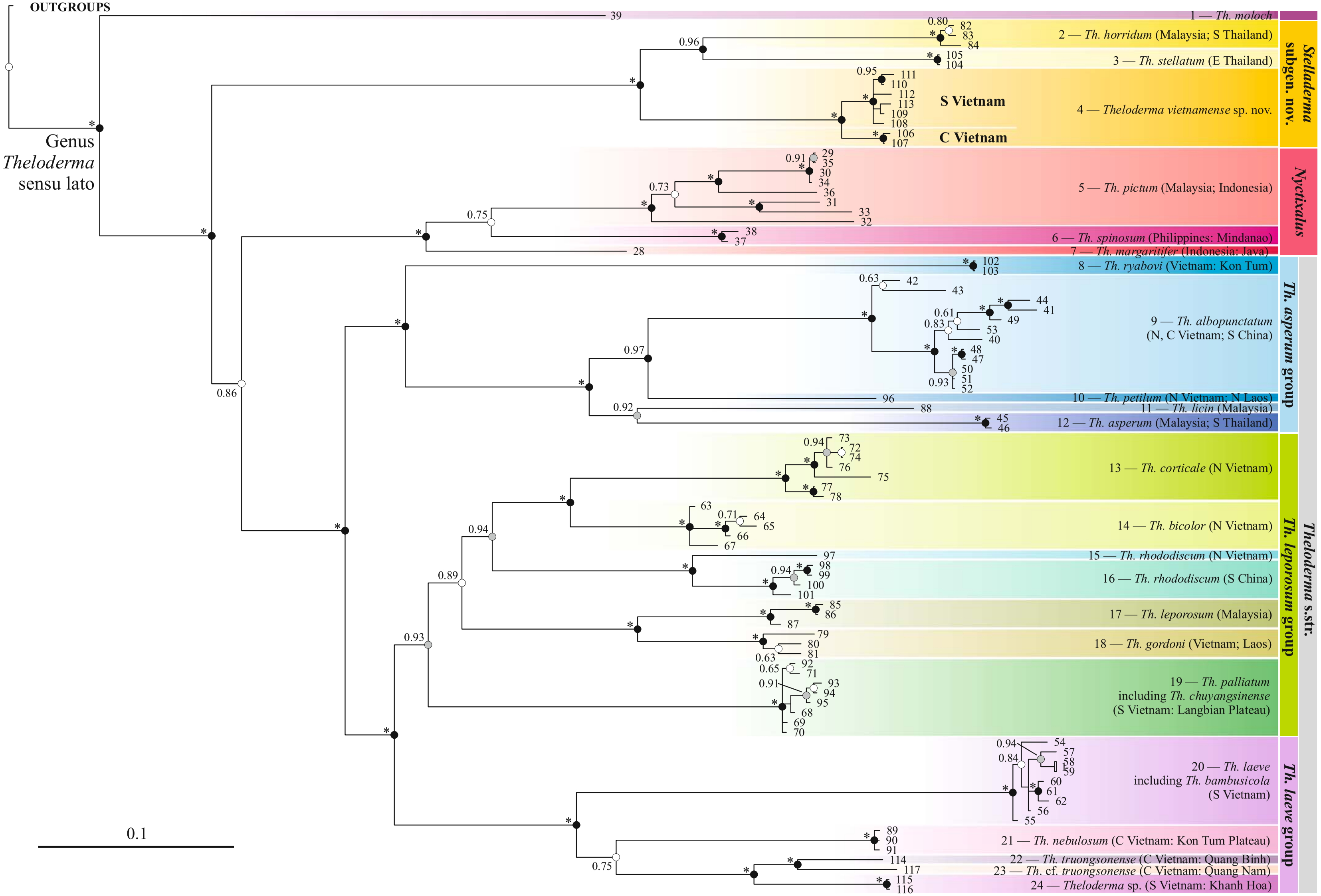

Fig. 3. Bayesian inference dendrogram of *Theloderma* and its relatives derived from the analysis of 1987 bp of 12SrRNA – 16S rRNA mtDNA gene fragment, showing differentiation within *Theloderma sensu lato*. Voucher specimen IDs and Genbank accession numbers are given in Table 1. For outgroups see Fig. 2. Color of node correspond to the support value (black — highly supported; gray — moderate support; white — no significant support). Star indicate significant values of PP node support (PP > 0.95). Numbers near branches represent posterior probability (PP) for poorly supported nodes. Numbers of specimens (No. 1 – 117) correspond to those in Table 1.

of the *Th. asperum* group is divided into the two well-supported subgroups corresponding to Indochinese (*Th. petilum* from Laos and Vietnam (clade 10) and *Th.* "*asperum*" populations from Vietnam and southern China (clade 9); monophyly support BPP = 0.97) and Malayan (*Th. licin* (clade 11) and *Th. asperum sensu stricto* (clade 12), both from peninsular Malaysia; monophyly support BPP = 0.92) populations. Thus, our results clearly indicate the paraphyly of *Th. asperum* sensu lato with respect to *Th. licin* and *Th. petilum*. Genetic differentiation between Malayan and Indochinese *Th. asperum* lineages is quite profound ($p = 12.24\%$, see Table 2). According to the recently published paper by Dever et al. (2015) the poorly known species *Th. phrynoderma* is also likely a member of the *Th. asperum* group. We also report a certain genetic variation within *Th. asperum* from Indochina ($p = 3.16\%$, see Table 2).

The second group, comprising the rest of *Theloderma* taxa, is also divided into the two subgroups. The first subgroup joins small-sized *Theloderma* taxa from southern and central Vietnam (Fig. 3, clades 20 – 24: *Th. bambusicola*, *Th. laeve*, *Th. nebulosum*, *Th. truongsonense*, and two unidentified lineages, allied to *Th. truongsonense*), which we indicate as *Th. laeve* group (see Fig. 3; monophyly support BPP = 1.0). The second subgroup joins all other *Theloderma* species (*Th. leporosum* group: clades 13 – 19; Fig. 3) and has a moderate value of monophyly support (BPP = 0.93, see Fig. 3). According to the phylogeny by Nguyen et al. (2015), the Indochinese species *Th. lateriticum* is also likely a member of *Th. leporosum* group.

However, phylogenetic structuring within both the *Th. laeve* and *Th. leporosum* groups received low support and relationships between members of these groups remain sufficiently unresolved and require further study.

Within the *Th. leporosum* group, *Th. corticale* (clade 13) and *Th. bicolor* (clade 14) form a monophyly (BPP = = 1.0, Fig. 3); these species appear to be closely related ($p = 6.09\%$). Certain differentiation is revealed between Vietnamese (sample 97) and Chinese (samples 98 – 101) populations of *Th. rhododiscum* ($p = 2.29\%$). An Indochinese species *Th. gordoni* (clade 18) appear to be a sister species to Sundanese and Malayan *Th. leporosum* (clade 17) ($p = 8.53\%$, monophyly support BPP = 1.0). Finally, we revealed minimal variation ($p = 0.65\%$) between *Th. chuyangsinense* from Chu Yang Sin Mt. in Dak Lak Province of Vietnam (Fig. 3, clade 19, samples 68 – 71) and *Th. palliatum* from Bi Doup and Hon Giao Mountains in Lam Dong Province of Vietnam (Fig. 3, clade 19, samples 92 – 95); samples from the two geographic populations are mixed and form a single clade which we indicate as *Th. palliatum*.

Within the *Th. laeve* group the species indicated as *Th. bambusicolum* by Orlov et al. (2012) from southern Vietnam forms a most basal split, quite distant from the other small-sized *Theloderma* ($p = 12.83 – 13.93\%$). Populations of this species from the 4 localities in Binh Phuok, Dong Nai and Lam Dong Provinces of Vietnam demonstrate low interpopulational differentiation ($p = = 0.92\%$; data for Dong Nai Province not included). Differentiation between populations of *Theloderma* cf. *truongsonense* from Quang Binh (see Fig. 3; type locality of *Th. truongsonense*, clade 22), Quang Nam (originally indicated as *Th. truongsonense* by Rowley et al., 2011; reindicated as *Th. laeve* by Orlov et al., 2012; clade 23) and *Theloderma* sp. from Khanh Hoa (clade 24) provinces of Vietnam varies from $p = 4.35$ to $p = 6.10\%$ (Table 2); taxonomic status of these populations requires further studies.

TAXONOMY

Status of "*Theloderma*" *moloch* (Annandale, 1912)

After its discovery by Annandale (1912) in Abor country, Arunachal Pradesh (India) and description as *Phrynoderma moloch*, this enigmatic species has changed its generic affiliation several times, being listed as *Rhacophorus*, *Nyctixalus*, and *Theloderma* (see Ahl, 1931; Dubois, 1981; Inger in Frost, 1985; Nguyen et al., 2015). Li et al. (2009) were the first to report the distant phylogenetic relationships between the specimen 6255Rao collected in Motuo (southern Tibet, China), which they identified as *Th. moloch*, and the rest of the *Theloderma*; the specimen 6255Rao was recovered in their tree as a sister clade with respect to *Philautus*. This result was also confirmed by the following research (Li et al., 2009; Pyron and Wiens, 2011). Therefore, inclusion of *Phrynoderma moloch* Annandale, 1912 in *Theloderma* was widely rejected, and the species is preliminary listed as "*Theloderma*" *moloch* in the Amphibian Species of the World database (Frost, 2015).

However, in a consequent paper, Li et al. (2013) showed that in the multilocus-based phylogeny of Rhacophoridae, the sample 6255Rao is nested in the well-supported Nyctixalini clade, together with *Theloderma sensu stricto* and *Nyctixalus*. In the recent paper, Nguyen et al. (2015) raised doubts on the validity of the phylogenetic analyses by Li et al. (2013), and assumed that the figure presented by the latter is incorrect. Though Nguyen et al. (2015) did not confirm monophyly of *Theloderma sensu lato*, their phylogenetic tree does not resolve the phylogenetic position of *Theloderma moloch*; monophyly of Nyctixalini and Rhacophorinae other than

Liuixalus is also not supported in the tree of Nguyen et al. (2015).

According to our phylogenetic analyses, the sequences of the sample 6255Rao form a well-supported clade with the rest of Nyctixalini (*Theloderma* + *Nyctixalus*); monophyly of the latter clade is also strongly supported (see Fig. 3). Thus, our results are in agreement with the data by Li et al. (2013), but they do not contradict the tree of Nguyen et al. (2015), since in their phylogram, the position of *Th. moloch* is unresolved as well as some basal nodes of the tree.

Thus, our data suggests the possible monophyly of *Th. moloch* with the rest of Nyctixalini. However, to date, all the debates on phylogenetic position of *Th. moloch* are based on the sequence data from a single specimen 6255Rao, identification and taxonomic status of which require clarification; it is not clear whether it really represents the species described by Annandale (1912) or not. Therefore, in our opinion, no taxonomic decision on *Th. moloch* is possible until a more detailed phylogenetic and taxonomic study on additional material of this taxon is performed, including careful comparison with the type specimens.

Relationships between *Theloderma* Tschudi, 1838 and *Nyctixalus* Boulenger, 1882

The classical works on morphology and taxonomy of Rhacophoridae (Taylor, 1962; Liem, 1970; Channing, 1989) indicated close proximity of the genera *Theloderma* and *Nyctixalus*, based on significant morphological and ecological similarities, especially similar breeding habits of these frogs, with no clear synapomorphies distinguishing *Theloderma* from *Nyctixalus*. The following molecular phylogenetic studies also reported *Nyctixalus* and *Theloderma* as sister genera, mostly due to the incomplete taxon sampling for both genera (Wilkinson et al., 2002; Frost et al., 2006; Li et al., 2008, 2009; Yu et al., 2009; Pyron and Wiens, 2011; Meegaskumbura et al., 2015). A number of studies (Rowley et al., 2011; Nguyen et al., 2014), however, recovered *Nyctixalus pictus* to be nested within *Theloderma*, which was later explained as a result of an insufficient taxon sampling and short sequences by Nguyen et al. (2015). Though Nguyen et al. (2015) state the opposite, this is not the case of the multilocus phylogenetic reconstruction by Li et al. (2013), which imbeds *Nyctixalus* within *Theloderma*, with a clade marked as “Unidentified species” [specimen ID: LJT W44-W45 from Malaysia; GenBank AN: KC465842-43, see Table 1] forming a basal split within Nyctixalini, being a sister clade to the rest of *Theloderma* + *Nyctixalus*. Examination of the sequences by Li et al. (2013) has shown that they correspond to *Theloderma horridum*, and therefore their study suggests paraphyly of *Theloderma* with respect to *Nyctixalus*. According to the divergence time estimates by Li et al. (2013), the divergence between *Th. horridum* clade, *Nyctixalus*, and *Theloderma sensu stricto* should have taken place within the time interval of 29 – 25 mya.

The study by Nguyen et al. (2015) provided evidence for monophyly of *Theloderma* other than *Th. moloch*, and *Nyctixalus* is recovered as a sister genus to the clade joining *Th. horridum* clade and *Theloderma sensu stricto* (the monophyly of the latter has not an absolute, but still a high level of support: MLBS/BPP 88/1.0). In our phylogeny, *Th. horridum* + *Th. stellatum* clade is a sister group to *Theloderma sensu stricto* + *Nyctixalus*, though the monophyly of the latter group has no significant support (BPP = 0.86) (Fig. 3). Therefore, our analysis shows the presence of the three deeply divergent groups of Nyctixalini (*Th. moloch* excluded) with practically unresolved phylogenetic relationships between them: *Th. horridum* + *Th. stellatum* clade, *Nyctixalus* and the rest species of *Theloderma sensu stricto*.

Thus, discussing the generic taxonomy of *Theloderma* Tschudi, 1838 and the related taxa, excluding *Th. moloch*, on which data are too scarce, the following should be considered:

1. The three Nyctixalini clades: *Th. horridum* + *Th. stellatum* clade, *Nyctixalus* and the rest species of *Theloderma sensu stricto*, are highly divergent from each other and have likely arisen within a narrow time interval (presumably, late Oligocene, ca. 29 – 25 mya, based on Li et al., 2013). The branching order between these three groups still remains controversial (e.g., compare Li et al., 2013 and Nguyen et al., 2015).
2. All the three groups share multiple morphological and ecological characters (Liem, 1970; Channing, 1989), including the peculiar mode of reproduction, which distinguish them from all other Rhacophoridae (Meegaskumbura et al., 2015).
3. Morphological differences between these groups are unclear; no synapomorphies are known to date to differentiate them from each other (Liem, 1970; Channing, 1989; Rowley et al., 2011; Dever et al., 2015).

Apparently, there are currently five alternative, equally valid taxonomic options:

1. Recognize no subgenera and place all of the species in *Theloderma*.

2 Recognize a genus *Theloderma*, with two subgenera, *Theloderma* and *Nyctixalus*.

3. Recognize three subgenera of *Theloderma*: *Theloderma*, *Nyctixalus* and the unnamed taxon for *Th. horridum* – *Th. stellatum* clade.

