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Review of the systematics, morphology and distribution of Asian Clawed Salamanders, genus *Onychodactylus* (Amphibia, Caudata: Hynobiidae), with the description of four new species

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Magnolia Press
Auckland, New Zealand

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(Zootaxa 3465)**

106 pp.; 30 cm.

7 Sept. 2012

ISBN 978-1-86977-995-5 (paperback)

ISBN 978-1-86977-996-2 (Online edition)

FIRST PUBLISHED IN 2012 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

<http://www.mapress.com/zootaxa/>

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ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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Abstract

We describe four new species of Asian Clawed salamanders of the genus *Onychodactylus* (Caudata: Hynobiidae), based on fresh material collected during fieldwork in Japan, Korea, the Russian Far East and northeastern China between 2003 and 2010, as well as older voucher specimens deposited in several museums. Our analyses comprise all species currently recognized within this genus across its entire distribution range. We follow an integrative taxonomic approach by combining detailed morphological comparative analyses with molecular phylogenetic analyses. We find significant differences among species in this genus, based on morphological and molecular data, which resulted in the recognition and description of four new species within this genus. The new species have uncorrected molecular divergences of over 4.5–7.4% and 1.9–4.1% to their closest relatives in the mitochondrial COI and 16S rRNA genes respectively. In the molecular analyses, we found two very divergent lineages in Korea and Japan that need further investigation, as detailed morphological data are not available for them. We also discuss our approach to delimit species on salamanders. For the new species described in this group we evaluate their threat status according to IUCN criteria: *O. koreanus* sp. nov. Min, Poyarkov & Vieites and *O. nipponoborealis* sp. nov. Kuro-o, Poyarkov & Vieites are classified as Least Concern, while *O. zhaoermii* sp. nov. Che, Poyarkov & Yan and *O. zhangyapingi* sp. nov. Che, Poyarkov, Li & Yan are classified as Vulnerable (Vu2a).

Keywords: Caudata, Hynobiidae, *Onychodactylus*, integrative taxonomy, Asia, salamander, *Onychodactylus koreanus*, *Onychodactylus nipponoborealis*, *Onychodactylus zhaoermii*, *Onychodactylus zhangyapingi*, new species

Introduction

Hynobiid salamanders constitute one of the most basal groups of salamanders worldwide (Zhang *et al.*, 2006; Vieites *et al.*, 2007), being currently restricted to Asia with few fossil representatives found in Europe (e.g. Venczel, 1999a; 1999b). This family includes some 53 species and 10 genera, with new species being described almost every year (Frost, 2011; AmphibiaWeb, 2012). Within this family, Asian Clawed salamanders, *Onychodactylus* Tschudi, 1838, represent a very divergent lineage from the rest of the genera which diverged during the Cretaceous (Zhang *et al.*, 2006). *Onychodactylus* is endemic to Northeast Asia – specifically, several Japanese islands, some mountains in the Korean peninsula and adjacent areas of China and Russia.

This genus represents the most specialized stream-dwelling form among all Hynobiidae, being characterized by a combination of derived and primitive characters (Kuzmin, 1995). *Onychodactylus* differs from other hynobiids by the absence of lungs (Dunn, 1923), presence of horny claws in larvae and adults (Temminck & Schlegel, 1838; Stejneger, 1907; Dunn, 1923), presence of skin folds on the limbs of larvae and hindlimbs of breeding males (Dunn, 1923), much larger genome size and chromosome number (Morescalchi *et al.*, 1979; Ikebe *et al.*, 1981; Sessions, 1982; Iizuka & Yazawa, 1994; Ikebe *et al.*, 1995; Litvinchuk *et al.*, 2004), numerous specific morphological and, in particular, osteological characteristics (Okajima, 1908; Okajima, 1922; Dunn, 1923; Smirnov, 1987; Smirnov & Vorobyeva, 1988; Kuzmin, 1995; Litvinchuk & Borkin, 2003), and long embryonic and larval development (Kudo, 1935; Emelianov, 1940; 1947; Regel & Epstein, 1977; Iwasawa & Kera, 1980; Hayase & Yamane, 1982) with signs of embryonization (Smirnov & Vassilieva, 2002). The combination of some characteristics, such as the presence of horny claws and skin folds in larvae and adults, and many characters of internal anatomy are unique to *Onychodactylus* and distinguish it from all other recent tailed amphibians (Dunn, 1923; Smirnov, 1987; Smirnov & Vorobyeva, 1988; Zhao & Hu, 1988; Kuzmin, 1995). Horny structures on the limbs are also present in the salamandrid genera *Calotriton* and *Euproctus*, and the latter shares also lunglessness with *Onychodactylus*.

