Zootaxa 4514 (1): 126–136
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4514.1.10
http://zoobank.org/urn:lsid:zoobank.org:pub:A70B1FF7-7237-42AB-8DC6-D128F969B96C

A review of the relationships of *Xenochrophis cerasogaster* Cantor, 1839 (Serpentes: Colubridae) to its congeners

JAYADITYA PURKAYASTHA[1,2,4], JATIN KALITA[2], RAJEEV KUNGUR BRAHMA[1], ROBIN DOLEY[3] & MADHURIMA DAS[1,2]

[1] *Help Earth, 16, RNC Path, Lachitnagar, Guwahati 781007, Assam, India*
[2] *Department of Zoology, Gauhati University, Jalukbari, Guwahati 781014. Assam, India*
[3] *Department of Molecular Biology and Biotechnology Tezpur University, Napaam, Tezpur 784028, Assam, India*
[4] *Corresponding author. E-mail: mail.jayaditya@gmail.com*

Abstract

We sampled snakes of the genus *Xenochrophis* from across Northeast India. The snakes were evaluated for both morphological and molecular parameters. Phylogenetic relationship was reconstructed using mitochondrial genes (Cytb, 12s rRNA, ND4). The genus *Xenochrophis* was found to be paraphyletic, *X. piscator* complex and *X. punctulatus* form a single clade with *Atretium schistosum* as their sister taxon. *X. cerasogaster* forms a distinct lineage. *X. vittatus* and *X. triangu-ligerus* are related to the genus *Rhabdophis*. Herein it is recommended that *X. piscator* complex, i.e. *X. asperrimus*, *X. flavipunctatus*, *X. melanzostus*, *X. piscator*, *X. sanctijohannis*, *X. schnurrenbergeri* and *X. tytleri*, as well as *X. punctulatus* be reallocated to the genus *Fowlea*

Key words: *Xenochrophis*, *X. piscator*, *X. cerasogaster*, *Rhabdophis*, Assam, India, morphology, phylogenetic relationship

Introduction

The snake family Colubridae is among the most diverse group of snakes containing more than 1910 species (Uetz *et al.* 2018). Of all the genera included in the subfamily Natricinae of the family Colubridae (see Pyron *et al.* 2011, 2013), the genus *Natrix* had become a very large and confusing group of snakes occurring throughout the globe including Europe, Africa, North America, Asia and Australasia. Malnate (1960) divided the genus *Natrix* (*sensu lato*) into five genera, namely *Macropophis* Boulenger, *Fowlea* Theobald, *Rhabdophis* Fitzinger, *Amphiesma* Duméril, Bibron & Duméril and *Natrix* Laurenti on the basis of (A) the number of maxillary and dentary teeth, and the arrangement of maxillary teeth which he classified into three groups- (i) teeth in a continuous series, with gradual increase in size posteriorly, (ii) teeth in a continuous series, with last two teeth prominently larger than the rest of the series and (iii) the last two teeth prominently larger than the rest of the series preceded by a diastema; (B) structure of internasals, which might be narrow or broad anteriorly; (C) position of nostrils placed laterally or dorso-laterally; and (D) shape of sulcus spermaticus being simple or forked.

Günther (1864) erected the genus *Xenochrophis* with the following diagnostic characters: body cylindrical, rather stout; head narrow, elongate; eye with round pupil; nostrils lateral, situated in the upper part of a single plate; shields of the head regular; scales keeled, in nineteen rows; ventrals rounded; anal bifid; subcaudals paired; no conspicuously longer teeth; they are widely set, those in middle of maxillary series and those in front of mandible being rather larger than the others. He included only *Xenochrophis cerasogaster* (Cantor, 1839**)** in this genus which was initially placed under the genus *Psammophis* Fitzinger and was thus the type species by monotypy of the genus *Xenochrophis*.

Theobald (1868) erected the genus *Fowlea* to accommodate a new species, *Fowlea peguensis*. Boulenger (1893) subsequently considered *F. peguensis* as a junior synonym of *Tropidonotus punctulatus* (Günther, 1858).

 Accepted by T. Nguyen: 18 Sept. 2018; published: 6 Nov. 2018

Theobald (1868) stated that snakes referred to the genus *Fowlea* are "*Tropidonotus*, with smooth scales and the aspect of *Hypsirhina*". It is difficult to ascertain what Theobald (1868) wanted to state, but we understand that the author meant that this new genus included a species similar to members of the genus *Tropidonotus* plus, as stated by "aspect of *Hypsirhina*", that these snakes were highly aquatic, perhaps it indicated the affinity of snake to aquatic mode of life. Malnate (1960) added to this definition of *Fowlea* and stated that the members of this genus have hemipenes and sulcus spermaticus divided; maxillary teeth fewer than 30, in continuous series, the teeth becoming larger posteriorly; internasals narrowed anteriorly, nostrils dorso-laterally; apical pits absent or obscure pits present on neck only. Malnate (1960) also assigned three species *piscator*, *punctulata* and *vittata* to the genus *Fowlea*.

The genus *Xenochrophis* has long been monotypic, with only the type species *X. cerasogaster*. Minton discovered *X. cerasogaster* in the lower Indus Valley (Malnate & Minton 1965) and compared it with the members of *Fowlea*. Striking similarities were found between *X. cerasogaster, F. piscator*, *F. punctulata* and *F. vittata*. It was concluded that *X. cerasogaster* and other species of *Fowlea* were congeneric. Thus, by principle of priority *Fowlea* (described in 1868) became a junior synonym of *Xenochrophis* (described in 1864). Subsequently, Malnate & Underwood (1988) studied Australasian Natricine snakes of the genus *Tropidonophis* and assigned *Macropophis maculata* Edeling, *Sinonatrix trianguligera* Boie and *Sinonatrix bellula* Stoliczka to *Xenochrophis*.

In this paper we evaluate the morphological and molecular relationships of *Xenochrophis cerasogaster* with species of the *X. piscator* complex (Vogel & David 2006; Vogel & David 2012), namely *X. asperrimus* (Boulenger), *X. flavipunctatus* (Hallowell), *X. melanzostus* (Gravenhorst), *X. piscator* (Schneider), *X. sanctijohannis* (Boulenger), *X. schnurrenbergeri* Kramer, and *X. tytleri* (Blyth).