4. Recognize two genera, with two subgenera of *Theloderma*, *Theloderma sensu stricto* and the unnamed taxon for *Th. horridum – Th. stellatum* clade.

5. Recognize three genera.

At the current state of phylogenetic and morphological knowledge, we tend to support the option 3. As noted by Wake (2013): an "effective way of attaining <...> a goal [to derive phylogenetic information from taxonomic ranks, without resorting to an alternative, non-Linnaean taxonomic system] is through the use of subgenera <...> this is especially effective when there is strong evidence of monophyly from diverse sets of biologically significant traits."

Hence, we propose a new subgenus to designate the clade encompassing *Th. horridum* and *Th. stellatum*, which we describe below as:

Stelladerma subgen. nov.

Type species. *Theloderma stellatum* Taylor, 1962.

Holotype. EHT 35441, by original designation; now FMNH 172249 (according to Frost, 2015).

Included species. *Theloderma* (*Stelladerma*) *horridum* (Boulenger, 1903); *Theloderma* (*Stelladerma*) *stellatum* Taylor, 1962; *Theloderma* (*Stelladerma*) *vietnamense* sp. nov. (described below).

Diagnosis. Frogs of the subgenus *Stelladerma* subgen. nov. are arboreal frogs of medium to large body size (adult SVL from 22 to 45 mm) and can be differentiated from other congeners by the following combination of morphological character states: (1) highly tuberculated skin on the dorsum with calcified warts and large asperities; (2) two slips of M. extensor digitorum communis longus (only shown for *Th. stellatum* by Liem, 1970); (3) Y-shaped terminal phalanges; (4) a distinct tympanum; (5) elongated snout with canthus rostralis rather sharpened than rounded, nostrils being slightly protuberant; (6) absence of bony ridges from canthus rostralis to occiput; (7) skin on head not co-ossified with skull; (8) reproduction in water-filled tree hollows and sometimes man-made waterbodies; (9) bluish coloration of sclera; (10) iris coloration uniform, brownish to dark golden with dark reticulations; (11) dark-brown to blackish belly coloration with light (whitish to bluish) markings forming star-like patterns or reticulations; (12) hand-webbing present, finger and toe discs wide and reddish in life; (12) vomerine teeth absent; (13) vocal openings in males present.

Phylogenetic definition. The most inclusive monophyletic taxon including the species *Theloderma stellatum* Taylor, 1962 and excluding the species *Th. asperum* (Boulenger, 1886).

Etymology. Derived from Latin "stella" for "star," what refers to the scientific name of the type species of the new subgenus — *Theloderma stellatum* Taylor, 1962 ("stellated") and also is a reference to the beautiful belly coloration of the members of this taxon with star-shaped or reticulated whitish to bluish pattern on dark background. Gender is neutral.

Distribution. To date known from southern Indochina (from central and southern Vietnam, Gia Lai and Kon Tum Provinces southwards to Phu Quoc Island and Con Dao Archipelago), eastern Cambodia, Cardamom Mountains in southern Cambodia and eastern Thailand, westwards to Uthai Thani Province of Thailand; extreme southern peninsular Thailand and Malaya south of the Isthmus of Kra, also including northern Borneo (Sabah, Malaysia, and possibly Brunei); also found in Pulau Tioman, West Malaysia.

The proposed preliminary taxonomy of Nyctixalini is provided in *Appendix 2*.

Taxonomic rearrangements within the *Theloderma asperum* group

Our data show monophyly and distinctiveness of the *Th. asperum* species group (Fig. 3), joining a number of small to large-sized *Theloderma*, all of which are characterized by presence of uniform reddish-brown iris and large white blotches on the rear part of the dorsum (with the exception of for *Th. petilum*, which has no white blotches). Phylogenetic relationships within this group are well-resolved and in general correspond well to those presented by Nguyen et al. (2015). The large-sized species *Th. ryabovi* (Fig. 3, clade 8) from central Vietnam is recovered as the most basal lineage in *Th. asperum* species group; it shows distant relationships to all other taxa of this group (see Table 2, $p = 14.66 – 16.61\%$). The rest of the taxa are divided in two subgroups, one of which joins populations from Indochina (Fig. 3, clades 9 – 10) while the other one encompasses populations of the Malayan Peninsula and Thailand south of the Isthmus of Kra (Fig. 3, clades 11 – 12). Our study confirms the assignment of *Th. petilum* to this group, made by Nguyen et al. (2014, 2015); though morphologically *Th. petilum* does not resemble other members of *Th. asperum* group (compare Fig. 1*x* to Fig. 1*e – j*).

Our study clearly indicates paraphyly of *Th. asperum* sensu lato with Indochinese populations, traditionally assigned to this species, forming a well-supported monophyly with *Th. petilum* (BPP = 0.97), while populations of *Th. asperum* from Perak (Malaysia) are closer to *Th. licin* with significant levels of support (BPP = 0.92). This species was described by Boulenger (1886) as *Ixalus asper* Boulenger, 1886, from "Hill Garden, Larut, Perak, at an altitude of 3300 feet." Later this species was transferred to the genus *Theloderma* by Taylor (1962). Meanwhile, a morphologically similar rhacophorid frog was described from "Yang-liu-chung, Yaoshan" in Guangxi Province of China as *Philautus albopunctatus* Liu et Hu, 1962. Later this rhacophorid was assigned to the genera *Aquixalus* and *Liuixalus* (Fei et al., 2009; Hertwig et al., 2012), until it was not synonymized with *Th. asperum* Boulenger (1886) by Yu et al. (2007; 2008). However, Yu et al. (2007; 2008) did not include any material from the vicinity of the type locality of *Th. asperum* or, at least, from the Malayan Peninsula. Although Orlov et al. (2010) reported a presence of distinct northern and southern populations of *Th. asperum* in Vietnam, our data indicate that genetic variation among these populations is quite limited ($p < 3.16\%$).

According to our data, *Th. asperum sensu lato* appears to be paraphyletic, with the Indochinese populations forming a distant ($p = 12.24\%$, see Table 1) and well-supported clade (Fig. 3, clade 9; BPP = 1.0), showing closer affinities to *Th. petilum* (Fig. 3, clade 10) than to morphologically more similar *Th. asperum* (Fig. 3, clade 12) and *Th. licin* (Fig. 3, clade 11) from the Malayan Peninsula. This paraphyly and genetic distinctiveness is a strong argument towards recognizing the Indochinese populations of *Th. asperum sensu lato* as a separate species. In this case, the name *Theloderma albopunctatum* (Liu et Hu, 1962) comb. et stat. nov. should be applied at least to the populations from southern China, central and northern Vietnam and Laos, though the extent of distribution of this species, as well as its genetic and morphological distinctiveness from other members of *Th. asperum* species complex, has still to be investigated.

Taxonomic status of small-sized *Theloderma* from southern Vietnam

Orlov and Ho (2005) described a small-sized rhacophorid frog from Quang Binh Province in central Vietnam as *Philautus truongsonensis* (Fig. 1*s*). Rowley et al. (2011) applied 16S rRNA sequences for molecular identification of the small-sized rhacophorid frogs from central and southern Vietnam and described the two new species — *Th. palliatum* from Bidoup and Hon Giao mountains in the Langbian Plateau, Lam Dong Province (Fig. 1*q*) and *Th. nebulosum* from highlands in Kon Tum Province (Fig. 1*u*), which were assigned to the genus *Theloderma* based on molecular and morphological data. In particular, the both new species demonstrated the bicolored iris, a character which, among the Southeast-Asian Rhacophoridae, they shared only with *Ph. truongsonensis* and *Nyctixalus*. Rowley et al. (2011) also showed that based on their phylogenetic data, the frog they identified as *Ph. truongsonensis* (from Quang Nam Province, central Vietnam) is also nested in the genus *Theloderma*, and assigned it as *Th. truongsonense*.

Later, Orlov et al. (2012) argued that the specimen which was identified as *Th. truongsonense* by Rowley et al. (2011) was identified incorrectly. Orlov et al. (2012) claimed that it is different from the type *Philautus truongsonensis* Orlov and Ho, 2005 due to the smooth skin on the dorsum and almost lacking asperities, and likely corresponds to the species, which was identified as *Philautus laevis* Smith, 1924 in the previous works (Inger et al., 1999; Orlov and Ananjeva, 2007). Orlov et al. (2012) proposed a new combination *Th. laeve* for this species (Fig. 1*v*). In the same paper, Orlov et al. (2012) described the two new small-sized *Theloderma* species. *Th. chuyansinense* was described from a single specimen from Chu Yang Sin Mountain in the northern edges of the Langbian Plateau (Fig. 1*r*), and is morphologically similar to *Th. palliatum*. *Th. bambusicolum* was described from low altitudes in southern foothills of the Langbian Plateau (Fig. 1*t*); this species was assigned to the genus *Theloderma* mainly by presence of the bicolored iris and based on its reproductive biology — it breeds in water-filled bamboo internodes and is strictly associated with bamboo forests. However, in contrast to the other *Theloderma* species, *Th. bambusicolum* has a completely smooth skin with no signs of warts or asperities. The status and phylogenetic position of all these taxa remained controversial.

Our phylogenetic data (Fig. 3) indicate the following:

(1) Samples of *Th. palliatum* from the type locality (Bidoup Mt.) and *Th. chuyangsinense* from the type locality (Chu Yang Sin Mt.) form a clade with no clear structuring and low intergroup genetic distances, $p < < 0.65\%$ (Fig. 3, clade 19). In our opinion, this clearly indicates that the two taxa are conspecific and *Th. chuyangsinense* Orlov et al., 2012 should be considered as a subjective junior synonym of *Th. palliatum* Rowley et al., 2011. Possibly, taking into account conservation treats due to fragmentation of Langbian forests and isolated position of Chu Yang Sin Mountain at the northern edge of the plateau, a subspecific status would be more appropriate for the Chu Yang Sin population of *Th. palliatum*.

(2) The small-sized *Theloderma* of southern and central Vietnam form a clade (Fig. 3, *Th. laeve* group) with the poorly resolved phylogenetic relationships. Populations, indicated by Orlov et al. (2012) as *Th. bambusicolum* (Fig. 1*t*), form a lineage (Fig. 3, clade 20), which is quite distant from the other members of the group ($p = 12.83 - 13.93\%$, see Table 2) (the correct Latin name should be modified to "*bambusicola*" as a noun in preposition from "bambusa" (bamboo) and "-cola" (tiller, inhabitant); gender is masculine).

(3) *Th. nebulosum* from Kon Tum Province represents a divergent lineage (Fig. 3, clade 21); it appears that

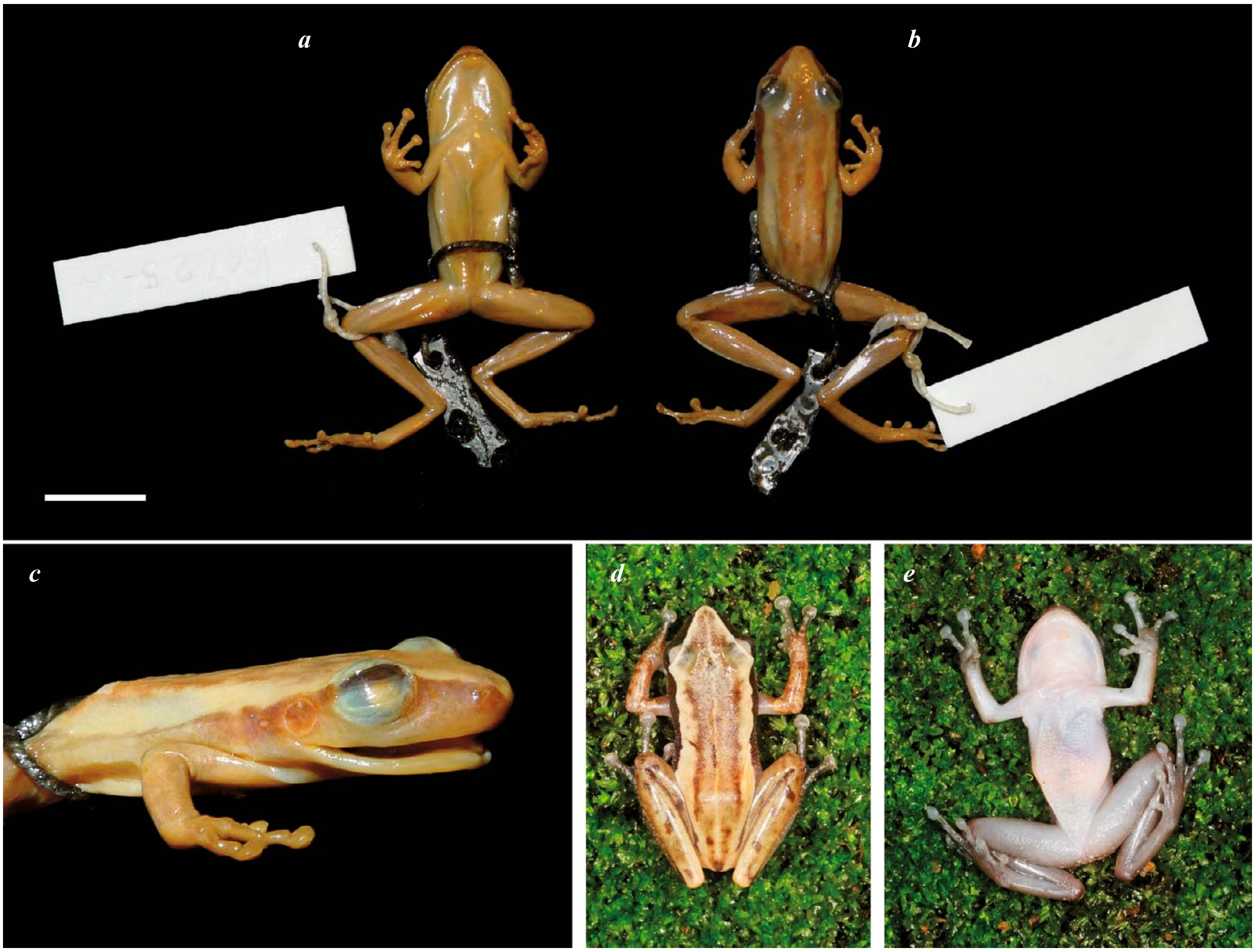

Fig. 4. Type specimens of *Philautus laevis* Smith, 1924 and *Theloderma bambusicolum* Orlov, Poyarkov, Vassilieva, Ananjeva, Nguyen, Sang et Geissler, 2012. *Philautus laevis* holotype BMNH 1947.2.5.94 (formerly 1924.1.31.1) in preservative: ***a***, ventral view; ***b***, dorsal view; ***c***, lateral view (photos A. V. Abramov); *Theloderma bambusicolum* holotype ZMMU A-4569 (field ID ZMMU NAP-02908) in life: ***d***, dorsal view; ***e***, ventral view (photos N. A. Poyarkov).

this species was misidentified with *Th. truongsonense* (as *Philautus truongsonensis*) in some of the previous works (Orlov and Ananjeva, 2007; Orlov et al., 2012).