Several phylogenetic studies have recovered this genus as basal, highly divergent and sister to other hynobiid genera (Zhang *et al.*, 2006; Zhang & Wake, 2009; Peng *et al.*, 2010) based on analyses of complete mitochondrial genomes.

Originally, two species are currently recognized within the genus *Onychodactylus*. The first species described was *O. japonicus* (Houttuyn, 1782), which was brought to Europe from Japan, where they were already well known and hunted by local people for food and medicinal purposes. Many years later, the continental species *O. fischeri* (Boulenger, 1886) was described from the Far East of Russia and was originally assigned to a separate genus *Geomolge* Boulenger, 1886 based on the absence of claws and the form of vomerine tooth series. Dunn (1918) synonymised it with *Onychodactylus*; the same author studied specimens from newly reported populations within the Korean peninsula and considered them as conspecific with Russian populations, assigning them as *O. fischeri*.

One of the few taxonomic revisions ever conducted within the genus *Onychodactylus* is the paper by Dunn (1923) where he compared large series of *O. japonicus* and specimens of *O. fischeri* from Wonsan, Korea. In that study he determined that these two species “are extremely closely related” (p. 511, 514) and raised some doubts on the validity of the continental species *O. fischeri*: “Far being generally distinct it is doubtful if any constant character separates the two species” (p. 511). However, we have observed that neither E.R. Dunn nor any other specialists who had worked on the taxonomy of hynobiids had the opportunity to compare the actual specimens of *Onychodactylus fischeri* from Russia, which in reality corresponds to Boulenger’s description. The same was true for specialists from the former Soviet Union who had no access to materials from China, Korea or Japan. Hence, following Dunn’s opinion, the name *O. fischeri* was applied to Korean and Chinese populations of *Onychodactylus* for nearly a century, but comparative works on geographic variation were lacking. Despite impressive geographic variation in color and patterns of dorsal markings in Japanese species (described by Sato, 1943), interspecific taxonomy of *O. japonicus* was not studied. Ikebe *et al.* (1995) reported intrapopulational chromosomal polymorphism in four populations of *O. japonicus* from central and northern Honshu and noted that the northernmost population from Jokagura (Tohoku district) was distinct from other Japanese populations showing karyotypes resembling those of the chromosomes of *O. fischeri* from Korea. However, this discovery also had no taxonomic consequences.

Yoshikawa *et al.* (2008) presented an extensive study of molecular differentiation and phylogeography of *O. japonicus* using cytochrome b (CytB) mtDNA sequences. They studied 250 specimens from 87 localities, covering

the entire species range, reporting the presence of four highly divergent lineages within the Japanese species, each with strong phylogeographic structuring. In the same study they used *O. fischeri* from Korea (3 specimens from 2 populations) and Russia (3 specimens from 2 populations) as outgroups, suggesting that *O. fischeri* populations do not form a clade. Assuming the broad distribution of *O. fischeri*, that spans through various biogeographic regions in northeastern Asia and several isolated mountain systems, it could be expected that this species might contain similar cryptic diversity as revealed recently within *O. japonicus*, and in fact might consist of several distinct cryptic species.

Recently, Yoshikawa *et al.* (2010a, 2010b) presented an extensive study of allozyme variation in *O. japonicus*, including all previously revealed mtDNA lineages in their analysis from 17 populations covering the entire species range. Based on the results of this electrophoretic survey, the authors confirmed the presence of six well-supported genetic groups (N-Tohoku, S-Tohoku, Tsukuba, SW-Honshu, Kinki and Shikoku) that were largely concordant with clades recognized in the previous mtDNA study. Genetic distances were not small, reaching species-levels for amphibians (mean Nei's D=0.146–0.471). The authors report sympatric occurrence of two different allozyme groups (SW-Honshu and Shikoku) in western Honshu. Although several possible hybrid individuals were found, hybridization between these two groups seem to occur very rarely, thus genetic isolation of two sympatric populations was assumed, indicating that at least the Shikoku population may represent a distinct species from the nominative form of *O. japonicus* from Honshu. If this assumption is correct, it is not yet clear which name should be applied to the Shikoku population: among all known synonyms of *O. japonicus*, *Salamandra unguiculata* Temminck & Schlegel, 1838 was described both from Hondo (Honshu) and Shikoku, so the assessment of type materials is needed to clarify the status of this name.