Materials and method

The sampling and collection of the specimen were done following Visual Encounter Survey (Crump & Scott 1994) and randomized walk (Lambert 1984) along with active search (Rolfe & McKenzie 2000). Specimens were collected from fishing nets whenever possible. Collected specimens were preserved in 10% formaldehyde. Measurements were taken using Mitutoyo dial calipers with 0.02 mm precision (Appendix 1). Ventral scales and the subcaudals were counted excluding the terminal scute (Dowling 1951).

The adult male specimens of *Xenochrophis* were collected, euthanized and their hemipenes was fully everted by injecting water into the tail at the position of 12^{th} subcaudal. Prior to fixing the specimen, the fully everted hemipenes were measured and photographed. The characters and classification of the hemipenes were done according to Dowling & Savage (1960) and Rösler & Böhme (2006).

The bone structure of the skull was studied with the aid of computerized tomography with Siemens Somaton Definition AS 128 slice duel energy CT scan with EffMaS (mili ampere/second): 20 and KV: 80slice 1mm 3d.

Tissues of voucher specimens were preserved in absolute alcohol or RNA later. DNA isolation was carried out using DNeasy mini kit standardised spin column protocol and/or Phenol Chloroform Isoamyl alcohol method. The isolated DNA was subjected to 0.8% Agarose gel electrophoresis to check the yield and presence of isolated DNA. PCR amplification of 12S rRNA , ND4 and Cyt b genes were done.

The chemicals and reagents were obtained as follows: DyNAzyme II DNA polymerase and dNTPs, was from Thermo Scientific® (Pittsburgh, USA). DNeasy blood and tissue kit and QIAquick gel extraction kit were from Qiagen (Hilden, Germany).

For isolation of DNA, tissues (liver) around 25mg was taken in a vial and cut into small pieces, 150µl of TE (tris EDTA buffer) was added to the vial, 100µl of Guanidine-HCl was added to it. Next, 3µl of proteinase K was added, the vials were then incubated at 50^0C to 55^0C in a hot water-bath, till the tissues were lysed. In case the tissues were kept overnight, 1% SDS may be added after incubation overnight for further lysis. 250µl of Phenol:Chloroform: Isoamyl alcohol (25:24:1) was added next and centrifuged at 12000rpm for 10 mins, the aqueous layer was pipetted out from the top and poured in different vials. 250µl of chloroform was then added to the vials and centrifuged at 12000rpm for 5–10 mins, the aqueous layer was again pipetted out and poured in a separate vial, 100% ethanol 250µl was added and centrifuged at 12000rpm for 5 mins. The supernatant was discarded and to the pellet again 250µl cold 70% ethanol was added and the samples were centrifuged at 12000rpm for 5mins. The supernatant was discarded and the pellets were dried and 40µl molecular biology grade water was added to the pellet. Bands were observed by 0.8% Agarose Gel electrophoresis.

For polymerase chain reaction, 12S rRNA, Cytochrome b and ND4 genes were amplified using gene-specific primers. Primers were obtained commercially (Table 1), according to Dubey *et al.* (2012), Kumazawa *et al.* (2004) and Are´valo *et al.* (1994). For amplification, a total of 0.2 µM of the primer sets, 0.2 mM dNTP mix, 1–2 µg of template DNA were used in a 30 µl PCR reaction mixture. The amplification was carried out using DyNAzyme II DNA polymerase. Polymerase Chain Reaction (PCR) was performed in an ARKTIK Thermal cycler (Thermo Scientific, Pittsburgh, USA) as follows: One cycle of 94ºC for 5 min; 30 cycles of 94ºC for 30 s, 50ºC for 1 min, 72ºC for 2 min; and final extension of 72ºC for 10 min for 12s rRNA and Cytb genes. For ND4 gene, denaturation was done for 7 min at 94ºC, followed by 94ºC for 40s, annealing at 46ºC for 30s and elongation for 1 min at 72°C. The reaction was carried out for 40 cycles. The amplified DNA was electrophoresed on 0.8% agarose gel and visualized under UV light.

TABLE 1. Primers for PCR amplification

Gene	Primer	Primer sequence (5`–3`)	Annealing temperature	Source
Cytochrome b	RC2F	GAAAAACCACCGTTGTTAATCAACTA	50ºC	Dubey *et al*. 2012
	RC2R	TTACAAGAACAATGCTTT		Dubey *et al*. 2012
12S rRNA	RT1F	AAAGCACGGCACTGAAGATGC	51ºC	Kumazawa *et al.* 2004
	RT1R	TTTCATGTTTCCTTGCGGTAC		Dubey *et al.* 2012
ND4	ND4	CACCTATGACTACCAAAAGCTCATGTAGAAGC	46ºC	Are´valo *et al*. 1994
	Leu	CATTACTTTTACTTGGATTTGCACCA		Are´valo *et al.* 1994

The DNA sequences of 12S rRNA, Cytb and ND4 were submitted to GenBank using BankIt submission tool of National Center for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov/genbank/) (Table 2). For phylogenetic analysis 3864 aligned base pairs of concatenated and partitioned data of Cytb (1139 bases), 12S rRNA (1852 bases) and ND4 (873 bases) were used. The sequences were aligned with Mega 7 using Muscle algorithm with default parameter settings (Kumar *et al*. 2016; Tamura & Nei 1993). Phylogenetic relationships were reconstructed using Maximum Likelihood (ML) and Bayesian Inference (BI). Data were partioned by gene and codon position (single partition for 12s rRNA, and three partition each for Cytb and ND4). Partitioned ML analyses were conducted using RaxmlGUI v1.3 (Silvestro & Michalak 2012) using GTRGAMMA model for both genes following Pyron *et al*. (2013) with 1000 rapid bootstraps. Partitioned Bayesian analyses were carried out in MrBayes 3.2.1 (Ronquist *et al*. 2012) with 500000 generations, sampling every 5000 generations with the first 25% discarded as burn-in. *Coelognathus radiatus* was assigned as the out-group.

Abbreviations used: JP: personal collection of Jayaditya Purkayastha; HE: Help Earth; ZSI: Zoological Survey of India, Kolkata; VR/ERS/ZSI: Eastern Regional Station, Zoological Survey of India, Shillong; MNHN: Muséum national d'Histoire naturelle, France.