(4) The topotypic *Th. truongsonense* from Quang Binh (Fig. 3, clade 22), showing presence of dermal *asper*ities on the dorsum (Fig. 1*s*), forms a well-supported clade with the smooth *Theloderma*, lacking dorsal asperities (Fig. 1*v*), previously indicated as *Th. truongsonense* by Rowley et al. (2011) and as *Th. laeve* by Orlov et al. (2012) (Fig. 3, clade 23) ($p = 4.35\%$). An unidentified *Theloderma* sp. from Khanh Hoa province with a moderate level of dorsal asperities development (Fig. 1*w*) is recovered as a sister clade of *Th. truongsonense* (Fig. 3, clade 24; $p = 5.78 – 6.10\%$, Table 2). Thus, the clades 22, 23, and 24 from central and southern Vietnam are closely related to each other and show certain variation in dorsal skin structure from the well-developed tiny dermal asperities in *Th. truongsonense* to almost completely smooth dorsum in *Th.* cf. *truongsonense*. Here we tentatively join all these three lineages under the name *Th. truongsonense* (see below).

In order to clarify taxonomic relationships within the *Th. laeve* group, we had a chance to examine the holotype of *Philautus laevis* Smith, 1924, stored in BMNH 1947.2.5.94 (formerly 1924.1. 31.1; formerly M. Smith 2439) (Fig. 4*a* – *c*). Smith (1924) described this species from “Sui Kat, alt. 1000 m., Langbian Plateau, S. Annam” (now in Lam Dong Province, Vietnam). In all major diagnostic characters, the type of Smith (1924) is indistinguishable from the form, described by Orlov et al. (2012) as *Th. bambusicolum*; photos of the *Th. bambusicolum* holotype ZMMU A-4569 (Field ID ZMMU NAP-02908) are given in Fig. 4*d*, *e*. During the recent field surveys in Lam Dong Province (Bao Loc District) of Vietnam, we discovered several new populations of *Th. bambusicola* from altitudes up to 800 – 900 m a.s.l., almost at the same altitudes and in geographic proximity to the type locality of *Philautus laevis* Smith, 1924. Therefore, we consider that *Th. bambusicolum* Orlov, Poyarkov, Vassilieva, Ananjeva, Nguyen, Sang et Geissler, 2012 should be considered a subjective junior synonym of *Philautus laevis* Smith, 1924.

Differentiation within *Theloderma* (*Stelladerma*) *stellatum* Taylor, 1962 species complex

Our work also sheds some light on taxonomy of *Theloderma stellatum* Taylor, 1962, a medium-sized species inhabiting southern Indochina from eastern Thailand to southern and central Vietnam.

Molecular differentiation. Results of our molecular analyses clearly indicate paraphyly of *Th. stellatum sensu lato* with respect to *Th. horridum*: it appears that the Thai populations of *Th. stellatum* form a sister clade to *Th. horridum* (Fig. 3) while *Th.* cf. *stellatum* from Vietnam is a more distant lineage. Genetic differentiation of *Th.* cf. *stellatum* from Vietnam to closest congeners is quite significant (*p*-distance = 9.38 and 10.28% to *Th. stellatum sensu stricto* and *Th. horridum*, respectively; see Table 2). This degree of pairwise divergence in the 12S rRNA and 16S rRNA genes is greater than that usually representing differentiation at the species level in Anura (Vences et al., 2005a, 2005b; Vieites et al., 2009). Together with non-monophyly of *Th. stellatum sensu lato* this suggests a species status for the Vietnamese populations.

Known distribution of the *Theloderma stellatum* species complex is shown in Fig. 5: filled icons correspond to populations, taxonomic identification of which was checked by mtDNA sequencing [NB: populations 17 (Con Dao) and 19 (Binh Chau) were identified using different genetic markers, therefore are not included in Table 1]. As Fig. 5 shows, the range of the species complex lasts from central to eastern Thailand, then eastwards along the Cardamom Mountains to southern Cambodia, southern and central Vietnam, including Phu Quoc and Con Dao islands. The type locality of *Th. stellatum* Taylor, 1962 is situated in Khao Se Bab, Nam Tok Plew (Phliu) National Park, Chanthaburi Province (locality *10*, Fig. 5). Our molecular phylogenetic analysis assessed the two populations of *Th. stellatum* Taylor, 1962 from Thailand, including the close vicinity of the type locality in Chanthaburi Province (locality *9*, Fig. 5); other populations from Thailand and neighboring areas of Cambodia were tentatively assigned to *Th. stellatum* Taylor, 1962; their taxonomic status requires further investigations.

Known distribution of the Vietnamese form of *Th.* cf. *stellatum* lasts from Gia Lai province in central Vietnam southwards to Con Dao and Phu Quoc Islands; this species is also recorded from Mondulkiri Province of Cambodia. The extent of the Vietnamese form of *Th.* cf. *stellatum* distribution in Cambodia is unknown. Similar distribution pattern was reported for Indochinese reptiles (Hartmann et al., 2013) and amphibians (Geissler et al., 2015); it is interpreted as a role of the Mekong River basin as a zoogeographical barrier for herpetofauna (see Bain and Hurley, 2011; Geissler et al., 2015 for discussion).

Thus, based upon the phylogenetic analysis of the 12S rRNA — 16S rRNA mtDNA sequence fragments, the *Th.* cf. *stellatum* from Vietnam represents a highly divergent mtDNA lineage, clearly distinct from all other *Theloderma* species for which comparable mtDNA sequences are available.

Morphological differentiation. Specimens of the *Theloderma* cf. *stellatum* from southern Vietnam and *Theloderma stellatum* from Thailand are morphologically obviously different from other congeners (see comparison). Hence, other taxa of *Theloderma* were not included in the PCA. Total samples of 10 adults of *Th.* cf. *stellatum* from central Vietnam (5 males; 5 females), 9 adults of *Th.* cf. *stellatum* from southern Vietnam (7 males; 2 females) and 6 adults (all males) of *Th. stellatum sensu stricto* from eastern Thailand were included in the PCA. The morphological characters used in the PCA are listed in Table 3 and are also marked (* or **) in Table 4. The performed PCA discriminated well between the two species (see Fig. 6); it also clearly distinguished the sample sets from southern and central parts of Vietnam. As the result of the PCA, the F1 had an eigenvalue explaining 53.53% of variability, the F2 explained 23.44% of variability and the F3 just 5.54% (see Fig. 6).

At the same time, from the external appearance, specimens of *Th. stellatum* from Thailand (Fig. 1*b*; Fig. 7) and *Th.* cf. *stellatum* from southern and central Vietnam (Fig. 1*c*; Fig. 8) look fundamentally similar to each other and their diagnostics is very complicated, partially due to the high individual variation in coloration. This variation is enhanced by the presence of the lighter night (Fig. 7*b*, *c*; Fig. 8*d*) and darker day coloration (Fig. 7*a*; Fig. 8*a* – *c*), different degrees of the dorsal dark markings development and a high variation in extend of whitish or beige blotches on the rear of the dorsum. In the original description Taylor (1962) reported presence of trifoliate dark pattern on the dorsum; we also observed a trifoliate-shaped marking in all the Thai specimens we had a chance to examine, whereas in Vietnamese populations the most common dark pattern in shoulders area was a chevron in a shape of an inverted U or sometimes Λ. In agreement with description of Taylor (1962), in life Thai specimens have pinkish coloration of finger and toe

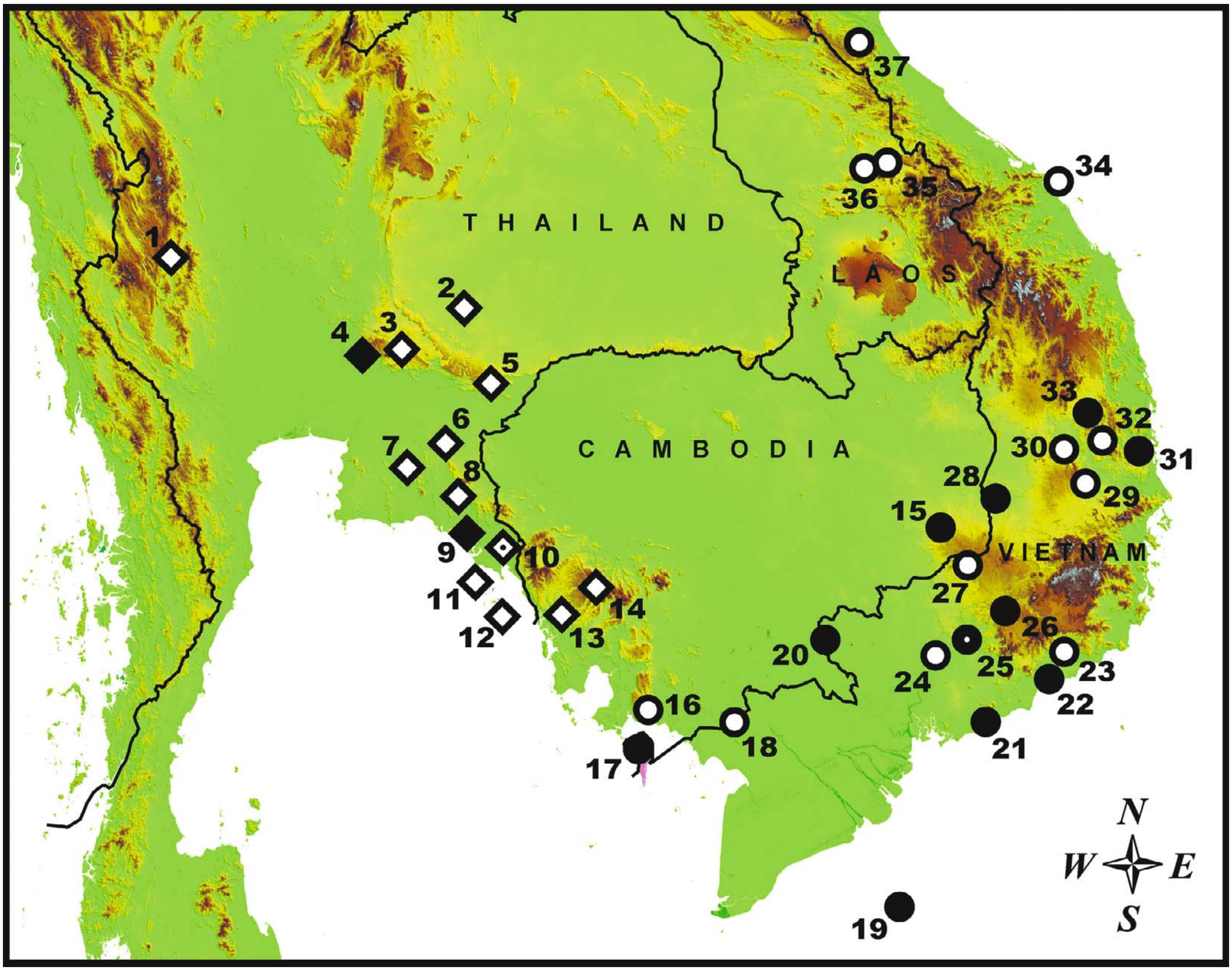

Fig. 5. Distribution of *Theloderma stellatum* complex in southern Indochina and Thailand. A dot in the center of an icon indicates the type locality. Filled icon indicates that the population has been assessed molecularly and its identification was confirmed by mtDNA sequencing. Locality information. *Theloderma stellatum*: Thailand: *1*, Hauy Kha Khaeng Wildlife Sanctuary, Uthai Thani Province (this paper); *2*, Wangnamkhiew District, Nakor Ratchasrima Province (this paper); *3*, Khao Yai National Park, Nakhon Nayok Province (this paper); *4*, Nang Rong waterfall, Nakhon Nayok Province (this paper); *5*, Pangsida National Park, Sa Kaew Province (this paper); *6*, Khao Soi Dao Wildlife Sanctuary, Chanthaburi Province (this paper); *7*, Khao Ang Rue Nai Wildlife Sanctuary, Chonburi Province (this paper); *8*, Khao Kitchakut National Park, Chanthaburi Province (this paper); *9*, Phliu waterfall envrions, Chanthaburi Province (this paper); *10*, Khao Se Bab, Nam Tok Plew (Phliu) National Park, Chanthaburi province (type locality of *Theloderma stellatum* Taylor 1962); *11*, Koh Chang National Park, Trad Province (this paper); *12*, Koh Kut, Trad Province (this paper); Cambodia: *13*, Koh Kong Province (Neang and Holden, 2008); *14*, Central Cardamom Protected Forest, Pursat Province (Neang and Holden, 2008); *Theloderma vietnamense* sp. nov.: Cambodia: *15*, Khao Seima National Park, Mondulkiri Province (Neang and Holden, 2008; Rowley et al., 2011); *16*, Steng Chhral, Kampot Province (this paper); Vietnam: *17*, Phu Quoc National Park, Phu Quoc, Kien Giang Province (Nguyen and Nguyen, 2008; Nguyen et al., 2009; this paper); *18*, Nui Dai Mt., An Nong, Tinh Bien Commune, An Giang Provine (Ngyen Ngoc Hung, communication; this paper); *19*, Con Dao National Park, Con Son Island, Ba Ria — Vung Tau Province (Poyarkov and Vassilieva, 2011; this paper); *20*, Lo Go – Xa Mat National Park, Tay Ninh Province (this paper); *21*, Binh Chau — Phuok Buu National Park, Ba Ria — Vung Tau Province (this paper); *22*, Binh Thuan Province (Rowley et al., 2011); *23*, Bac Binh District, Binh Thuan Province (NCSM 80384; Dever et al., 2015); *24*, Ma Da Forestry, Dong Nai Biosphere Reserve, Dong Nai Province (Nguyen et al., 2009); *25*, Cat Tien National Park, Dong Nai Biosphere Reserve, Dong Nai Province (type locality of *Theloderma vietnamense* sp. nov., this paper); *26*, Loc Bac (Loc Bao) Forestry, Lam Dong Province (this paper); *27*, Bu Gia Map National Park, Binh Phuok Province (this paper); *28*, Yok Don Mt., Yok Don National Park, Dak Lak Province (Nguyen et al., 2009; this paper); *29*, Krong Pa, Gia Lai Province (Nguyen et al., 2009); *30*, Kon Ka Kinh Nature Reserve, Gia Lai Province (Nguyen et al., 2009); *31*, Phu Yen Province (Nguyen et al., 2014); *32*, K'Bang; Kon Cha Rang Nature Reserve, Gia Lai Province (Nguyen et al., 2014); *33*, Mang Canh environs, Kon Plong, Kon Tum Province (Orlov and Ananjeva, 2007; Nguyen et al., 2014; this paper); *34*, Nui Son Tra Mt., Danang City (this paper); *35*, Nam Sagi River Drainage Basin, Vilabouli District, Savannakhet Province, Laos (NCSM 76485-8; Dever et al., 2015); *36*, Tham Bing Cave, Xepon Mines, Vilabouli District, Savannakhet Province, Laos (NCSM 76490; Dever et al., 2015); *37*, Phong Nha – Ke Bang National Park, Quang Binh Province (Luu et al., 2013).

disks (Fig. 7), whereas in Vietnamese populations digit disks are usually brick-reddish or rusty (Fig. 8). Finally, we have observed relatively stable differences in the belly pattern (Fig. 9). The three species of the subgenus *Stelladerma* subgen. nov. show an increasing degree of development of the dark (blackish to dark-brown) spots on the belly, with *Th.* cf. *stellatum* from southern Vietnam (Fig. 9*a*) having the darkest ventral pattern with comparatively sparse light (whitish to bluish) thin reticulations on the belly and rare minute whitish dots on the throat. *Th. stellatum sensu stricto* from eastern Thailand (Fig. 9*b*) shows a lighter ventral pattern, formed by the thick irregular white or bluish star-shaped spots and reticulations, usually connected to each other, and more pronounced white spotting on the throat. Finally, *Th.*

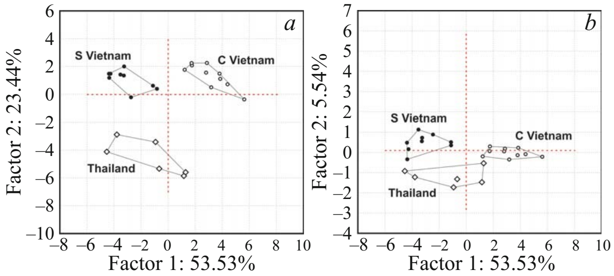

Fig. 6. Two-dimensional principal component plot showing the success of multivariate morphometrics in discriminating the members of *Theloderma stellatum* complex: *Th. stellatum* from Thailand (diamonds), *Th. vietnamense* sp. nov. from southern Vietnam (black circles) and *Th. vietnamense* sp. nov. from northern Vietnam (white circles): *a*, the first two factors of PCA; *b*, the first and third factors of PCA.