However, other cases of sympatry between six genetic groups of *O. japonicus* were not reported both for mtDNA and allozyme data. In the paper by Yoshikawa *et al.* (2010a) the sampling was not complete enough to cover the presumed contact zones between them. The authors concluded that by applying the D value of 1.60 as the criterion for separating species in amphibians, it could be assumed that some or all of these groups might represent different species. However, the obtained allozyme perspective confirms the high level of genetic divergence among Japanese populations and indicates that the situation might not be so simple and that further genetic and morphological comparisons are necessary for solving the taxonomic problem.

Recent molecular surveys on Chinese tailed amphibians also revealed deep divergence between populations of *Onychodactylus fischeri* from Liaoning and Jilin provinces (Che *et al.*, 2012; Xia *et al.*, 2012). The taxonomic status of these lineages is not clear and requires further examination with greater amounts of material to be studied and as well as the application of both molecular and morphological taxonomic methods.

Onychodactylus are strict stream-dwellers and inhabit only clean mountain streams with water temperature not higher than 10° C throughout the year. Based on these criteria, Kuzmin (1995) and Kuzmin & Maslova (2005) summarized data on their distribution, natural history and conservation. *O. japonicus* is a common species in Japan and it is abundant in mountains of the Japanese islands of Honshu (Hondo) and Shikoku from the sea-level to 2.600–2.700 m a. s. l. However, the species is absent in Hokkaido, Kyushu and smaller islands in the Sea of Japan (Ohno, 1982; Akita, 1996). On the Asian continent, *O. fischeri* is not very common, inhabiting mountainous areas above 300 m a. s. l. from the Korean peninsula (Won, 1971; Yang *et al.*, 2001) to northeastern China, where it is present in Liaoning and Jilin provinces (Ji *et al.*, 1987; Fei *et al.*, 1999; 2006). The species also inhabits the southern part of the Sikhote-Alin Mountains in the Maritime Territory (Primorye Territory, or Primorskiy krai) of Russia; and most likely this portion of the species range is isolated from the Korean and Chinese populations (see analysis of species distribution in Russia in Kuzmin & Maslova, 2004; 2005). Because of low migration and dispersal abilities, as well as dependence of specific habitats, diversification and speciation events in hynobiid salamanders are thought to be strongly influenced by geo-historical events (Matsui *et al.*, 2006; Zeng *et al.*, 2006; Fu & Zeng, 2008; Zhang *et al.*, 2006; Peng *et al.*, 2010), which is likely the case in *Onychodactylus* as well.

Here, we present the results of a long-term study of the geographic variation within Asian Clawed salamanders of the genus *Onychodactylus*, covering most of the distributional range of the genus. We followed an integrative taxonomic approach, combining comparative morphological and genetic analyses, with extensive field sampling throughout the ranges of currently described species. We here follow several congruent lines of evidence to support new species recognition, that include having significant differences in morphological diagnostic traits, together with being well supported in our phylogenetic analyses as distinct clades, and showing a certain degree of genetic differentiation compared to other lineages in mtDNA considered for amphibians (see Vieites *et al.*, 2009). We explicitly state that the lineages for which we do not have any morphological data, neither nuclear data, are

considered for the moment unconfirmed candidate species pending further works. This resulted in identifying four confirmed candidate species (*sensu* Vieites *et al.*, 2009), which we describe here, as well as two unconfirmed candidate species that need further data to resolve their taxonomic status.