Results

Xenochrophis cerasogaster, the type species of *Xenochrophis*, showed morphological differences to the other species of the *X. piscator* complex: (1) head not distinct from the neck (vs. distinct in the *X. piscator* species complex); (2) only the 4th supralabial touching the eye (vs. 4th and 5th supralabials touching the eyes in the *X. piscator* species complex); (3) body slender (vs. robust in the *X. piscator* species complex); (4) body reddish-brown with brown stripe (vs. with chequered, blotches or stripped pattern, more or less pale coloured in the *X. piscator* species complex); (5) ventrals marbled with red (vs. off-white in the *X. piscator* species complex); (6) 68–80 subcaudals in males (vs. 77–99 in the *X. piscator* species complex) (see Vogel & David 2006, 2012); (7) tail much longer, TL/Tol 0.198–0.28 in males and 0.206–0.242 in females (vs. 0.257–0.353 in males and 0.215–0.306 in females) (see Vogel & David 2006, 2012).

From a comparative study of the skull of *X. cerasogaster* with those of *X. piscator* and *X. schnurrenbergeri, X. cerasogaster* was observed to have an arrow head shaped skull with a sharp tapering anterior part, much narrower than in *X. piscator* and *X. schnurrenbergeri*; the baso-occipital bone fused with the parietal pushing inwards

forming a narrow V shape; the quadrate joined the dentary bone, forming a wider angle with parietal than in *X. piscator* and *X. schnurrenbergeri*; the suture between nasal and premaxilla narrow and the premaxilla extends well beyond the dentary. In contrast, the skull of *X. schnurrenbergeri* is a broad V-shape, the baso-occipital bone fused with the parietal forming a narrow U shape; the quadrate joined the dentary bone, forming a wide angle (narrower than in *X. cerasogaster*) with parietal; the joint between nasal and premaxilla in broad V shaped and that of *X. piscator* in broad U shape; the baso-occipital bone fused with parietal pushing inwards forming a wide V shape. The quadrate joined the dentary bone, forming a wide angle (narrower than in *X. cerasogaster*) with the parietal and is the thickest of all the studied congeners; the joint between nasal and premaxilla narrow (Fig. 1).

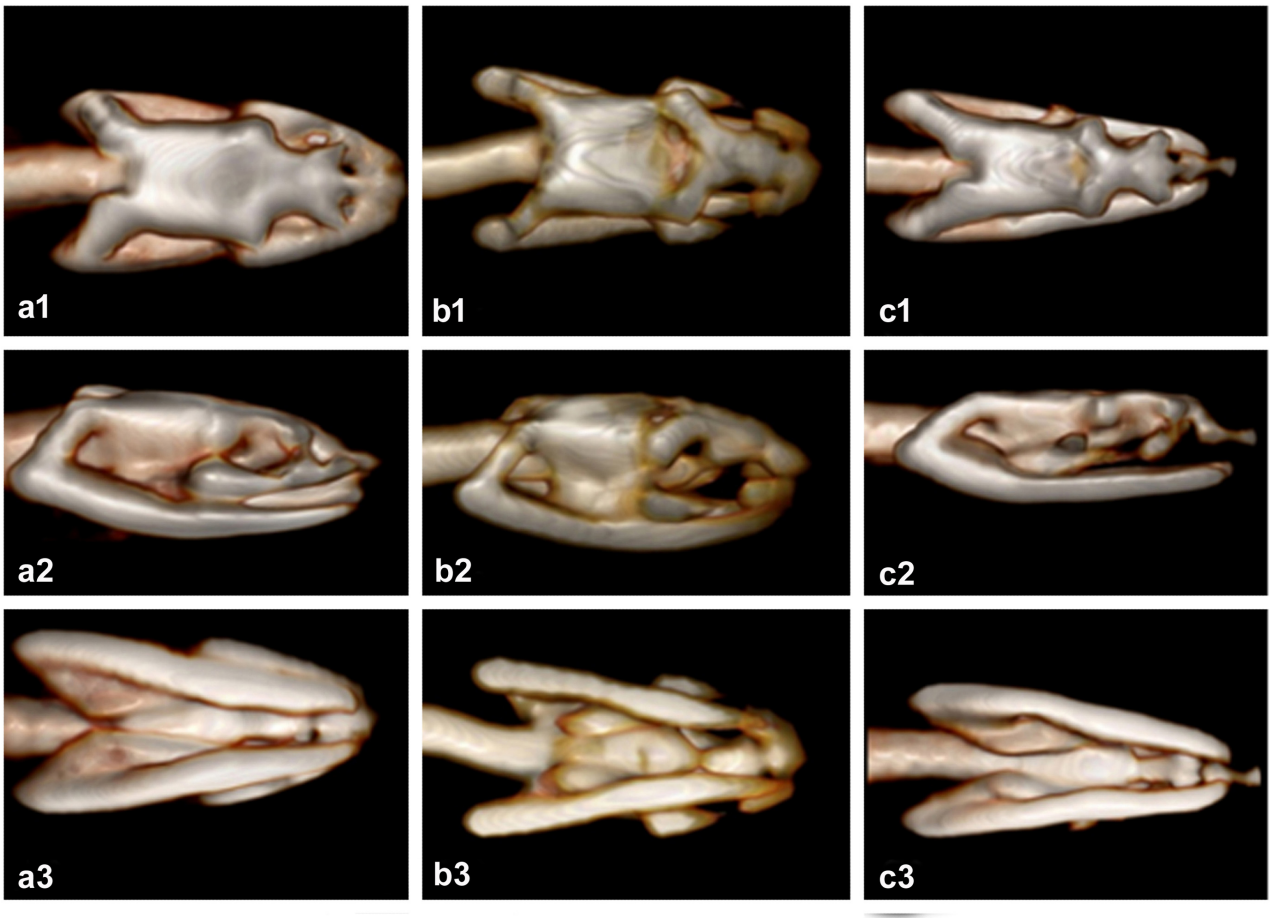

FIGURE 1. Skull structure of *Xenochrophis piscator* (JP225) from Guwahati, Assam (a1: dorsal view, a2: lateral view, a3: ventral view); *Xenochrophis schnurrenbergeri* (JP0102), Guwahati, Assam (b1: dorsal view, b2: lateral view, b3: ventral view); *Xenochrophis cerasogaster* (JP201),Guwahati, Assam (c1: dorsal view, c2: lateral view, c3: ventral view).