TABLE 3. Measurements of the Examined Series of *Theloderma stellatum* and *Theloderma vietnamense* sp. nov.

Character	*Th. vietnamense* sp. nov.												*Th. stellatum*		
	Central Vietnam						Southern Vietnam						Thailand		
	males (*N* = 5)			females (*N* = 5)			males (*N* = 7)			females (*N* = 2)			males (*N* = 6)		
	aver.	max	min	aver.	max	min	aver.	max	min	aver.	max	min	aver.	max	min
SVL	32.60	35.10	30.20	32.80	35.80	30.20	29.85	31.94	28.02	29.96	30.14	29.78	30.69	36.90	22.70
A-G	17.18	17.90	16.40	17.96	20.40	16.50	15.48	17.16	13.74	17.53	17.64	17.41	14.02	15.90	12.50
HW	13.44	14.10	12.90	14.20	16.20	12.40	11.76	12.99	10.52	11.73	11.88	11.57	12.15	13.20	11.19
HL	14.92	16.20	13.50	14.28	15.80	13.70	11.30	12.53	10.15	11.86	12.36	11.36	11.42	12.70	10.70
HD	6.06	6.30	5.80	6.54	7.10	6.00	4.20	4.69	3.90	4.23	4.27	4.18	3.63	4.19	3.40
UEW	4.22	4.40	4.00	4.70	5.60	4.10	2.80	3.10	2.54	2.64	2.71	2.56	3.47	4.00	2.54
IOD	5.26	5.70	5.00	5.82	6.80	5.10	3.51	3.83	3.12	3.59	3.74	3.44	3.77	4.70	3.10
IND	3.56	3.80	3.30	3.88	4.70	3.40	2.17	2.44	1.81	2.09	2.18	1.99	2.56	3.10	2.13
ED	4.78	5.20	4.60	4.94	5.60	4.30	3.94	4.20	3.67	3.87	3.91	3.82	3.80	4.40	3.00
TD	4.14	4.70	3.70	4.68	5.30	3.60	2.17	2.39	1.89	2.37	2.37	2.37	3.05	3.90	2.40
ESL	6.00	6.80	5.10	6.30	7.30	5.30	4.92	5.39	4.38	4.58	4.72	4.44	6.35	8.90	4.42
TED	1.36	1.40	1.30	1.42	1.80	1.20	1.07	1.28	0.88	1.21	1.30	1.11	1.71	2.30	1.30
END	3.80	4.10	3.60	4.34	5.30	3.60	3.59	3.99	3.26	3.44	3.51	3.37	5.43	9.70	3.59
FLL	23.60	25.40	21.80	24.92	29.60	21.90	18.16	18.89	17.00	19.83	20.11	19.55	16.53	19.10	14.00
FFL	3.80	4.00	3.50	4.00	4.70	3.60	2.65	2.96	2.26	2.97	3.08	2.85	3.21	4.10	2.30
TFL	7.30	7.60	7.00	7.58	8.00	7.20	5.44	5.89	4.80	5.73	5.84	5.62	7.27	9.60	4.70
FTD	1.86	2.20	1.60	1.86	2.20	1.60	1.84	2.06	1.66	1.98	2.17	1.78	2.37	2.80	1.90
NPL	3.22	3.50	2.90	—	—	—	2.48	2.99	1.26	—	—	—	2.57	3.30	1.51
MKTe	—	—	—	—	—	—	0.96	1.26	0.66	0.65	0.80	0.50	1.36	2.50	1.00
HLL	55.40	59.70	52.30	58.98	69.10	51.40	44.97	48.44	41.40	45.70	47.56	43.84	50.81	61.50	42.30
FL	14.08	14.90	13.70	14.72	16.40	13.80	13.62	14.81	12.31	13.90	14.43	13.37	14.79	18.80	11.10
TL	17.92	19.10	16.90	19.68	22.90	15.80	15.30	16.92	13.79	16.01	16.08	15.94	16.34	16.80	15.36
FOT	23.40	25.70	21.40	24.58	29.80	21.50	20.06	22.21	18.20	19.78	20.16	19.40	23.81	32.70	19.96
FTL	3.38	3.60	3.20	3.72	4.30	3.30	2.75	3.23	2.31	2.89	2.98	2.79	3.72	4.70	3.30
FFTL	9.32	10.00	8.80	9.78	11.50	8.70	7.93	9.94	6.82	8.40	8.74	8.06	12.48	12.60	7.98
HTD	1.12	1.40	0.90	1.22	1.60	0.90	1.25	1.51	1.05	1.17	1.45	0.88	2.50	4.10	1.48
MTTi	—	—	—	—	—	—	1.33	1.55	1.12	1.31	1.39	1.23	1.66	2.40	1.30

For abbreviations see *Material and Methods*; “aver.” for “average.” All measurements are given in mm.

TABLE 4. Mean Values and Standard Deviation of Morphometric and Characters of *Theloderma vietnamense* sp. nov. and *Th. stellatum*

Character	*Th. vietnamense* sp. nov. ($n = 19$)	*Th. stellatum* ($n = 6$)	p-value
SVL	31.36 ± 2.21	30.69 ± 4.77	
A-G/SVL	53.54 ± 2.69	46.27 ± 5.93	**
HW/SVL	40.86 ± 2.14	40.26 ± 5.62	
HL/SVL	41.61 ± 3.81	37.87 ± 5.76	
HD/SVL	16.82 ± 2.79	12.05 ± 2.03	**
UEW/SVL	11.56 ± 2.41	11.55 ± 2.57	
IOD/SVL	14.51 ± 2.78	12.39 ± 1.59	
IND/SVL	9.40 ± 2.27	8.49 ± 1.63	
ED/SVL	14.06 ± 1.30	12.41 ± 1.23	*
TD/SVL	10.60 ± 3.26	9.96 ± 1.44	
ESL/SVL	17.55 ± 1.80	20.94 ± 2.61	*
TED/SVL	3.98 ± 0.51	5.76 ± 2.22	**
END/SVL	12.18 ± 0.95	17.89 ± 2.64	**
FLL/SVL	68.42 ± 7.03	55.13 ± 11.13	**
FFL/SVL	10.59 ± 1.64	10.43 ± 1.82	
TFL/SVL	20.72 ± 2.41	23.90 ± 5.06	*
FTD/SVL	5.96 ± 0.61	7.83 ± 1.58	**
NPL/SVL	2.69 ± 1.46	8.4 ± 1.86	
MKTe/SVL	6.44 ± 1.53	4.44 ± 1.62	
HLL/SVL	163.48 ± 13.91	167.31 ± 10.98	
FL/SVL	44.89 ± 1.94	49.29 ± 3.93	
TL/SVL	54.70 ± 4.26	54.50 ± 7.03	
FOT/SVL	70.22 ± 4.78	78.54 ± 13.41	*
FTL/SVL	10.12 ± 1.15	12.35 ± 2.54	**
FFTL/SVL	28.09 ± 2.39	34.14 ± 11.09	*
HTD/SVL	3.816 ± 0.61	8.20 ± 2.87	**
MTTi/SVL	5.37 ± 2.30	5.45 ± 1.36	

Notes. All morphometric characters are given as % of SVL. Character abbreviations are explained in *Material and Methods*.
*$p < 0.5$, **$p < 0.05$.

TABLE 5. Temporal and Frequency Characteristics of Advertisement Call Parameters for *Theloderma stellatum* and *Theloderma vietnamense* sp. nov. [means ± SE (range)]

Parameters	*Th. vietnamense* sp. nov.	*Th. stellatum*
Number of calls	16	32
Call duration, msec	161 ± 3 (125 – 175)	85 ± 2 (65 – 108)
Intercall interval duration, sec	2 ± 0.02 (1.91 – 2.2)	0.88 ± 0.08 (0.38 – 2.39)
Calling rate, calls/sec	0.47	0.95
Number of harmonics	2.6 ± 0.1 (2 – 3)	2.1 ± 0.1 (2 – 3)
F_{beg}, Hz	1230 ± 10 (1180 – 1290)	1480 ± 10 (1350 – 1740)
F_{end}, Hz	1330 ± 10 (1180 – 1290)	1400 ± 20 (1220 – 1550)
F_{min}, Hz	1220 ± 10 (1160 – 1290)	1380 ± 20 (1220 – 1520)
F_{max}, Hz	1340 ± 10 (1310 – 1370)	1580 ± 10 (1220 – 1740)
F_{range}, Hz	120 ± 10 (60 – 170)	200 ± 12 (80 – 370)
Frequency modulation	weak lift	arched
$F_{peak\ 1}$, Hz	1300 ± 10 (1270 – 1330)	1530 ± 30 (1370 – 1720)
$F_{peak\ 2}$, Hz	2550 ± 10 (2540 – 2560)	2910 ± 10 (2840 – 2970)

horridum shows the lightest ventral coloration (Fig. 9*c*), with dark coloration on the belly being reduced to numerous blotches of irregular shape and distinct light reticulations on the throat. Based on the material we had a chance to examine (see *Appendix 1*), we consider that these differences in belly coloration are usually stable.

We also found stable differences between the three *Stelladerma* subgen. nov. species in the body morphometrics, degree of finger and toe webbing development and hand morphology. These characters are discussed in details in the *Comparisons*.

Acoustics. The advertisement calls of *Theloderma* cf. *stellatum* from southern Vietnam and *Theloderma stellatum* Taylor, 1962 from eastern Thailand differ both by temporal and frequency characteristics (see Fig. 10, Table 5). Moreover, the advertisement calls of *Theloderma* cf. *stellatum* from southern Vietnam have longer call and intercall durations and show lower frequency range than calls of *Theloderma stellatum sensu stricto*. Though differences in frequencies and temporal parameters may be partially related to minor differences in temperature conditions of the recordings or may reflect differences in body size of calling males. The frequency of maximum amplitude coincides with the fundamental frequency in 87.5% calls of *Theloderma* cf. *stellatum* from southern Vietnam and only in 34.4% calls of *Theloderma stellatum*. Finally, these two species significantly differ by the shape of the frequency modulation — arched in *Theloderma stellatum* Taylor, 1962 (see Fig. 10*a*; Table 5) vs. weak lift in *Theloderma* cf. *stellatum* from southern Vietnam (see Fig. 10*b*; Table 5).

Taxonomic part

Thus, our molecular, morphological and acoustic analyses (see below) provide solid evidence that the Vietnamese populations previously referred as *Th. stellatum* represent a distinct yet undescribed species of *Theloderma*, clearly distinguishable from *Th. stellatum sensu stricto* from Thailand and other congeners, which we describe below as:

Theloderma vietnamense sp. nov.

Synonymy. *Theloderma stellatum* Taylor, 1962 (partim) — Tarkhnishvili (1994, 1995); Kuzmin and Tarkh-

Fig. 7. *Theloderma stellatum sensu stricto* from Thailand in life: ***a***, adult male from Nakhon Nayok Province, Khao Yai Nature Reserve; ***b***, juvenile from Uthai Thani Province, Hauy Kha Khaeng Wildlife Sanctuary; ***c***, adults from Uthai Thani Province, Hauy Kha Khaeng Wildlife Sanctuary (photos P. Pawangkhanant).

nishvili, 1997; Orlov (1997; 2005); Inger et al. (1999); Orlov et al. (2002; 2006; 2010); Orlov and Ho (2005); Nguyen et al. (2005; 2009); Stuart et al. (2006); Nguyen and Nguyen (2008); Rowley et al. (2011); Nguyen et al. (2014; 2015).

Holotype. ZMMU A-5387 (field number NAP-05238) collected on February 4th, 2015, by Anna B. Vassilieva and Anna V. Moiseeva in Vietnam, Dong Nai Province, Dong Nai Biosphere Reserve (former Cat Tien National Park), Nam Cat Tien Sector, environs of Cat Tien National Park headquarters, in a water-filled hollow in a *Lagerstroemia calyculata* (Lythraceae) tree, approximate coordinates: 11°25′43″ N 107°25′38″ E; altitude ca. 110 m a.s.l. (Figs. 11 – 13).

Paratypes. ZMMU A-4661 (NAP-00081): Cat Tien National Park, Dong Nai Province, Vietnam (1 sp., paratype); ZMMU A-5456 (NAP-03406): Loc Bac (Loc Bao) forestry, Bao Loc district, Lam Dong Province, Vietnam (1 sp., paratype); ZMMU A-4525 (NAP-02998): Con Son island, Road to So Ray, Con Dao Archipelago, Ba Ria — Vung Tau Province, Vietnam (1 sp., paratype); ZMMU A-5385 (NAP-03723 – 03725; NAP-03811; NAP-03824): Phu Quoc National Park, Phu Quoc Island, Kien Giang Province, Vietnam (5 sp., paratypes); ZISP 12212 (NAP-03825): Phu Quoc National Park, Phu Quoc Island, Kien Giang Province, Vietnam (1 sp., paratype).