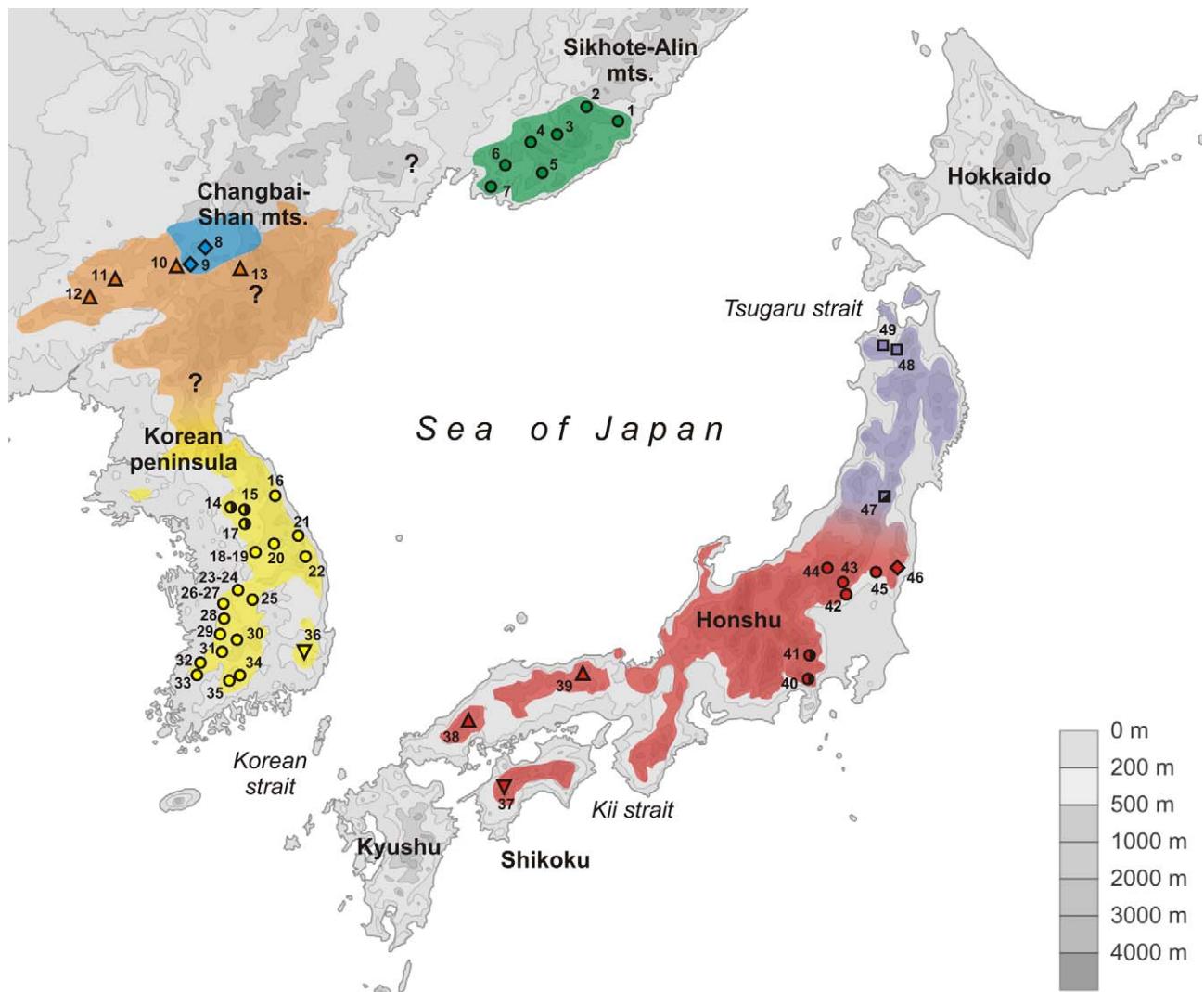


FIGURE 1. Distribution (shaded) and sampling localities of *Onychodactylus*. Legend: *O. fischeri* (Primorye, Russia)—green: circles—clade A; *O. zhangyapingi* (China, Jilin)—blue: diamonds—clade C; *O. zhaoermii* (China, Liaoning)—orange: triangles—clade B; *O. koreanus* (Korean peninsula)—yellow: circles—clade D; *Onychodactylus* sp. (Yangsan, Korea)—yellow: inverted triangle—clade E; *O. japonicus* species complex (Honshu and Shikoku, Japan)—red: inverted triangle—clade F; triangles—clade G; circles—clade H; diamond—clade I; *O. nipponoborealis* (Tohoku, Japan)—purple: squares—clade J. For locality numbers refer to TABLE 1 and FIGURE 3; icons reflecting revealed lineages also given in FIGURE 3.