The molecular phylogenetic study using concatenated data of Cytb, 12S rRNA and ND4 gene by using Maximum Likelihood (Fig. 2) and Bayesian Inference (Fig. 3) suggest a distinct divergence between *X. cerasogaster* and the *X. piscator* species complex. The ML tree is well supported with an average bootstrap value 69.69 (56% of nodes have a bootstrap value > 70) with all the important relationships having strong support value. Similarly, the BI tree is also well supported with an average posterior probability value of 87.44 (74.4% of nodes have posterior probability >85). Specimens of *X. piscator* (JP336, JP341, JP335, JP54, JP0225) from northern part of study area (Brahmaputra Valley) were seen to form a separate clade from the specimen (JP348, JP349) from the southern part of study area (Barak valley). A specimen of *X. piscator* (HE58) from Hyderabad is clustered as sister taxon to *X. tytleri.*

These results showed that (1) *X. cerasogaster* occupies a separate branch from rest of the species of *Xenochrophi*s with *A. schistosum* taking up an intermediate position; (2) *X. punctulatus, X. schnurrenbergeri, X. flavipunctatus,* and *X. asperrimus* were nested within the same clade whereas all the members of *X. piscator* from

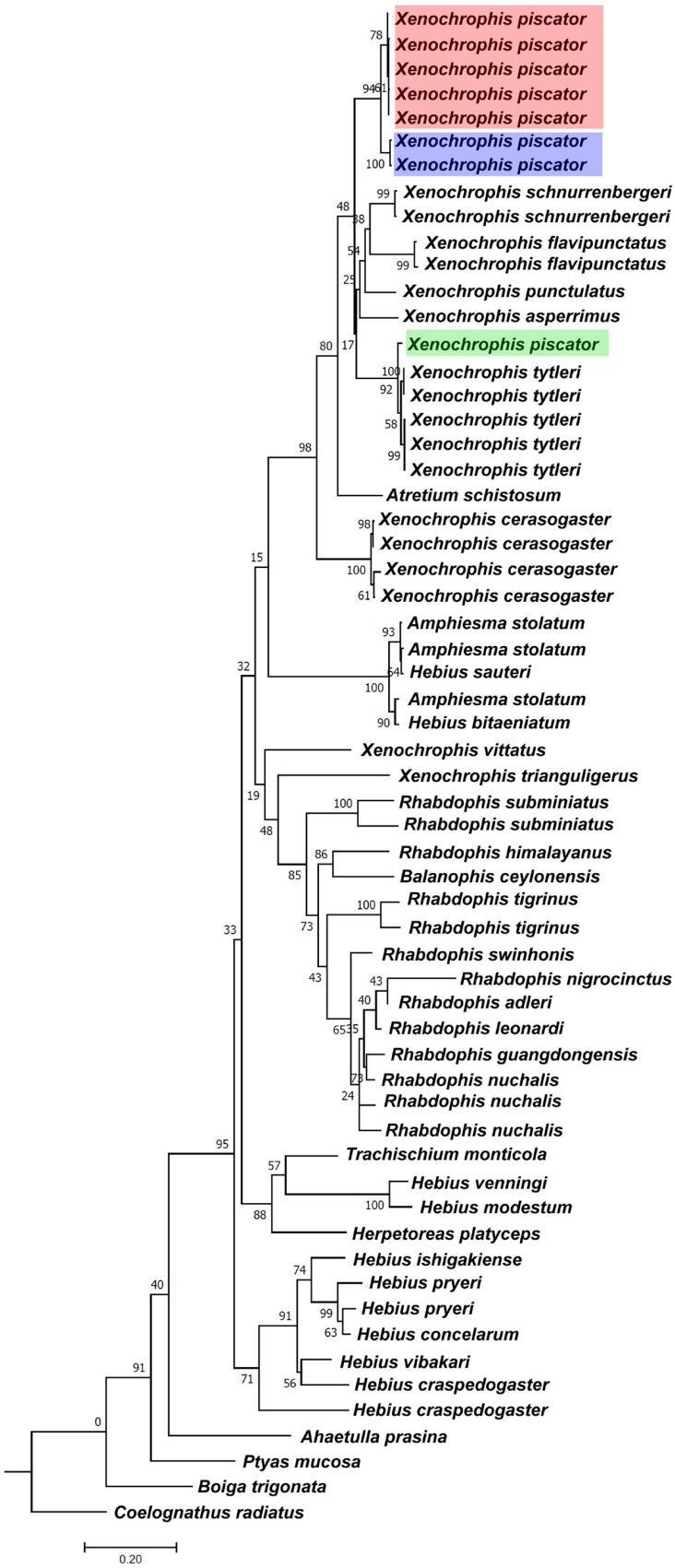

FIGURE 2. Cladogram using Maximum likelihood with concatenated data from Cytochrome b, 12S rRNA, and ND4 gene sequences with *Coelognathus radiatus* as the out-group (Red: specimens from Northern Assam, Blue: Specimen from Southern Assam, Green: Specimen from Hyderabad)

Assam embeded in a separate clade; (3) *X. piscator* from Hyderabad, near the type locality of *X. piscator* (Visakhapatnam), showed distinct divergence from the species occurring in Northeast India, and was sister taxon to *X. tytleri*; (3). *X. schnurrenbergeri* was closely related to *X. flavipunctatus* than both of them to *X. punctulatus* with *X. asperrimus* as the most distant relative; (4) *X. vittatus* and *X. trianguligerus* were closely related to the genus *Rhabdophis*; and (5) There are two distinct groups of *X. piscator* from the state of Assam, occurring in the northern (Brahmaputra Valley) and southern (Barak Valley), part of the region, respectively.