Referred materials. Adults: ZMMU A-5457: Bu Gia Map National Park, Binh Phuok Province, Vietnam (1 sp.); ZMMU A-3172-1-2: Ma Da Forestry, Dong Nai Province, Vietnam (2 sp.); ZMMU A-3778: Lo Go – Xa Mat National Park, Tay Ninh Province, Vietnam (2 sp.); ZMMU A-3951: Phu Quoc National Park, Phu Quoc Island, Kien Giang Province, Vietnam (1 sp.); ZMMU A-5460: Binh Chau – Phuok Buu National Park, Ba Ria – Vung Tau Province, Vietnam (2 sp.); ZMMU A-3758:

Fig. 8. *Th. vietnamense* sp. nov. from Vietnam in life: southern Vietnam: ***a***, Kien Giang Province, Phu Quoc Island, Phu Quoc N. P. (photo N. A. Poyarkov); ***b***, Lam Dong Province, Loc Bac (Loc Bao) (photo N. A. Poyarkov); central Vietnam: ***c***, Gia Lai Province, Kannack, Tram Lap (photo N. L. Orlov); ***d***, Kon Tum Province, Kon Plong, Mang Canh (photo N. L. Orlov).

Mondulkiri Province, Cambodia (1 sp.); ZMMU A-3773: Steng Chhral, Kampot Province, Cambodia (1 sp.); ZISP 7556a-7556b; FMNH 253617 – – 253626: Tram Lap, 40 km northwest of the town of Kannack, 900 m a.s.l. (Tay Nguyen Plateau), Gia Li Province, Vietnam (10 sp.); Larvae: ZMMU NAP-02442: Cat Tien National Park, Dong Nai Province, Vietnam (2 sp.); ZMMU NAP-02827: Loc Bac Forestry, Lam Dong Province, Vietnam (1 sp.); ZMMU NAP-03680: Lo Go – Xa Mat National Park, Tay Ninh Province, Vietnam (1 sp.); ZMMU ABV-00832: Cat Tien National Park, Dong Nai Province, Vietnam (2 sp.); ZMMU A-3172-3: Ma Da Forestry, Dong Nai Province, Vietnam (1 sp.).

Etymology. The specific name "*vietnamense*" is a Latin toponymic adjective in the nominative singular (neutral gender), referring to distribution of the new species covering central and southern parts of Vietnam.

Recommended vernacular name. We recommend the following trivial name in English: *South-Vietnamese Bug-Eyed Frog*. Recommended vernacular name in Vietnamese: *Ech Cay San Viet Nam*.

Diagnosis. The new species is assigned to the genus *Theloderma* by (1) having some degree of calcified tuberculate skin, (2) presence of a distinct tympanum, (3) having terminal phalanx with a Y-shaped distal end, (4) presence of the intercalary cartilage between the terminal and penultimate phalanges of digits, (5) tips of digits expanded into large disks bearing circummarginal grooves, (6) reproductive behavior of depositing eggs in water-filled tree hollows, karst crevices etc. (Liem, 1970; Rowley et al., 2011; Nguyen et al., 2015), and molecular data (see Fig. 3). *Theloderma vietnamense* sp. nov. is distinguished from all other *Theloderma* by a combination of the following morphological attributes: (1) absence of co-ossification of the head skin to the skull; (2) absence of bony ridges from canthus rostralis to occiput; (3) highly tuberculated skin on the dorsum with calcified warts and large asperities; (4) elongated snout with canthus rostralis rather sharpened than rounded, nostrils be-

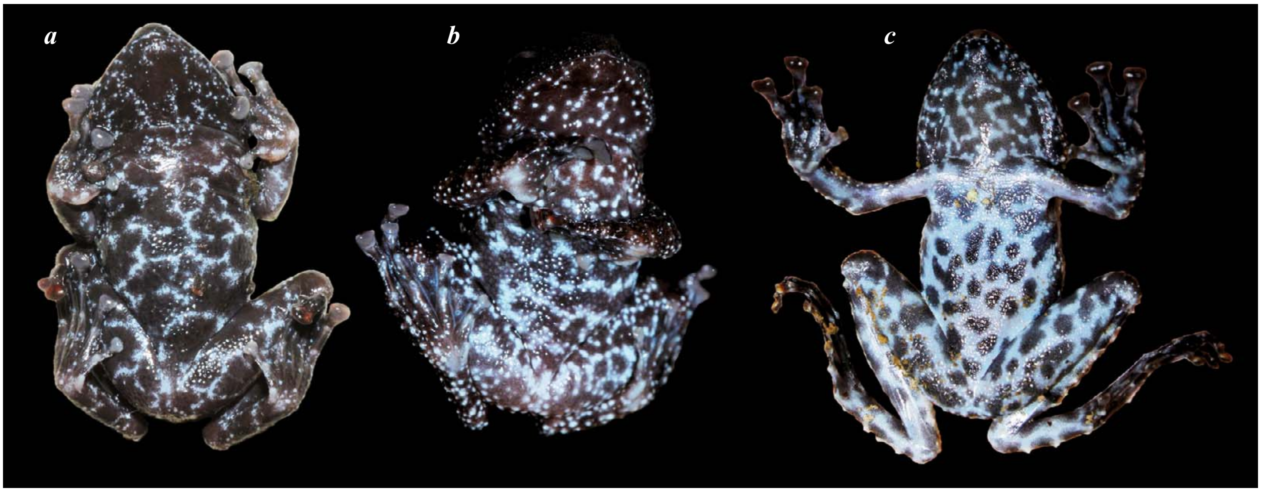

Fig. 9. Ventral patterns in three species of *Theloderma* (*Stelladerma* subgen. nov.) in life: ***a***, *Th. vietnamense* sp. nov. (Vietnam, Dong Nai Province, Cat Tien N. P.; photo E. A. Galoyan); ***b***, *Th. stellatum sensu stricto* (Thailand, Nakhon Nayok Province, Khao Yai N. P.; photo P. Pawangkhanant); ***c***, *Th. horridum* (Thailand, Satun Province, Tha Le Ban N. P.; photo P. Pawangkhanant).

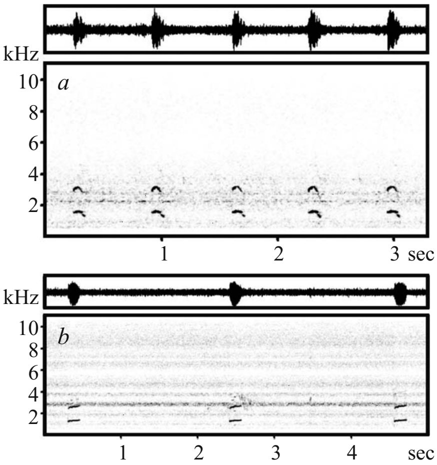

Fig. 10. Oscillograms (top) and sonograms (bottom) of male advertisement calls of *Th. stellatum* complex, recorded at 25.5°C. ***a***, *Theloderma stellatum* (Thailand, Nakhon Nayok Province, Khao Yai N. P.); ***b***, *Theloderma vietnamense* sp. nov. (Vietnam, Dong Nai Province, Cat Tien N. P.).

ing slightly protuberant; (5) vocal opening in males present; (6) absence of vomerine teeth; (7) male of medium body size (SVL 28.0 – 35.1 mm, mean SVL 31.2 mm), female (SVL 29.8 – 35.8 mm, mean SVL 32.0 mm); (8) small tympanum size, tympanum diameter to eye diameter (57% in males, 61% in females), tympanum almost completely smooth; (9) dorsal surface with distinct calcified, white-tipped warts and small asperities (size ranging from 0.1 – 0.5 mm in diameter), regularly scattered across the dorsum, but being larger and denser at the head basis; (10) ventral surfaces, including throat, covered with numerous minute asperities giving it a slightly granular appearance; (11) rudimentary webbing between fingers (basal between all fingers; Fig. 12*b*); (12) finger and toe discs wide with dorsal surfaces reddish in life; (13) supernumerary tubercles on palmar surface absent, inner metacarpal tubercle present, elongated, single outer metacarpal tubercle; (14) toe webbing extensive, webbing formula **I** 1 – $2^{1}/_{4}$ **II** 1 – 2 **III** 1 – $2^{1}/_{4}$ **IV** $2^{1}/_{4}$ – $1^{1}/_{2}$ **V**; (15) inner metatarsal tubercle present; outer metatarsal tubercle absent; (16) iris coloration uniform, brownish to dark golden with brown veins, dark radiating streaks and dark vertical stripe in the lower part of iris; (17) bluish coloration of sclera; (18) brown dorsum with irregular brown or rusty with white, occasionally lavender gray markings, irregular brownish black spots on dorsum, darker brown inguinal (groin) spots, rear back and heels usually white, dark transverse stripes on limbs, and darker, inverted U-pattern between shoulders on lighter background; (19) dark-brown to blackish belly coloration with slight whitish to bluish interrupted reticulations, belly looks dark; throat with minute light dots; (20) head size to SVL ratio (16.82 ± 2.79); eye diameter to SVL ratio (14.06 ± 1.30); eye to nostril distance to SVL ratio (12.18 ± 0.95). The new species is also markedly distinct from all congeners for which comparable sequences are available (12S rRNA to 16S rRNA mitochondrial DNA fragment; uncorrected genetic distance >9.38%). The advertisement call of the new species, consisting of a tonal call with frequency modulation expressed in the weak lift of fundamental frequency during the call, average call duration 160 ± 4 msec, and with an average dominant frequency of 1.23 – 1.33 kHz, also dis-

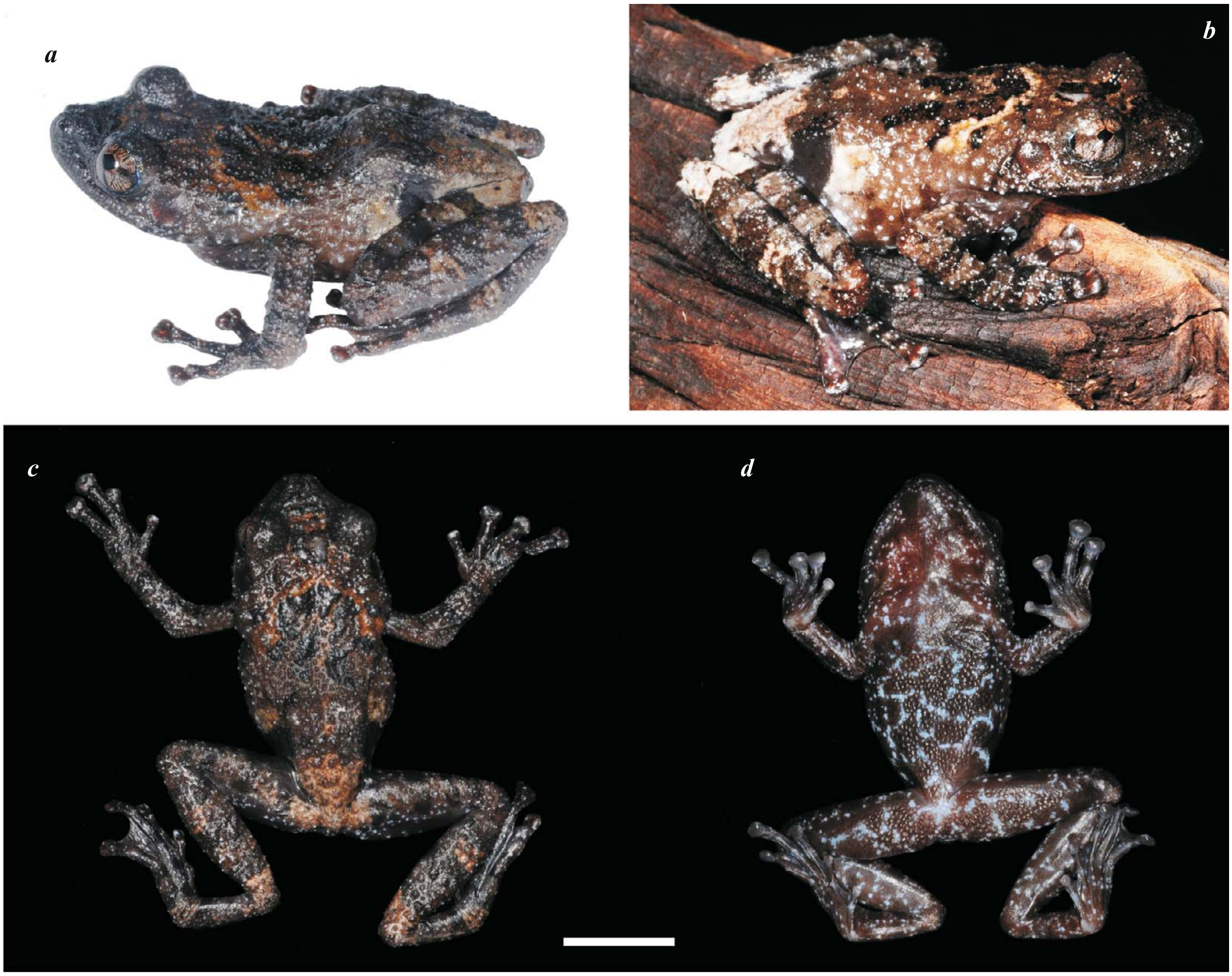

Fig. 11. Holotype *Theloderma vietnamense* sp. nov. (ZMMU A-5387, male; filed number NAP-05238) in life: ***a***, diurnal coloration; ***b***, nocturnal coloration; ***c***, dorsal view; ***d***, ventral view. Scale bar 10 mm. Photos by N. A. Poyarkov.

tinguishes the new species from *Theloderma* species for which calls are known.