Materials and methods

Sample collection

We collected salamanders by opportunistic searching in streams and their surroundings. Specimens were euthanized in a chlorobutanol solution, fixed in 95% ethanol or formaldehyde, and preserved in 70% ethanol. Localities were georeferenced with GPS receivers using the WGS84 datum system, and plotted on maps (Fig. 1, Table 1). For molecular analyses, muscle or liver tissue samples were taken from freshly euthanized specimens in the field and preserved in 98% ethanol or frozen. In some cases, tail tips were taken and the animal was released. Our sampling covered most of the geographic range of the genus. For the Japanese species *O. japonicus* we studied 81 specimens from 13 populations, representing main lineages within the species as revealed by Yoshikawa *et al.*

(2008) and used published data by these authors for CytB sequences for comparison. For Russian populations of the continental species *O. fischeri* we studied 48 specimens from 7 populations. For Chinese populations of *O. fischeri* we studied 15 specimens from 6 localities and also used the published sequences of Chinese *O. fischeri* from Zhang *et al.* 2006 (accession number DQ333820). For Korean populations of *O. fischeri* we analyzed 76 specimens from 23 localities which thoroughly covers the species range in the southern part of the Korean peninsula (see Fig.1). The only blank spot on the map of our sampling area is from North Korea from which we could not obtain any materials due to logistical reasons.

Morphological studies were based on the analysis of 223 specimens of adult and larvae of *Onychodactylus* species, including vouchers stored in the following herpetological collections: Zoological Museum of Moscow State University (ZMMU), Moscow, Russia; Zoological Institute of R.A.S. (ZISP), St.-Petersburg, Russia; Museum of Vertebrate Zoology (MVZ), U.C., Berkeley, USA; Chengdu Institute of Biology C.A.S. (CIB), Chengdu, Sichuan, China; Kunming Institute of Zoology C.A.S. (KIZ), Kuming, Yunnan, China; National Museum of Natural History – Naturalis (RNHM), Leiden, the Netherlands; Zoologisches Forschungsmuseum Alexander Koenig (ZMK), Bonn, Germany; Senckenberg Forschungsinstitut und Naturmuseum (SMF), Frankfurt –a. M., Germany; National Museum of Nature and Science (NSMT), Tokyo, Japan; and Ewha Women's University Natural History Museum (EWNHM), Seoul, Korea. Included in the morphological analysis were the type specimens of *Salamandra unguinulata* Temminck & Schlegel, 1838 and *Onychodactylus schlegeli* Tschudi, 1838, which were housed in the RMNH. Overall, studied specimens can be assigned to 37 populations, which fit well with the sampling areas used for molecular analysis. For detailed information on populations used in the morphological analysis, refer to Appendix 1.

Genome size measurements were conducted for 17 specimens of *Onychodactylus* from six localities (two from Japan, two from China, one from Korea, and one from Russia) by DNA flow cytometry using BD FACSaria flow cytometer and followed standard protocols for this method (Murphy *et al.*, 1997).

DNA isolation, PCR and sequencing

Total genomic DNA was extracted from ethanol-preserved or frozen muscle tissues using standard phenol-chloroform with proteinase K (final concentration 1 mg/ml) isolation method (protocols followed Hillis *et al.*, 1996 and Sambrook & Russell, 2001), or using the standard salt extraction protocol (Bruford *et al.*, 1992), for most of the samples. For the rest we used a glass-fiber automatic DNA isolation protocol following Ivanova *et al.* (2006). We amplified three mitochondrial markers for phylogenetic purposes – 16S rRNA, Cytochrome oxidase I (COI) and Cytochrome B (CytB). Those are among the most widely used markers for amphibian phylogenetics and taxonomic studies (e.g. Weisrock *et al.*, 2001; Vences *et al.*, 2005a; Vences *et al.*, 2005b; Smith *et al.*, 2008; Fu & Zeng, 2008; Yoshikawa *et al.*, 2008). All primers for PCR and sequencing used in this study are summarized in Table 2. The obtained fragments were sequenced in both directions for each sample, and a consensus sequence was generated. Fragment length varied among taxa due to missing nucleotides at the beginning or end of the sequences or by different length of variable regions corresponding to loops in the secondary structure of the 16S rRNA molecule.