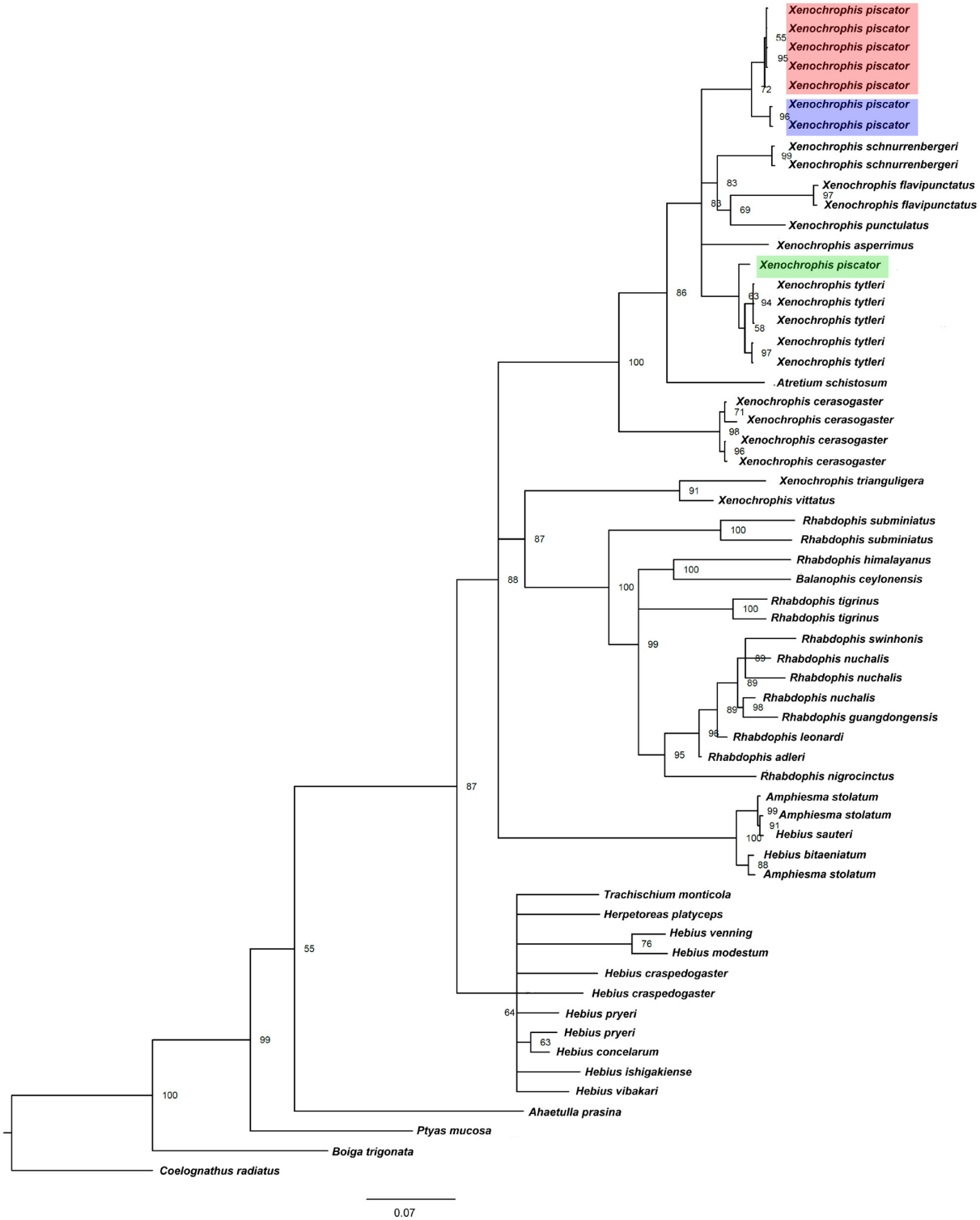

FIGURE 3. Cladogram using Bayesian inference with concatenated data from Cytochrome b, 12S rRNA, and ND4 gene sequences with *Coelognathus radiatus* as the out-group. (Red: specimens from Northern Assam, Blue: Specimen from Southern Assam, Green: Specimen from Hyderabad)

TABLE 2. Sequences used for analysis in this paper (*: specimens sequenced in this study)

Accession no.	Gene Name	Species	Locality
KT373883	12S rRNA	*Xenochrophis piscator**	India: Guwahati
KT373881	12S rRNA	*Xenochrophis piscator**	India: Guwahati
KT373884	12S rRNA	*Xenochrophis schnurrenbergeri**	India: Guwahati
KT373882	12S rRNA	*Xenochrophis schnurrenbergeri**	India: Guwahati
KT373885	12S rRNA	*Xenochrophis cerasogaster**	India: Guwahati
KT373880	12S rRNA	*Xenochrophis cerasogaster**	India: Guwahati
KY379927	12S rRNA	*Xenochrophis piscator**	India: Guwahati
KY379928	12S rRNA	*Xenochrophis piscator**	India: Dwarband
KY379929	12S rRNA	*Xenochrophis piscator**	India: Silchar
KY379931	12S rRNA	*Xenochrophis cerasogaster**	India: Guwahati
KY379932	12S rRNA	*Xenochrophis cerasogaster**	India: Guwahati
KY379933	12S rRNA	*Rhabdophis subminiatus**	India: Guwahati
KY379908	Cyt b	*Xenochrophis piscator**	India: Guwahati
KY379909	Cyt b	*Xenochrophis piscator**	India: Guwahati
KY379910	Cyt b	*Xenochrophis cerasogaster**	India: Guwahati
KY379913	Cyt b	*Rhabdophis subminiatus**	India: Guwahati
KY379914	Cyt b	*Xenochrophis piscator**	India: Silchar
KY379915	Cyt b	*Xenochrophis piscator**	India: Guwahati
KY379918	Cyt b	*Xenochrophis cerasogaster**	India: Guwahati
KY379919	Cyt b	*Xenochrophis piscator**	India: Guwahati
KY379920	Cyt b	*Xenochrophis cerasogaster**	India: Guwahati
KY379921	Cyt b	*Xenochrophis piscator**	India: Guwahati
KY379922	Cyt b	*Xenochrophis schnurrenbergeri**	India: Guwahati
KY379923	Cyt b	*Xenochrophis cerasogaster**	India: Guwahati
KY379924	Cyt b	*Xenochrophis schnurrenbergeri**	India: Guwahati
KY379925	Cyt b	*Xenochrophis piscator**	India: Guwahati
KC347487	Cyt b	*Atretium schistosum*	China
JQ687432	Cytb	*Amphiesma stolatum*	China
KJ685693	Cytb	*Amphiesma stolatum*	China: Guangdong
KJ685702	Cytb	*Hebius sauteri*	Taiwan
KJ685667	Cytb	*Hebius bitaeniatum*	Viet Nam: Ha Giang
AF471030	Cytb	*Amphiesma stolatum*	Mtanmar: Bago Division
GQ281777	Cytb	*Rhabdophis subminiatus*	China: Hainan
KF800929	Cytb	*Rhabdophis himalayanus*	Myanmar
KC347474	Cytb	*Balanophis ceylonensis*	Unknown
AB842176	Cytb	*Rhabdophis swinhonis*	Unknown
KF800936	Cytb	*Rhabdophis nigrocinctus*	Myanmar
KF800931	Cytb	*Rhabdophis adleri*	China
KF800932	Cytb	*Rhabdophis leonardi*	China
KF800930	Cytb	*Rhabdophis guangdongensis*	China
KF800935	Cytb	*Rhabdophis nuchalis*	China
AF402907	Cytb	*Rhabdophis nuchalis*	Unknown

.....continued on the next page

TABLE 2. (Continued)