Description of holotype. Medium-sized specimen in good state of preservation; body habitus relatively robust (Figs. 11 and 13). The holotype has no dissections; the distal phalanx of the right third finger is absent; the right fourth finger of the holotype is slightly damaged at the basis (Fig. 11*c*, *d*; Fig. 13). Head. Head slightly longer than wide (HW/HL 0.91), flattened; top of head sculptured with calcified warts; snout comparatively short (ESL/HL 0.37), obtusely truncate in dorsal view (Fig. 11*c*; Fig. 13*a*) and gently rounded in profile (Fig. 12*a*), snout slightly projecting beyond margin of the lower jaw; nostril slightly oval-shaped, surrounded by a slightly raised notably protuberant dermal rim (Fig. 11*a*), with a distinct skin flap laterally, located much closer to the tip of the snout than to the eye (Fig. 12*a*); loreal region distinctly concave; canthus rostralis relatively distinct, rounded; eyes rather large (ED/HL 0.30), eye diameter slightly less than snout length (ED/ESL 0.82), notably protuberant in dorsal view and in profile (Fig. 13*a*, *c*), pupil horizontal, diamond-shaped; tympanum distinct, round with vertical diameter being equal to the horizontal diameter (vertical diameter to horizontal diameter (TD) ratio 1.0), tympanic rim elevated relative to skin of temporal region, tympanum relatively small comprising 67% of eye diameter (TD/ED 0.67); tympanic rim notably elevated relative to skin of temporal region; vomerine teeth absent; pineal ocellus absent; skin not co-ossified to skull; choanae oval, at margins of mouth roof; vocal sac openings present; tongue wide, attached anteriorly with the free posterior end, notched at posterior tip; supratympanic fold indistinct, being only notable in the posterior edge of tympanum, running down towards an area posteriorly to the corner of the mouth, not reaching the level of axilla, supratympanic ridge indistinct (Fig. 12*a*). Forelimbs. Forelimbs slender, thin; relative length of fingers **I** < **II** < < **IV** < **III**; tips of all fingers with the well-developed disks with distinct circummarginal grooves (Fig. 12*b*), disks moderately wide compared to finger width (third finger disk width 161% third finger width), disks slightly wider than long, the third finger disk width 136% of third finger disk length; third finger disk width 73% of tympanum diameter; dermal fringing developed at all fingers (Fig. 12*b*); finger webbing rudimentary, basal between all fingers, reaching the level of the most proximal articular tubercles at the inner sides of the first and second fingers, not reaching the level of the most proximal articular tubercles on the outer surfaces of all fingers, finger-webbing formula **I** 2 – 3$^{1}/_{4}$ **II** 3 – 3 **III** 2$^{3}/_{4}$ – 2$^{3}/_{4}$ **IV**; subarticular tubercles small, slightly protruding, rounded, distinct on all fingers, finger subarticular formula **I** (1), **II** (1), **III** (1), **IV** (1) [subarticular tubercles indistinct at distal articulations of fingers **III** and **IV**]; on the ventral surface of the proximal parts of the third and fourth fingers a low dermal midventral ridge present; supranumary tubercles absent; nuptial pad present, elongated, oval-shaped, covering prepollex area; a single indistinctly paired outer metacarpal (palmar) tubercle is barely distinct [the holotype was collected out of the breeding season] (Fig. 12*b*). Hindlimbs. Hindlimbs slender, relatively long, heels overlap when legs are at the right angles to the body, but tibiotarsal articulations reaches the level of the middle of the eye, but not exceeding beyond the front of the eye; tibia half of the snout-vent length (TL/SVL ration 0.51); toes fully webbed, toe-webbing formula **I** 1 – 2$^{1}/_{4}$ **II** 1 – 2 **III** 1 – 2$^{1}/_{4}$ **IV** 2$^{1}/_{4}$ – 1$^{1}/_{2}$ **V** with dermal fringes reaching to disks at all toes. Tips of toes bearing disks with distinct circummarginal and transverse grooves; disks slightly smaller than those of the fingers; relative toe length **I** < **II** < **III** < **V** < **IV**; round yet indistinct subarticular tubercles on all toes, toe subarticular formula **I** (1), **II** (1), **III** (2), **IV** (3), **V** (2); oval-shaped inner metatarsal tubercle well pronounced and slightly protuberant, 2.2 times longer than wide, outer metatarsal tubercle absent (Fig. 12*c*). Skin texture and skin glands. Dorsal skin covered with calcified, white-tipped small pearly asperities, quite evenly distributed as single warts on dorsum, body flanks and around the vent, but tending to form several clumps on forehead and on the area posterior to tympanum (Fig. 13*a*), upper eyelid with small tubercles (Fig. 12*a*); tympanum almost completely smooth with 3 tiny asperities discernable (Fig. 12*a*); ventral surface of thighs and posterior surface of belly coarsely granular, chest and throat smooth (Fig. 11*d*; Fig. 13*b*).

Fig. 12. Holotype *Theloderma vietnamense* sp. nov. (ZMMU A-5387, male; filed number NAP-05238) in life: ***a***, head, lateral view; ***b***, volar view of the left hand; ***c***, plantar view of the left foot. Scale bar 10 mm. Photos by N. A. Poyarkov.

Dermal fringes and pointed projection at tibiotarsal articulation absent.

Color of holotype in life. Dorsal surface diurnally dark brownish-gray, with distinct dark blackish-brown blotches and warm brown markings (Fig. 11*a*, *c*). At night coloration more contrasting with dark-gray ground color turning to warmer and lighter brown tint, with dark dorsal markings being well-distinct (Fig. 11*b*). In the center of the dorsum large blackish-brown blotch of irregular shape lasts towards the scapular area, forming a distinct dark-brown chevron of an inverted U-shape (Fig. 11*a* – *c*), anteriorly edged with light warm beige (nocturnally, Fig. 11*b*) to rusty brown (diurnally, Fig. 11*a*, *c*). Irregular diamond-shaped interorbital blotch located between the posterior edges of the inner margins of the orbital bulge, is also edged with light-brown (Fig. 11*b*). A single dark brown pelvic band runs across the body between the dark-blackish inguinal spots. Rear of the dorsum, body flanks, dorsal surface at the basis of hindlimbs and around the tibiotarsal articulation has much lighter ground color, varying from dull gray-brown (diurnally, Fig. 11*a*) to beige or creamy white (nocturnally, Fig. 11*b*). Three small (ca. 1 mm in diameter) creamy spots in the middle of the dorsum between the scapular chevron and the transverse pelvic dark band (Fig. 11*b*). Dorsum is covered by numerous whitish or bluish-white asperities, being brighter and more distinct at night (Fig. 11*b*); they are also well-discernable on dorsal and lateral surfaces of the head (Fig. 12*a*). Tympanum uniformly colored, purplish-brown (Fig. 12*a*). Lateral surfaces of the body lighter than the dorsum, gray-brown, with two distinct uniformly black large inguinal spots

Fig. 13. Holotype *Theloderma vietnamense* sp. nov. (ZMMU A-5387, male; filed number NAP-05238) in preservative: ***a***, dorsal view; ***b***, ventral view. Scale bar 10 mm. Photos by N. A. Poyarkov.

(Fig. 11*a*, *b*). Small pale bluish speckles on flanks and in the groin region (Fig. 11*a*, *b*; Fig. 12*a*). Three dark blackish-brown bands run across the dorsal side of forearm, smaller transverse dark bands continue on fingers. Three dark blackish-brown bands running across the dorsal surfaces of tibiotarsus and thigh; when leg is adpressed, the medial dark band forms a continuous line with the dark inguinal spot, which, in its turn, continues to the dorsal pelvic band. Thigh has an extra-band proximally than the knee; knee with a dark-brownish patch, forming a dark knee cap. Dorsal surfaces of finger and toe disks dark brick-reddish with lighter gray margins; finger disks are brighter than the disks on toes. Dorsal and ventral surfaces of arms, hands and feet grayish brown with faint bluish speckling (Fig. 11*a*, *b*; Fig. 12*b*, *c*). Ventral surfaces dark blackish-brown with a purple tint being especially prominent in the throat and chin area, covered with faint pale bluish white thin reticulations forming a network-like pattern (Fig. 11*d*). Throat with faint white to bluish speckling (Fig. 11*d*), it extends laterally onto the upper lip and flanks (Fig. 12*a*); minute bluish speckles also present on ventral surfaces of limbs (Fig. 12*b*, *c*).

Pupil horizontally oval; iris coloration uniform, brownish to dark golden with brown veins, dark horizontal radiating streaks and a more distinct dark vertical stripe in the lower part of iris (Fig. 12*a*). Sclera light bluish (Fig. 11*b*; Fig. 12*a*).

Color of holotype in preservative. The coloration of specimens in ethanol depends on its color before euthanasia. In preservative, the reticulated ventral pattern is distinct, and the inguinal dark spot remains blackish. In general, coloration remains much resembling the one observed in life, but the dark brown base color of the dorsal surface looses warm tints in tone and look darker, brownish-gray; light ochre spots on dorsum fade to grayish creamy-white, ventral coloration is also less warm in tone (Fig. 13*a*). The white reticulations on the ventral surface look more distinct and contrasting, though the bluish tint fades completely (Fig. 13*b*).

Measurements of the holotype (all in mm). SVL 33.53; A-G 16.76; HW 12.98; HL 14.32; HD 5.84; UEW 2.68; IOD 3.39; IND 2.22; ED 4.34; TD 2.90; ESL 5.28; TED 0.87; END 4.13; FLL 20.58; FFL 3.19; TFL 5.69; FTD 2.12; NPL 2.09; MKTe 1.06; HLL 48.86; FL 14.97; TL 16.99; FOT 22.07; FTL 3.05; FFTL 8.05; HTD 1.40; MTTi 1.34.

Variation. All individuals in the type series are generally similar in morphology and body proportions; variation of the studied specimens (including the type series) in morphometric characters is shown in Table 3. We found no clear differences in body size between the sexes based upon the series examined from both the southern and central Vietnam (see Table 3).

Specimen coloration may vary greatly in the number and size of black spots on dorsum, in shape of dark inguinal spots, dark dorsal pattern (may vary from an inverted V or U-shaped chevron to almost trifoliate figure or separate dark blotches), in presence and size of the white blotches (in some specimens they are completely indistinguishable, whereas in others they may occupy the larger part of the dorsum) (Fig. 8*c*, *d*).

Like other rhacophorids (including most species of *Theloderma*, see McLeod and Norhayati, 2007; Rowley et al., 2011; Orlov et al., 2012), *Theloderma vietnamense* sp. nov. can vary the pigmentation of portions of its skin in response to diel period, stress and microhabitat conditions. Similar to other *Theloderma* (McLeod and Norhayati, 2007; Rowley et al., 2011), in life, both sexes of the new species show much lighter coloration of dorsum (to grayish-brown or dark beige), belly (dark brown with purple tint) and throat nocturnally (Fig. 8*d*; Fig. 11*b*) than during the day time (Fig. 8*a* – *c*; Fig. 11*a*). Diurnally coloration is much darker, dorsum turns dark warm chocolate-brown, belly also turns much darker, colored blackish-brown with violet tint and clear thin bluish-white reticulations. White blotches on the rear of dorsum are quite clear during night, whereas diurnally or when handled and stressed; they turn grayish-beige and may be almost indistinguishable. Similarly, beige or ochre edging of dorsal blotches and the dark pattern in scapular area become much less distinct during the day.

Though we revealed certain differences in body morphometrics between central and southern Vietnamese populations of *Theloderma vietnamense* sp. nov. (see Table 3 for details), in general morphology and body coloration, population from Kontum Province corresponds well to the type series (see Fig. 14).

Larval stage. Morphological description of larval stages is based on eight tadpoles (Gosner stages 25 – 35) collected in tree hollows filled with water: ZMMU NAP-02442 (2 specimens, Cat Tien National Park, Dong Nai Province), ZMMU NAP-02827 (Loc Bac Forestry, Lam Dong Province), ZMMU NAP-03680 (Lo Go – Xa Mat National Park, Tay Ninh Province) (see *Appendix 2*).

The main morphometric parameters of the tadpoles are given in Table 6. Body proportions are given as mean ± SD. We also included data on two tadpoles at hatching (Gosner stage 25) ZMMU ABV-00832 (2 specimens, Cat Tien National Park, Dong Nai Province; not included in Table 6).

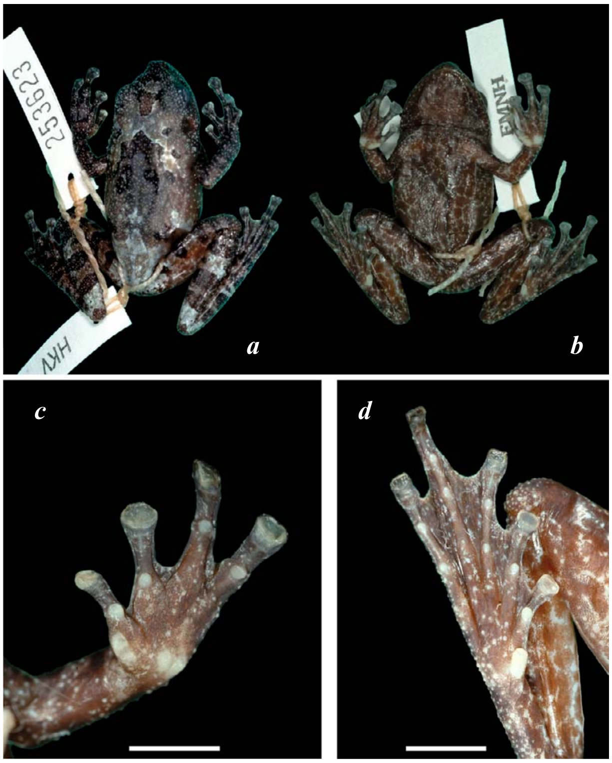

Fig. 14. *Theloderma vietnamense* sp. nov. (FMNH 253623, male) in preservative: ***a***, dorsal view; ***b***, ventral view; ***c***, volar view of the left hand; ***d***, plantar view of the right foot. Scale bar 10 mm. Photos by N. L. Orlov.

External morphology. Body broadly oval (BW/BL = 0.73 ± 0.04), depressed dorsoventrally (Fig. 15); snout broad, rounded; in fixed specimens lateral lymphatic sacs visible on each side of the body as thickened horizontal ridges extending along the posterior half of the body. Eyes small (ED/BL = 0.06 ± 0.02), smaller at early developmental stages (mean ED/BL = = 0.05) and slightly larger at more advanced stages (mean ED/BL = 0.09), dorsal, pupils oriented dorsolaterally. Tail relatively short (TaL/BL = 1.20 ± 0.1), slightly longer at more advanced stages, with rounded tip and well developed muscular part. Upper and lower fins reach their maximum height in the medium tail part, with the upper fin being slightly higher or approximately equal to the lower fin in height (UF/LF = 1.1 ± 0.17), not extending on the trunk. Spiracle sinistral, lateroventral, representing short tube fused to the body wall without free distal portion, with aperture directed posterodorsally; spiracle opening margins even, without serration. Vent tube medial, attached to the lower fin, short, with oblique aperture oriented ventrocaudally. Narial apertures small, rounded, oriented rostrolaterally, surrounded by a slightly raised rim; positioned closer to the snout tip than to the eyes (NP/RN = 1.85 ± 0.50). Mouth anteroventral.

Fig. 15. Tadpole of *Theloderma vietnamense* sp. nov. (stage 35) in life in dorsal view. Photo by E. A. Galoyan.

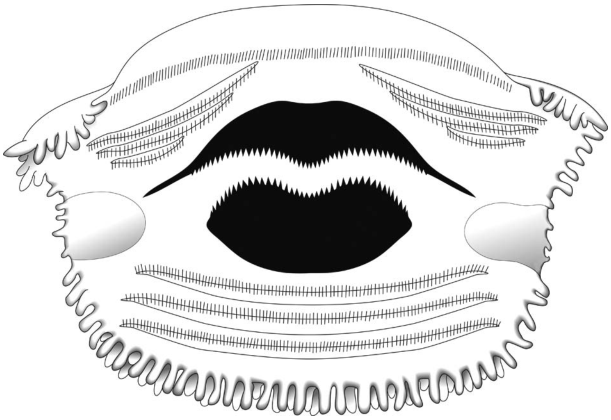

Fig. 16. Oral disc morphology of *Theloderma vietnamense* sp. nov. tadpole (NAP-02827, stage 35). Drawing by A. B. Vassilieva and V. L. Trounov.

Tadpoles hatch at stage 25 with the fully developed opercular fold. At hatching, mouth sheaths are well formed, labial teeth are still developing. Digestive tract filled with yolk. Two tadpoles at hatching had TL 10.8, SVL 3.7 and TL 9.6, SVL 3.4 mm, respectively.