PCRs were performed in 25 µl reactions using ca. 50 ng genomic DNA, 10 pmol of each primer, 15 nmol of each dNTP, 50 nmol additional MgCl₂, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl₂ and 0.01% gelatine) and 1 U of Taq DNA polymerase. The PCR conditions were: an initial denaturation step at 95° C for 3 min; 35–39 cycles at 95° C for 30 s, annealing for 1 m, extension at 72° C for 2 min and final extension of 5 min at 72° C. Annealing temperatures varied for amplifications of different makers: 48° C for 16S rRNA, 49–53° C for COI and 46–51° C for CytB. PCR products were loaded onto 1% agarose gels, stained with GelStar gel stain (Cambrex), and visualized in a Dark reader transilluminator (Clare Chemical). If results were satisfying, 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 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). Obtained sequences were deposited in GenBank under accession numbers JN700874–JN700875; JN712107–JN712110; JN712112–JN712120; JX157963–JX158323; see Table 1). Full mitochondrial genomes of hynobiid salamanders published by Zhang *et al.* (2006) and Peng *et al.* (2010) were used as outgroup taxa (GenBank accession numbers: NC004021; DQ333808–DQ333822; FJ532058–FJ532060).

TABLE 1. Species, sampling localities, locality numbers, sample sizes used for molecular phylogenetic analysis, revealed clades and GenBank accession numbers.

Species	Sampling locality	N	Clade	GenBank Acc. No.
<i>Onychodactylus fischeri</i> (Primorye, Russia)				
1	Primorye territory; Olga	5	A	JX157963-57967; JX158078-158082; JX158200-158204
2	Primorye territory; Serebryannaya R.	2	A	JX157968; JX158083; JX158205
3	Primorye territory; Fadeevo	4	A	JX157969; JX158084; JX158206
4	Primorye territory; Partizan	6	A	JX157970; JX158085; JX158207
5	Primorye territory; Tigrovoy	15	A	JX157971-157984; JX158086-158099; JX158208-158221
6	Primorye territory; Shkotovo	10	A	JX157985; JX158100-158102; JX158222-158223
7	Primorye territory; Anisimovka	6	A	JX157986-157987; JX158103-158104; JX158224-158225
Total for the group:		48		
<i>Onychodactylus zhangyapingi</i> (Jilin, China)				
8	Jilin; Linjiang	4	C	JN700874; JX157988-157991; JX158229
9	Jilin; Tonghua	3	C	JX157992-157994; JX158109-158111; JX158230-158231
Total for the group:		7		
<i>Onychodactylus zhaoermii</i> (Jilin and Liaoning, China)				
10	Jilin; Laoling Mts.	2	B	JX157995-157996; JX158112-158113; JX158232-158233
11	Liaoning; Sanjiazi	2	B	JX157997; JX158114-158115; JX158234
12	Liaoning; Xiuyan	3	B	JN700875; JX157998-158000; JX158116-158118; JX158235-158237
13	Jilin; Changbaishan Mt. ¹	1	B	DQ333820
Total for the group:		8		
<i>Onychodactylus koreanus</i> (Korea)				
14	Gangwon-do; Seo-myeon	7	D1	JX158001-158004; JX158119-158122; JX158238-158241
15	Gangwon-do; Dongnae-myeon	7	D1	JX158005-158008; JX158123-158126; JX158242-158245
16	Gangwon-do; Seoraksan NP	1	D2	JX158009; JX158127; JX158246

.....continued on next page

TABLE 1. (Continued)