Accession no.	Gene Name	Species	Locality
GQ281786	Cytb	*Rhabdophis nuchalis*	China: Sichuan
GQ281785	Cytb	*Rhabdophis tigrinus*	China: Liaoning
AB663628	Cytb	*Rhabdophis tigrinus*	Japan: Kagoshima
EF395895	Cytb	*Xenochrophis vittatus*	Unknown
KJ685690	Cytb	*Herpetoreas platyceps*	China: Xizang
KJ685700	Cytb	*Hebius venningi*	Thailand
KJ685671	Cytb	*Hebius modestum*	China: Yunnan
JQ687435	Cytb	*Trachischium monticola*	China
KC010339	Cytb	*Ahaetulla prasina*	Unknown
KR814695	Cytb	*Ptyas mucosa*	Unknown
KC347475	Cytb	*Boiga trigonata*	Unknown
DQ902121	Cytb	*Coelognathus radiatus*	Myanmar
KX017176	ND4	*Xenochrophis tytleri*	Unknown
KX017175	ND4	*Xenochrophis tytleri*	Unknown
KX017174	ND4	*Xenochrophis tytleri*	Unknown
KX017173	ND4	*Xenochrophis tytleri*	Unknown
KX017170	ND4	*Xenochrophis tytleri*	Unknown
AB989304	ND4	*Hebius vibakari*	Japan: Kyoto
JQ687412	ND4	*Amphiesma craspedogaster*	China
AB989286	ND4	*Hebius ishigakiense*	Japan: Okinawa
AB989172	ND4	*Hebius pryeri*	Japan: Okinawa
AB989270	ND4	*Hebius concelarum*	Japan: Okinawa
AB989104	ND4	*Hebius pryeri*	Japan: Kagoshima
JQ687418	ND4	*Amphiesma craspedogaster*	China
JQ687419	ND4	*Rhabdophis tigrinus*	China
JQ687413	ND4	*Rhabdophis nuchalis*	China
JQ687411	ND4	*Rhabdophis subminiatus*	China
U49325	ND4	*Rhabdophis subminiatus*	Unknown
U49321	ND4	*Xenochrophis trianguligeru*	Unknown
JQ687425	ND4	*Amphiesma stolatum*	China
DQ902317	ND4	*Coelognathus radiatus*	Thailand
KC347525	ND4	*Atretium schistosum*	Unknown
AY487074	ND4	*Xenochrophis punctulatus*	Myanmar
MH807258	ND4	*Xenochrophis piscator**	India: Hyderabad

Discussion

Günther (1864) stated that members of genus *Xenochrophis* have lateral nostrils, situated in the upper part of a single plate and jaws without conspicuously longer teeth, those in middle of maxillary series and those in front of mandible being rather larger than others. But, we observed that, in case of members of *X. piscator* species complex, the nasal is partially divided (Fig. 4) and the maxillary teeth gradually becomes larger posteriorly (Fig. 5). Malnate & Minton (1965) agreed on the fact that *X. cerasogaster* differs significantly from *X. piscator* in the form of maxillary and dentary dentition and less strongly developed processes of the posterior cranial elements.

The molecular phylogenetic analysis showed that the genus *Xenochrophis* seems to be paraphyletic. The *X.*

piscator complex (Vogel & David 2006), *X. punctulatus* and *A. schistosum* are sister clades to *X. cerasogaster.* From this, it can be inferred that *X. cerasogaster* is not congeneric with *X. piscator* complex and *X. punctulatus*. On the other hand *X. vittatus* and *X. trianguligerus* are sister taxa to the genus *Rhabdophis*, a point which agrees with the inference of the previous studies (Pyron *et al*. 2011, Dubey *et al*. 2012).

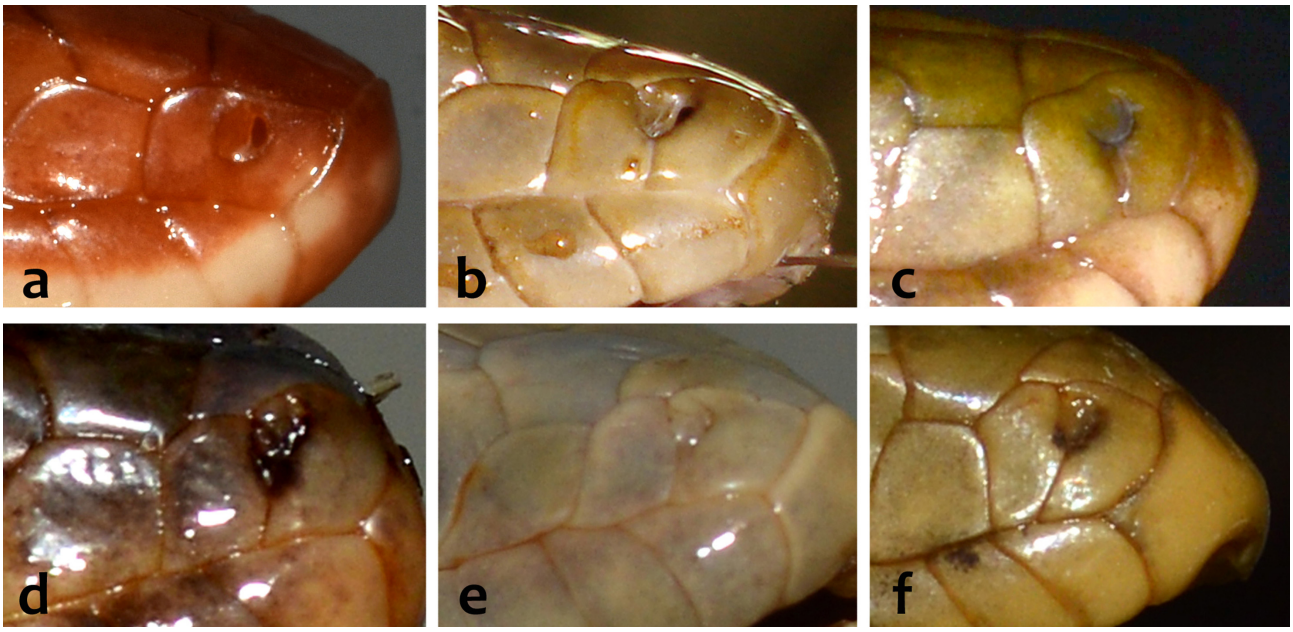

FIGURE 4. The structure of the nasal a: *X. cerasogaster* (JP201), b*: X. piscator* (JP225), c: *X. schnurrenbergeri* (JP0102), d: *X. melanzostus* (ZSI21214), e: *X. asperrimus* (ZSI 16649), f: *X. flavipunctatus* (ZSI18115).