Oral disc. Oral disc (Fig. 16, based on NAP-02827, Gosner stage 35) moderately wide (ODW/BW = 0.36 ± ± 0.04), elliptical; mouth corners and lower labium fringed with continuous double (occasionally triple) row of soft conical papillae. Mouth sheaths with densely serrated cutting edges; upper sheath wide arch-shaped, lower sheath smoothly U-shaped. Spike-like labial denticles arranged along the upper labium edge and flat unpigmented ridges having horizontal orientation: a single undivided and several (2 – 4) divided rows on the upper labium and invariably 3 rows on the lower labium. LTRF 1:3+3/3 (variants 1:2+2/3 or 1:4+4/3 are also observed).

Coloration. Coloration in life (Fig. 15) and in preservative are similar, slightly variable from dark brown to yellowish brown on the dorsal and lateral surfaces of the body and tail; ventral surface is paler, semi-transparent, grayish or yellowish. Eyes and keratinized mouthparts are black. Lines of neuromasts are faintly visible on the dorsal surfaces of the head, trunk and tail.

TABLE 6. Main Morphometric Parameters of *Theloderma vietnamense* sp. nov. Tadpoles

Character	NAP-02827	NAP-02827	NAP-02442	NAP-03680	NAP-03680	NAP-02442	NAP-02827	NAP-02827
Stage	25	25	25	27	28	31	31	35
TL	15.5	16.6	20.2	23.9	26.7	26.1	30.8	34.1
BL	7.0	7.6	9.2	11.5	12.8	11.6	13.5	14.1
TaL	8.5	9.0	11.0	12.4	13.9	14.5	17.3	19.7
BW	5.7	5.9	6.5	8.0	9.1	8.6	9.5	9.9
BH	3.7	3.8	4.2	5.8	6.5	5.6	6.2	7.0
TH	5.3	4.5	4.0	4.8	5.1	4.9	6.3	6.2
SVL	7.0	7.6	9.2	11.5	12.8	11.6	13.7	14.6
SSp	5.1	5.5	6.4	8.2	9.5	8.3	9.8	10.2
UF	1.5	1.4	1.2	1.6	1.6	1.3	2.1	1.8
LF	1.8	1.3	1.3	1.2	1.4	1.3	1.6	1.7
IN	1.4	1.4	1.6	1.8	2.1	2.1	2.3	2.4
IP	2.6	2.9	2.7	3.1	3.4	3.3	4.0	4.1
RN	0.5	0.6	0.8	1.5	1.7	1.0	1.6	2.0
NP	1.3	1.5	1.7	1.9	2.3	2.1	2.4	2.7
ED	0.4	0.4	0.6	0.5	0.7	1.0	0.8	1.3
ODW	1.7	1.8	2.3	2.8	3.5	3.1	4.0	3.8
LTRF	1:2+2/3	1:2+2/3	1:2+2/3	1:3+3/3	1:2+2/3	1:2+2/3	1:4+4/3	1:3+3/3

Note. For abbreviations see *Materials and Methods*.

Advertisement call. The advertisement call of *Theloderma vietnamense* sp. nov. recorded at 25.5°C represents a tonal call with a weak frequency modulation (see Fig. 10; Table 5).

Call duration varied from 125 to 175 (160 ± 4) msec. The interval between successive calls in one individual varied from 1.91 to 2.20 (2 ± 0.02) sec. The call repetition rate in a series of successive calls was 0.47 calls per second. The initial (1230 ± 10 Hz) and final fundamental frequency in a single call (1330 ± 10 Hz) also represented the minimum and the maximum fundamental frequencies, respectively. Thus, the frequency modulation was expressed in the weak lift of fundamental frequency during the whole call; such pattern was recorded in all calls. The frequency range varied from 60 to 170 Hz (120 ± 10). All calls contained the clearly visible lower harmonic and 37.5% of them also contained the second poorly distinguishable harmonic. The maximum amplitude frequency in individual calls (1298 ± 10 Hz) coincided with the fundamental frequency except for the two calls where the maximum amplitude frequency coincided with the lower harmonic (2550 ± 10 Hz) (Table 5). Around 43.8% of the calls of the new species showed presence of the nonlinear acoustic phenomenon — subharmonics.

Position in mtDNA phylogeny and sequence divergence. According to our mtDNA data, the new species belongs to the subgenus *Stelladerma* subgen. nov. together with *Th. horridum* and *Th. stellatum sensu stricto* (see Fig. 3). Uncorrected genetic *p*-distances between *Theloderma vietnamense* sp. nov. 12S rRNA and 16S rRNA sequences and all homologous sequences of congeners available on GenBank and included in the analysis (see Table 1) varied from 9.38% (with *Th. stellatum sensu stricto*) to 20.19% (with *Th. laeve*) (see Table 2). This degree of pairwise divergence is considered to be high, notably greater than the genetic divergence thresholds representing species level differentiation in frogs (Vences et al., 2005a, 2005b; Vieites et al., 2009). Intraspecific variation in these gene fragments for *Theloderma vietnamense* sp. nov. less than $p = 1.90\%$.

Distribution and biogeography. The known distribution of *Theloderma vietnamense* sp. nov. is shown in Fig. 5. The new species has been so far recorded from a number of localities in southern and central Vietnam and adjacent parts of Cambodia (localities *15 – 35*, Fig. 5) from the Con Dao archipelago in the south (Con Son Island, locality *18*, Fig. 5) to as far as Kon Tum Province of Central Vietnam in the north (Mang Canh environs, locality *33*, Fig. 5), or even, possibly, penetrating to central Laos (localities *35*, *36*, Fig. 5), occupying altitudes from the sea level up to 1500 m a.s.l. The species is also recorded from the neighboring areas of Cambodia, including mountain areas in Mondulkiri Province (locality *15*, Fig. 5), biogeographically belonging to the western edges of the Langbian Plateau, a part of southern Annamites (Truong Son) (Stuart et al., 2006). We recorded *Th. stellatum* in Nui Son Tra, Danang City (locality *34*, Fig. 5; specimen not collected), Dever et al. (2015) report on *Th. stellatum* samples from Savannakhet Province of Laos (localities *35*, *36*, Fig. 5), whereas Luu et al. (2013) report on *Th. stellatum* from Phong Nha – Ke Bang National Park in Quang Binh Province of Vietnam (locality *37*, Fig. 5), which is to date the northernmost country record for this species. We assume that these localities likely correspond to the new species, *Theloderma vietnamense* sp. nov. However, they are situated quite far to the north from the known distribution area in Kon Tum Province, and the status of these localities has to be clarified by further studies.

Most localities of the new species known to date are recorded eastwards from the Mekong River basin (localities *19 – 35*, Fig. 5), with the exception of the Phu Quoc Island population (locality *17*, Fig. 5); taxonomic attribution of which to *Theloderma vietnamense* sp. nov. was confirmed by molecular phylogenetic analyses (see *Results*). From the point of biogeography and geology (see reviews in Bain and Hurley, 2011) the Phu Quoc Island is a part of the Cardamom Mountains of the southern Cambodia and eastern Thailand; though the island shows a specific zoogeographic attribution in the biogeographical analysis of the south-Indochinese batrachofauna by Geissler et al. (2015). We had a chance to examine a single specimen from Steng Chhral, Kampot Province, Cambodia (ZMMU A-3773, see *Appendix 1*; locality *16*, Fig. 5), a locality, situated just across the sea strait separating the Phu Quoc Island from the mainland eastern Cambodia. Unfortunately, a correct identification of the new species is only reliable with application of molecular genetic methods; however, based on the preliminary analyses of morphological diagnostic features (degree of toe webbing, morphometrics), we tentatively assign this population to *Theloderma vietnamense* sp. nov. The population of *Theloderma* cf. *stellatum* discovered in Nui Dai Mt., An Giang Province (locality *18*, Fig. 5; Nguyen Ngoc Hung, personal communication) is quite interesting since it fills the gap between the Phu Quoc population and the rest of the range of *Theloderma vietnamense* sp. nov.; however, the correct identification of this population would be only possible with application of molecular genetic methods. Therefore, the extent of *Theloderma vietnamense* sp. nov. distribution in Cambodia, as well as a reliable taxonomic assignment of the Cardamom Mountain populations, requires further studies using morphological, molecular and acoustic lines of evidence.

Fig. 17. Typical breeding habitat of *Theloderma vietnamense* sp. nov. is located in numerous water-filled hollows in the roots of a giant *Tetrameles nudiflora* (Tetramelaceae), Cat Tien National Park, Dong Nai Province, Vietnam. Photo by A. V. Tchabovsky.

The distribution pattern of *Th. stellatum* and *Th. vietnamense* sp. nov. closely resembles the distribution of other cryptic species, such as *Calotes mystaceus* and *C. bachae*, being also likely separated from each other by the Mekong River (Hartmann et al., 2013). The described differentiation within the *Theloderma stellatum* species complex gives another example of the role of the Mekong Basin as an important zoogeographical barrier for herpetofauna in southern Indochina (Hartmann et al., 2013; Geissler et al., 2014, 2015).

Natural history notes. The new species inhabits various types of dense evergreen and semideciduous forests in lowlands and hilly areas at elevations from the sea level up to 1500 m a.s.l., being most abundant at elevations up to 800 m a.s.l. In the area 2 – 5 km around the type locality near Cat Tien National Park headquarters the new species was mostly found in the dense monsoon tropical semideciduous forests with closed canopy at altitudes up to 200 m a.s.l., dominated by *Lagerstroemia calyculata* (Lythraceae), *Afzelia xylocarpa* (Fabaceae), and *Dipterocarpus alatus* (Dipterocarpaceae), with occasional trees of *Tetrameles nudiflora* (Tetramelaceae) (see Fig. 17). Most specimens of the *Theloderma vietnamense* sp. nov. were collected in the water-filled tree-hollows in trunks and roots of *Lagerstroemia calyculata*, *Tetrameles nudiflora*, and other tree species. Occasionally in some areas the reproductive groups of the new species were recorded in man-made waterbodies (water-filled barrels, etc.) within the secondary forest. *Theloderma vietnamense* sp. nov. is a very secretive species and is usually observed in water-filled tree-hollows (also serving as shelters during the day time) or in their vicinity (at night). Activity is strictly nocturnal and highly arboreal. The new species feeds mainly on beetles, ants, caterpillars and spiders (Kuzmin and Tarkhnishvili, 1997).

Reproduction. In southern Vietnam, breeding period usually lasts from April to November; spawning was recorded even during the dry season after occasional rains. The new species is a strict phytothelm breeder: spawning occurs in the water-filled tree hollows. Commonly, a single tree-hollow is inhabited by a reproductive group consisting of one male and 2 – 3 females. Males call on vegetation near the hollows or from inside the hollow (see Advertisement call). Egg-clutches usually include 4 – 8 pigmented eggs (diameter 2.5 – 3 mm) embedded in a transparent gelatinous mass, which is placed on hollow wall above the water surface (Fig. 18). Hatched tadpoles drop into the water and continue development in the hollow cavity until metamorphosis is completed, which takes up to three months. Tadpoles of different ages can be often recorded in the same tree hollow.

Conservation status. *Theloderma vietnamense* sp. nov. has a wide distribution in southern and central Vietnam, including adjacent territories of eastern Cambodia (see Fig. 5), and may be locally quite common. However, as a strict phytothelm-breeding specialist, the new species is associated with water-filled tree hollows, usually observed in the big trees within the primary monsoon tropical forests; these are scarce, thus the new species is never observed in large numbers. Moreover, the monsoon tropical forests of southern Vietnam have been subject to severe anthropogenic habitat transformation and destruction during the last 40 years; Vietnam has the second highest rate of deforestation of primary forests in the world (Meijer, 1973; De Koninck, 1999; Laurance, 2007; Meyfroidt and Lambin, 2008). Therefore, the relevant conservation status of the new species still has to be estimated. Given the available information, we suggest *Theloderma vietnamense* sp. nov. to be considered as a Data Deficient species following IUCN's Red List categories (IUCN 2001).

Comparisons. Photos of the Indochinese and Thai species of *Theloderma* for comparison purposes are presented in Fig. 1. The small to medium body size, absence of vomerine teeth and presence of small dorsal asperities and warts on dorsum distinguishes *Theloderma vietnamense* sp. nov. from the large-sized *Theloderma* species: *Th. bicolor*, *Th. corticale*, *Th. gordoni*, *Th. kwangsiense*, *Th. leporosum*, *Th. nagalandense* (vs. large body size, large dorsal asperities, and vomerine teeth present in these taxa). *Th. moloch* can also be differentiated from the new species by the presence of large dorsal asperities and vomerine teeth. Presence of a distinctly bicolored iris allows distinguishing *Th. laeve*, *Th. nebulosum*, *Th. palliatum*, *Th. truongsonense* from the new species (vs. iris is brownish to dark-golden with black reticulations in *Theloderma vietnamense* sp. nov.) and taxa of the subgenus *Nyctixalus*: *Th. margaritifer*, *Th. pictum*, *Th. spinosum*. Presence of the rudimentary webbing on hands separates the new species from *Th. albopunctatum*, *Th. andersoni*, *Th. asperum*, *Th. baibengense*, *Th. bicolor*, *Th. gordoni*, *Th. laeve*, *Th. lateriticum*, *Th. leporosum*, *Th. moloch*, *Th. nebulosum*, *Th. palliatum*, *Th. rhododiscum*, *Th. truongsonense*. The Malayan species *Th. licin* can be distinguished from *Theloderma vietnamense* sp. nov. by much smoother skin (vs. decent warts and dorsal asperities present in the new species), whitish coloration of the whole dorsum (vs. white blotches that may be present in the rear of dorsum in the new species), by whitish belly with brown reticulations (vs. blackish belly with white-bluish thin reticulations in *Theloderma vietnamense* sp. nov.), by smooth tympanum (vs. three tiny tubercles on the tympanum in the new species, see Fig. 12*a*), by presence of three distinct metacarpal tubercles (vs. two metacarpal tubercles in *Theloderma vietnamense* sp. nov.) and by the red coloration of iris (vs. golden-brownish iris with black reticulations in the new species). *Th. phrynoderma* can be differentiated from the new species by larger size (SVL 41.4 – – 44.6 mm), by more extensive hand webbing with one-third webbing between fingers II and III and nearly one-half webbing between fingers III and IV (vs. webbing basal or always less than one-third between all fingers in the new species), by much better developed dorsal asperities arranged in groups of large warts (vs. comparatively small asperities and warts on dorsum in the new species), by the presence of a few large round bumps on throat (vs. no bumps on throat in *Theloderma vietnamense* sp. nov.), and by uniform grayish coloration of dorsum (vs. brown with white or lavender-gray markings on dorsum with a distinct dark inverted U- or V-shaped figure in the new species). *Th. petilum* can be easily differentiated from the new species by almost completely smooth skin with minor asperities on head posterior surfaces of the dorsum and dorsal surfaces of limbs (vs. distinct asperities and warts on dorsum in the new species) and by characteristic coloration with two chocolate-

Fig. 18. Clutch of *Theloderma vietnamense* sp. nov. before hatching, Cat Tien National Park, Dong Nai Province, Vietnam. Photo by P. Geissler.

brown bands running from lateral surfaces of head towards groin, distinctly separated from the beige-brownish dorsum and edged with white (vs. no dark lateral bands in *Theloderma vietnamense* sp. nov.). *Th. ryabovi* can be diagnosed from the new species by notably larger size in adults (SVL up to 64.58 mm), by dorsal coloration varying from almost completely black to beige with black spots (vs. brownish dorsal coloration with an inverted U- or V-shaped figure in the new species) and by dark-gray belly coloration without pattern (vs. dark brownish-black belly with thin whitish reticulated pattern in *Theloderma vietnamense* sp. nov.).

Theloderma vietnamense sp. nov. is morphologically most similar to the other members of the subgenus *Stelladerma* subgen. nov.: *Th. horridum* and, especially, to *Th. stellatum*, and comparisons with these two species are the most pertinent ones.

Th. horridum can be easily distinguished from the new species by its large body size (SVL up to 45 mm, Fig. 1*a*) (vs. SVL up to 35.8 mm, Fig. 1*c* in *Theloderma vietnamense* sp. nov.), much lighter belly pattern: bluish-white background covered with numerous dark blotches of irregular shape and distinct light reticulations on the throat (Fig. 9*c*) (vs. dark belly pattern, blackish ground color with thin whitish reticulations in the new species; Fig. 9*a*), by half-webbed fingers (webbing formula: **I** $1^{1}/_{2} – 1^{1}/_{4}$ **II** $1 – 1^{3}/_{4}$ **III** $1^{1}/_{2} – 1$ **IV**) and complete webbing on feet (webbing formula: **I** 1 – 1 **II** 1 – 1 **III** 1 – 1 **IV** 1 – 1 **V**) (vs. basal webbing on both hands (**I** $2 – 3^{1}/_{4}$ **II** 3 – 3 **III** $2^{3}/_{4} – 2^{3}/_{4}$ **IV**) and feet (**I** $1 – 2^{1}/_{4}$ **II** 1 – 2 **III** $1 – 2^{1}/_{4}$ **IV** $2^{1}/_{4} – 1^{1}/_{2}$ **V**) in *Theloderma vietnamense* sp. nov.), by large irregular prominent warts on dorsum, forming large groups in the head basis and scapular area (vs. absence of enlarged warts in scapular area in the new species), by the snout being longer than the eye diameter (vs. shorter snout in the new species), by long legs, with tibiotarsal articulation reaching the tip of the snout when leg is adpressed to body (vs. shorter legs, with tibiotarsal articulation of an adpressed leg reaching the middle of the orbit in *Theloderma vietnamense* sp. nov.), by absence of white blotches in the rear part of the dorsum (vs. white spots in the posterior part of the dorsum usually discernable in the new species), by large tympanum, usually as big as eye (vs. small tympanum, always much smaller than the eye diameter in *Theloderma vietnamense* sp. nov.).

The new species is morphologically hardly distinguishable from *Th. stellatum sensu stricto* from eastern Thailand; these two species can be considered cryptic (sibling) species. However, there are some significant differences between the two forms in multiple lines of evidence.

Adult morphology. *Th. stellatum sensu stricto* can be diagnosed from the new species by the following combination of morphological attributes: by comparatively longer legs, with tibiotarsal articulation reaching the level behind the eye and the snout tip when leg is adpressed to body (vs. comparatively shorter legs, with tibiotarsal articulation of an adpressed leg reaching the middle of the orbit in *Theloderma vietnamense* sp. nov.), by comparatively better developed webbing: fingers about one-third webbed (webbing formula: **I** $2 – 2^{1}/_{2}$ **II** $1^{3}/_{4} – 3$ **III** 2 – 2 **IV**), toes about fourfifths webbed (webbing formula: **I** 1 – 2 **II** 1 – 2 **III** 1 – 2 **IV** 2 – 1 **V**) (vs. basal webbing on both hands (**I** $2 – 3^{1}/_{4}$ **II** 3 – 3 **III** $2^{3}/_{4} – 2^{3}/_{4}$ **IV**) and feet (**I** $1 – 2^{1}/_{4}$ **II** 1 – 2 **III** $1 – 2^{1}/_{4}$ **IV** $2^{1}/_{4} – 1^{1}/_{2}$ **V**) in *Theloderma vietnamense* sp. nov.), by dorsal pattern with clear trifoliate-shaped dark marking, edged with white or beige color (vs. dorsum with a dark chevron in a shape of an inverted U or V in the new species), by comparatively lighter belly pattern, consisting of the thick irregular whitish or bluish star-shaped blotches and reticulations, usually connected to each other, and distinct white spotting on the throat (Fig. 9*b*) (vs. dark belly pattern, blackish ground color with thin whitish reticulations, few bluish speckles on throat, in the new species; Fig. 9*a*), by a pair of outer metacarpal tubercles, clearly separated from each other (vs. a single indistinctly paired outer metacarpal tubercle in *Theloderma vietnamense* sp. nov.), and by a number of morphometric parameters (see Table 4): by a comparatively shorter axilla-groin distance, A-G/SVL ratio 46.27 ± 5.93 (vs. A-G/SVL = 53.54 ± 2.69 in the new species), by a comparatively smaller eye, ED/SVL ratio 12.41 ± 1.23 (vs. A-G/SVL = 14.06 ± 1.30 in *Theloderma vietnamense* sp. nov.), by a comparatively longer snout, ESL/SVL ratio 20.94 ± 2.61 (vs. ESL/SVL = 17.55 ± 1.80 in the new species), by a comparatively longer tympanum-eye distance, TED/SVL ratio 5.76 ± 2.22 (vs. TED/SVL = $= 3.98 \pm 0.51$ in *Theloderma vietnamense* sp. nov.) and by a comparatively longer eye-narial distance, END/SVL ratio of 17.89 ± 2.64 (vs. END/SVL = $12.18 \pm$ ± 0.95 in the new species).

Tadpole morphology. Though we had no chance to examine tadpole morphology of *Th. stellatum sensu stricto*, we rely on a detailed description by Wassersug et al. (1981), who studied a series of tadpoles from the vicinity of the type locality of this species in Chanthaburi Province of Thailand. These authors report for *Th. stellatum* the denticle formula LTRF 1:3+3/1+1:2, which is quite different from the oral disc morphology that we observed in *Theloderma vietnamense* sp. nov. (LTRF 1:3+3/3; 1:2+2/3; or 1:4+4/3). Wassersug et al. (1981) do not report the variation in the number of the divided denticle raws on the upper labium, as we did for the new species. Moreover, Wassersug et al. (1981) report that the upper denticle raw on the lower labium is always divided, while in *Theloderma vietnamense* sp. nov. samples it was invariably continuous. Whether or not these differences have any taxonomic value requires further consideration.

Acoustics. The advertisement calls of *Theloderma vietnamense* sp. nov. and *Th. stellatum* Taylor, 1962 differ both by temporal and frequency characteristics (see Fig. 10, Table 5). *Theloderma vietnamense* sp. nov. has longer call and intercall durations and shows lower frequency range than the calls of *Th. stellatum sensu stricto*. In *Theloderma vietnamense* sp. nov., the frequency of maximum amplitude coincides with the fundamental frequency in 87.5%, whereas in *Th. stellatum* it coincides in 34.4% calls. The two species can be easily distinguished by the shape of the frequency modulation, which has a form of a weak lift in *Theloderma vietnamense* sp. nov. (see Fig. 10*b*; Table 5) and is arched in *Th. stellatum* Taylor, 1962 (see Fig. 10*a*; Table 5).

mtDNA. Finally, the new species is markedly distinct from all other congeners for which comparable sequences are available, including its closest relatives — *Th. stellatum* and *Th. horridum* — by the relatively large genetic distances in 12S rRNA – 16S rRNA mtDNA gene fragment ($p = 9.38\%$ and 10.28%, respectively). Based on the data available to date, we assume that *Th. stellatum* and *Th. vietnamense* sp. nov. have allopatric distributions. However, taxonomic status of the populations from the southern Cambodia has to be clarified to shed light on this problem.

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APPENDIX 1.
Examined material on the subgenus *Stelladerma* subgen. nov., museum IDs given in bold

Theloderma vietnamense sp. nov. (Southern Vietnam)

Adults:

ZMMU A-5387 (NAP-05238): Cat Tien National Park, Dong Nai Province, Vietnam (1 sp., holotype); **ZMMU A-4661** (NAP-00081): Cat Tien National Park, Dong Nai Province, Vietnam (1 sp. paratype); **ZMMU A-5456** (NAP-03406): Loc Bac (Loc Bao) forestry, Bao Loc district, Lam Dong Province, Vietnam (1 sp., paratype); **ZMMU A-4525** (NAP-02998): Con Son island, Road to So Ray, Con Dao Archipelago, Ba Ria — Vung Tau Province, Vietnam (1 sp., paratype); **ZMMU A-5385** (NAP-03723 – 03725; NAP-03811; NAP-03824): Phu Quoc National Park, Phu Quoc Island, Kien Giang Province, Vietnam (5 sp., paratypes); **ZISP 12212** (NAP-03825): Phu Quoc National Park, Phu Quoc Island, Kien Giang Province, Vietnam (1 sp., paratype); **ZMMU A-5457**: Bu Gia Map National Park, Binh Phuok Province, Vietnam (1 sp.); **ZMMU A-3172-1-2**: Ma Da Forestry, Dong Nai Province, Vietnam (2 sp.); **ZMMU A-3778**: Lo Go – Xa Mat National Park, Tay Ninh Province, Vietnam (2 sp.); **ZMMU A-3951**: Phu Quoc National Park, Phu Quoc Island, Kien Giang Province, Vietnam (1 sp.); **ZMMU A-3758**: Mondulkiri Province, Cambodia (1 sp.); **ZMMU A-3773:** Steng Chhral, Kampot Province, Cambodia (1 sp.).

Tadpoles:

ZMMU NAP-02442: Cat Tien National Park, Dong Nai Province, Vietnam (2 sp.); **ZMMU NAP-02827**: Loc Bac Forestry, Lam Dong Province, Vietnam (1 sp.); **ZMMU NAP-03680**: Lo Go – Xa Mat National Park, Tay Ninh Province, Vietnam (1 sp.); **ZMMU ABV-00832**: Cat Tien National Park, Dong Nai Province, Vietnam (2 sp.); **ZMMU A-3172-3**: Ma Da Forestry, Dong Nai Province, Vietnam (1 sp.).

Theloderma vietnamense sp. nov. (Central Vietnam)

Adults:

ZISP 7556a-7556b; **FMNH 253617 – 253626**: Tram Lap, 40 km northwest of the town of Kannack, 900 m a.s.l. (Tay Nguyen Plateau), Gia Li Province, Vietnam (10 sp.).

***Theloderma stellatum* Taylor, 1962 (Thailand)**

Adults:

NHMT-119-1-00123: Bo thong waterfall, Khao Ang Rue Ni Wildlife sanctuary, Chon Buri Province, Thailand (1 sp.); **NHMT-119-3-00363**: Khao Ang Rue Ni Wildlife sanctuary, Phu Thai Protected Unit, Chon Buri Province, Thailand (1 sp.); **NHMT-119-5-11378-11379**: Khao Khit Chakut, Chanthaburi Province, Thailand (2 sp.); **NHMT-119-2-00258**: Khao Pra Buddha Baht Khao Kitchakut, Chanthabburi Province, Thailand (1 sp.); **ZMMU A-5386** (NAP-03961): Environs of Nang Rong waterfall, Nakhon Nayok Province, Thailand (1 sp.).

***Theloderma horridum* (Boulenger, 1903) (Thailand)**

Adult:

ZMMU A-5388 (NAP-04015): Satun Province, Thailand (1 sp.).

APPENDIX 2.
List of currently recognized species of the genus *Theloderma* Tschudi, 1838 and the proposed preliminary taxonomy for the genus

Genus *Theloderma* Tschudi, 1838
Unnamed subgeneric group

Theloderma moloch (Annandale, 1912)

Subgenus *Stelladerma* subgen. nov.

Theloderma (*Stelladerma*) *horridum* (Boulenger, 1903)

Theloderma (*Stelladerma*) *stellatum* Taylor, 1962

Theloderma (*Stelladerma*) *vietnamense* sp. nov.

Subgenus *Nyctixalus* Boulenger, 1882

Theloderma (*Nyctixalus*) *margaritifer* (Boulenger, 1882) comb. nov.

Theloderma (*Nyctixalus*) *pictum* (Peters, 1871) comb. nov.

Theloderma (*Nyctixalus*) *spinosum* (Taylor, 1920) comb. nov.

Subgenus *Theloderma* Tschudi, 1838

Theloderma asperum species group

Theloderma (*Theloderma*) *albopunctatum* (Liu et Hu, 1962) comb. et stat. nov.

Theloderma (*Theloderma*) *asperum* (Boulenger, 1886)

Theloderma (*Theloderma*) *baibengense* (Jiang, Fei et Huang, 2009) [corrected spelling due to gender correction; provisionally included based on the original description]

Theloderma (*Theloderma*) *licin* McLeod et Norhayati, 2007

Theloderma (*Theloderma*) *petilum* (Stuart et Heatwole, 2004)

Theloderma (*Theloderma*) *phrynoderma* (Ahl, 1927) [type species of the subgenus *Phrynoderma* Boulenger, 1893; provisionally included based on data of Dever et al., 2015]

Theloderma (*Theloderma*) *ryabovi* Orlov, Dutta, Ghate et Kent, 2006

Theloderma leporosum group

Theloderma (*Theloderma*) *andersoni* (Ahl, 1927) [provisionally included]

Theloderma (*Theloderma*) *bicolor* (Bourret, 1937)

Theloderma (*Theloderma*) *corticale* (Boulenger, 1903)

Theloderma (*Theloderma*) *gordoni* Taylor, 1962

Theloderma (*Theloderma*) *kwangsiense* (Liu et Hu, 1962) [provisionally included]

Theloderma (*Theloderma*) *lateriticum* Bain, Nguyen et Doan, 2009 [based on data of Nguyen et al., 2015]

Theloderma (*Theloderma*) *leporosum* Tschudi, 1838 [type species of the subgenus *Theloderma* Tschudi, 1838]

Theloderma (*Theloderma*) *nagalandense* Orlov, Dutta, Ghate et Kent, 2006 [provisionally included]

Theloderma (*Theloderma*) *palliatum* Rowley, Le, Hoang, Dau et Cao, 2011 [*Th. chuyangsinense* Orlov et al., 2012 is treated as a subjective junior synonym]

Theloderma (*Theloderma*) *rhododiscum* (Liu et Hu, 1962) [corrected spelling due to gender correction]

Theloderma laeve species group

Theloderma (*Theloderma*) *laeve* (Smith, 1924) [*Th. bambusicolum* Orlov et al., 2012 is treated as a subjective junior synonym and should be spelled as "*Th. bambusicola*"; name spelling corrected according to the rules of Latin grammar]

Theloderma (*Theloderma*) *nebulosum* Rowley, Le, Hoang, Dau et Cao, 2011

Theloderma (*Theloderma*) *truongsonense* (Orlov et Ho, 2005)

Theloderma (*Theloderma*) sp.

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