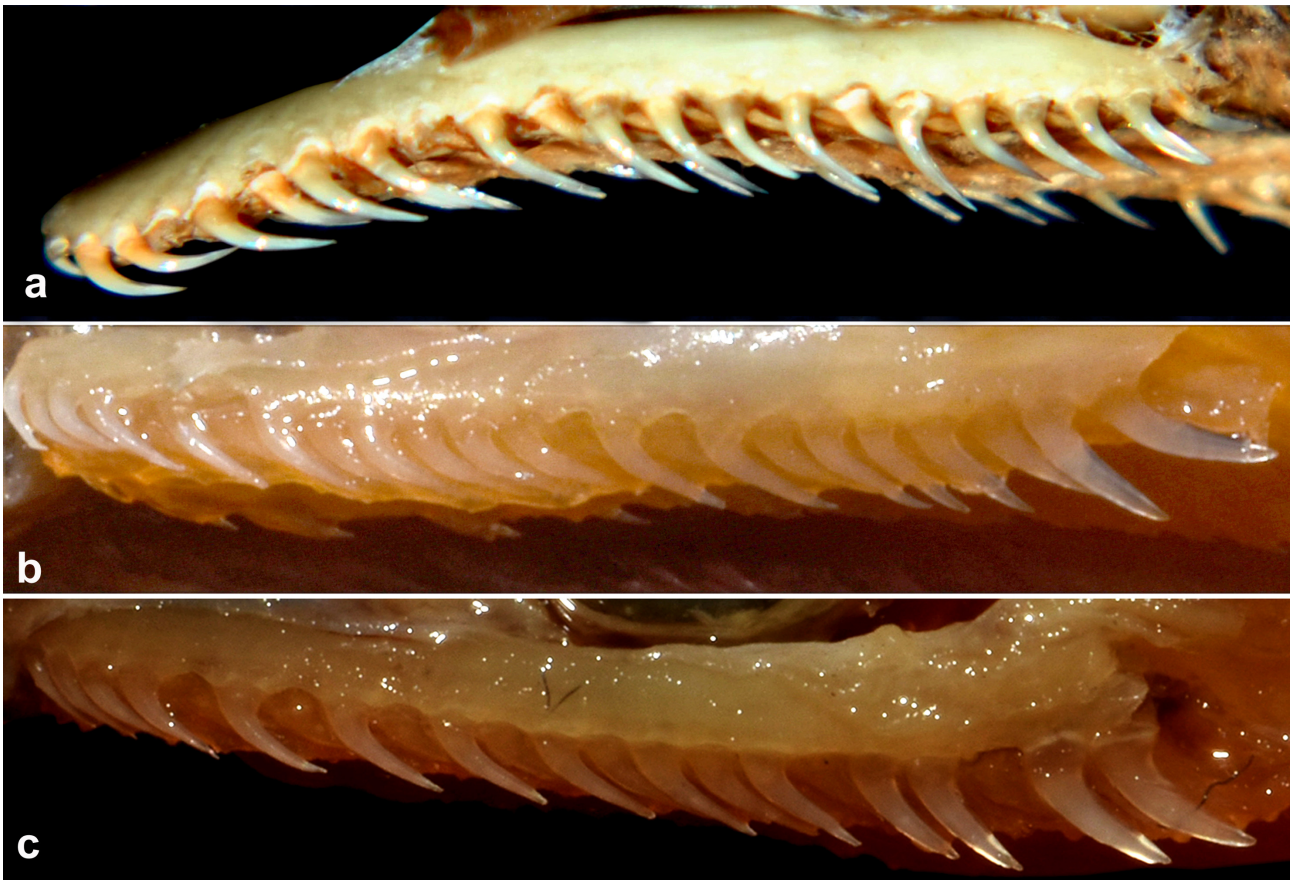

FIGURE 5. The structure of maxillary dentition, a: *X. cerasogaster* (JP201), b: *X. piscator* (JP225), c: *X. schnurrenbergeri* (JP0102).

Again, molecular phylogenetic analysis showed the presence of two distinct clades of *X. piscator* from Northeast India, occurring in northern and the southern part of the region, respectively. Vogel and David (2012) suggested the availability of the name *Xenochrophis mortuarius* Daudin for the large, dark colored, specimens from Northeastern India, that prove to be distinct from *X. piscator.* It is planned to discuss the status of these populations elsewhere.

As an output of this study, we recommend that the species of the *X. piscator* complex, i.e. *X. asperrimus*, *X. flavipunctatus*, *X. melanzostus*, *X. piscator*, *X. sanctijohannis*, *X. schnurrenbergeri* and *X. tytleri*, as well as *X. punctulatus* be reallocated to the genus *Fowlea*. Though *X. vittatus and X. trianguligerus* are sister taxa to the genus *Rhabdophis*, but due to limited data, conclusion cannot be drawn on their generic allocation and pending further study, they are provisionally kept in the genus *Xenochrophis* along with *X. bellulus* and *X. maculatus* which were not adressed in this study.

Acknowledgments

We would like to thank Assam Forest Department for their support in conducting this work. Thanks to Gernot Vogel, Patrick David and Truong Nguyen for their improvement of the manuscript. Thank you Ishan Agarwal, Puneeth Reddy and Anita Malhotra for sharing your knowledge on phylogenetic analysis. Thank you Suraj K. Chauhan for helping us with data for specimen of *X. piscator* from Hyderabad. Thank you Bhim. B. Biswa, Sumit Das, Gyanendra Deka, Somlee Gupta, Sayanti Basak, Anirban Chaudhuri for helping us in field study. JP would like to thank the Rufford Small Grants and Assam Science Technology & Environment Council for financial support during the project. MD would like to thank IBT Hub (Advanced level), Arya Vidyapeeth College and Molecular Toxinology Lab, MBBT, Tezpur University for laboratory support.

References

Are´valo, E., Davis, S.K. & Sites, J.W. (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in Central Mexico. *Systematic Biology*, 43, 387–418.
https://doi.org/10.1093/sysbio/43.3.387

Boulenger, G.A. (1893) *Catalogue of the snakes in the British Museum (Natural History), Vol. I., containing the families Typhlopidae, Glauconiidae, Boidae, Ilysiidae, Uropeltidae, Xenopeltidae, and Colubridae Aglyphae*, *part*. British Museum of Natural History, London, xiii + 448 pp., 28 pls.

Crump, M.L. & Scott, N.J. (1994) Visual encounter surveys. *In*: Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C. & Foster, M.S. (Eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C., pp. 84–92.

Dowling, H.G. & Savage, J.M. (1960) A guide to snake hemipenis: a survey of basic structure and systematic characteristics. *Zoologica*, 45, 17–28.

Dowling, H.G. (1951) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.

Dubey, B., Meganathan, P.R., Vidal, N. & Dubey, I.H. (2012) Molecular evidence for the nonmonophyly of the Asian natricid genus *Xenochrophis* (Serpentes: Colubroidea) as inferred from mitochondrial and nuclear genes. *Journal of Herpetology*, 46, 263–268.
https://doi.org/10.1670/10-116

Günther, A.C.L.G. (1864) *The Reptiles of British India*. Ray Society, London, xxvii + 452 pp., 26 pls.

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
https://doi.org/10.1093/molbev/msw054

Kumazawa, Y. & Endo, H. (2004) Mitochondrial genome of the Komodo Dragon: efficient sequencing method with reptile-oriented primers and novel gene rearrangements. *DNA Research*, 11, 115–125.
https://doi.org/10.1093/dnares/11.2.115

Lambert, M.R.K. (1984) Amphibians and reptiles. *In*: Cloudsley-Thompson, J.L. (Ed.), *Key environments: Sahara Desert*. Pergamon Press, London, pp. 205–227.

Malnate, E.V. (1960) Systematic division and evolution of the Colubrid snake genus *Natrix*, with comments on the subfamily Natricinae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 112 (3), 41–71.

Malnate, E.V. & Minton, S.A. (1965) A redescription of the natricine snake *Xenochrophis cerasogaster*, with comments on its taxonomic status. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 117 (2), 19–43.

Pyron, R.A., Burbrink, F.T., Colli, G.R., Montes De Oca, A.N., Vitt, L.J., Kuczynski, C.A. & Wiens, J.J. (2011) The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution*, 58, 329–342.
https://doi.org/10.1016/j.ympev.2010.11.006

Pyron, R.A., Kandambi, H.K.D., Hendry, C.R., Pushpamal, V., Burbrink, F.T. & Somaweera, R. (2013) Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. *Molecular Phylogenetics and Evolution*, 66 (3), 969–978.
https://doi.org/10.1016/j.ympev.2012.12.004

Rolfe, J.K. & Mckenzie, N.L. (2000) Comparison of methods used to capture herpetofauna: an example from the Carnarvon Basin. *Records of the Western Australian Museum*, 61, 361–370.
https://doi.org/10.18195/issn.0313-122x.61.2000.361-370

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
https://doi.org/10.1093/sysbio/sys029

Rösler, H. & Böhme, W. (2006) Peculiarities of the hemipenes of the Gekkonid lizard genera Aristelliger Cope, 1861 and Uroplatus Duméril, 1806. *In*: Vences, M., Köhler, J., Ziegler, T. & Böhme, W. (Eds.), *Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica*, Bonn, 2006, pp. 121–124.

Silvestro, D. & Michalak, I. (2012) raxmlGUI: A graphical front-end for RAxML. *Organisms Diversity and Evolution*, 12, 335–337.
https://doi.org/10.1007/s13127-011-0056-0

Tajima, F. & Nei, M. (1984) Estimation of evolutionary distance between nucleotide sequences. *Molecular Biology and Evolution*, 1, 269–285.
https://doi.org/10.1093/oxfordjournals.molbev.a040317

Theobald, W. (1868) *Catalogue of reptiles in the Museum of the Asiatic Society of Bengal*, Baptist Mission Press, Calcutta, 91 pp.

Uetz, P., Freed, P. & Hošek, J. (2018) The Reptile Database. Available from: http://www.reptile-database.org (accessed 16 March 2018)

Vogel, G. & David, P. (2007) On the taxonomy of the *Xenochrophis piscator* complex (Serpentes, Natricidae). *In*: Vences, M., Köhler, J., Ziegler, T. & Böhme, W. (Eds.), Herpetologia Bonnensis II. *Proceedings of the 13th Congress of the Societas Europaea Herpetologica*, Bonn, 2007, pp. 241–246.

Vogel, G. & David, P. (2012) A revision of the species group of *Xenochrophis piscator* (Schneider, 1799) (Squamata: Natricidae). *Zootaxa*, 3473, 1–60.

APPENDIX 1. Specimens examined

Rhabdophis subminiatus: JP337 from Guwahati in Assam, India

Xenochrophis asperrimus: ZSI 16649 from Sri Lanka

Xenochrophis cerasogaster: JP130JP131,–JP132, JP201, JP334, JP346, JP347 from Guwahati in Assam, India.

Xenochrophis flavipunctatus: ZSI18115

Xenochrophis melanzostus: ZSI21214

Xenochrophis piscator: JP54, JP225, JP335, JP336, JP341, JP348 and JP349 from Guwahati and VR/ERS/ZSI20390, from Kokrajhar in Assam, India; HE58 from Hyderabad (Telangana), India; VR/ERS/ZSI339, VR/ERS/ZSI340, VR/ERS/ZSI367 from Nokrek; VR/ERS/ZSI503, VR/ERS/ZSI3082, VR/ERS/ZSI6068, VR/ERS/ZSI8353, VR/ERS/ZSI39842 from East Khasi Hills and VR/ERS/ZSI8418 from West Khasi Hills in Meghalaya, India; VR/ERS/ZSI460 , VR/ERS/ZSI485 from Thoubal and VR/ERS/ZSI2379 from Domba in Manipur, India; VR/ERS/ZSI1004 from Siang, VR/ERS/ZSI35982 from Pasighat, VR/ERS/ZSI24646 from East Kameng in Arunachal Pradesh, India; VR/ZSI/ERS8928 from North Tripura in Tripura, India; ZSI25769 from Baripada in Orissa, India; ZSI21650 from Varanasi in Uttar Pradesh, India; ZSI23178 from Sunderbans, ZSI23938 and ZSI25595 from Kolkata, ZSI24406 from 24 Parganas, ZSI24407 from Midnipore in West Bengal, India; ZSI22789 from Goa, India.

Xenochrophis punctulatus: ZSI7579 from Yangon, Myanmar

Xenochrophis schnurrenbergeri: JP0073, JP0078, JP0102, JP217, JP337 from Guwahati, in Assam, India; ZSIK23176 andZSIK25734 from 24 Parganas in West Bengal, India; ZSIK23568 from Patna in Bihar, India