Species	Sampling locality	N	Clade	GenBank Acc. No.
<i>Onychodactylus koreanus</i> (Korea)				
17	Gangwon-do; Nae-myeon	7	D1	JX158010-158014; JX158128-158132; JX158247-158251
18	Gangwon-do; Chiaksan NP, Gillaji	2	D2	JX158015-158016; JX158133; JX158252-158253
19	Gangwon-do; Chiaksan NP , Chiak-san	1	D2	JX158017; JX158134; JX158254
20	Gangwon-do; Bongpyeong-myeon	2	D2	JX158018-158019; JX158135-158136; JX158255-158256
21	Gangwon-do; Seokbyeong-san	1	D2	JX158020-158021; JX158137-158138; JX158257-158258
				JN712107-712110; JX158022-
22	Gangwon-do; Singi-myeon	7	D2	158023; JX158139-158140; JX158259-158260
23	Chungcheongbuk-do; Naeam-myeon	7	D2	JX158024-158028; JX158141-158145; JX158261-158265
24	Cheongju-shi; Gadeok-myeon	2	D2	JN712112; JX158146
25	Gyeongsangbuk-do; Songni-san, Daemok-ri	2	D2	JX158147; JX158266
26	Daejeon; Jangtae-san	2	D2	JN712113-712114; JX158148
27	Chungcheongnam-do; Beolkok-myeon	3	D2	JN7112118-712120; JX158149
28	Chungcheongnam-do; Nonsan-shi; Boseoksa	1	D2	JN712115-712117; JX158150
29	Jeollabuk-do; Kunghangsan environs	1	D2	JX158151; JX158267
30	Jeollabuk-do; Jucheon-Myeon	2	D2	JX158029-158030; JX158152-158153; JX158268-158269
31	Jeollabuk-do; Naedong environs	2	D2	JX158031-158032; JX158154; JX158270-158271
32	Jeollabuk-do; Naejangsan NP (Naejang)	2	D2	JX158033; JX158155; JX158272
33	Jeollanam-do; Naejangsan NP (Sinung)	2	D2	JX158034; JX158156; JX158273-158274
34	Gyeongsangnam-do; Jirisan NP (Jiri-san)	8	D2	JX158035-158039; JX158157-158161; JX158275-158279
35	Jeollanam-do; Jirisan NP (Wonchon)	5	D2	JX158040; JX158162; JX158280
Total for the group:		74		
<i>Onychodactylus</i> sp. (Yangsan, Korea)				
36	Gyeongsangbuk-do; Yangsan-gun; Dong-myeon	2	E	JX158041-158042; JX158163-158164; JX158281-158282
Total for the group:		2		

.....continued on next page

TABLE 1. (Continued)

Species	Sampling locality	N	Clade	GenBank Acc. No.
<i>Onychodactylus cf. japonicus</i> (Shikoku, Japan)				
37	Ehime; Ishizuchi-San	6	F	AB452951-452953; AB452955; JX158283-158285
Total for the group:		6		
<i>Onychodactylus cf. japonicus</i> (western Honshu, Japan)				
38	Hiroshima; Yoshiwa	4	G	JX158043-158046; JX158165- 158166; JX158286-158289
39	Hyogo; Muraoka	4	G	JX158047-158049; JX158167- 158170; JX158290-158292
Total for the group:		8		
<i>Onychodactylus japonicus</i> s. str. (central Honshu, Japan)				
40	Kanagawa; Hakone-machi	10	H1	JX158050-158052; JX158171- 158172; JX158293-158295
41	Tokyo; Okutama envrions	8	H1	JX158053-158055; JX158173- 158175; JX158296-158298
42	Tochigi; Fujihara environs	5	H2	JX158056-158058; JX158176- 158178; JX158299-158301
43	Tochigi; Kinugawa-koen station	10	H2	JX158059-158061; JX158179- 158181; JX158302-158304
44	Fukushima; Hinoemata environs	13	H2	JX158062-158067; JX158182- 158189; JX158305-158310
45	Fukushima; Shirakawa	2	H2	AB452849; AB452884; AB452848; JX158311
Total for the group:		48		
<i>Onychodactylus cf. japonicus</i> (central Honshu, Japan)				
46	Fukushima; Iwaki	3	I	AB452846; JX158312-158313
Total for the group:		3		
<i>Onychodactylus nipponoborealis</i> (Tohoku, northern Honshu, Japan)				
47	Yamagata; Yamagata environs	2	J1	JX158068-158069; JX158190- 158191; JX158314-158315
48	Aomori; Hirakawa environs	11	J2	JX158070-158073; JX158192- 158196; JX158316-158319
49	Aomori; Hirosaki environs	3	J2	JX158074-158077; JX158197- 158199; JX158320-158323
Total for the group:		16		
Sum total:		112		

Note: 1—Locality uncertain (according to P. Zhang, personal comment), and probably refers to more western populations.

TABLE 2. DNA primers for PCR and sequencing used in the study.

Primer name	Primer sequence	Source
16S rRNA		
16Sar-L	5'-CGCCTGTTATCAAAAACAT-3'	Palumbi <i>et al.</i> 1991
16Sbr-H	5'-CCGGTCTGAACTCAGATCACGT- 3'	Palumbi <i>et al.</i> 1991
COI		
LepF1	5'-ATTCAACCAATCATAAAGATATTGG-3'	Hebert <i>et al.</i> , 2004b
VF1-d	5'-TTCTCAACCAACCACAARGAYATYGG-3'	Ivanova <i>et al.</i> , 2006
mLepF1	5'-GCTTCCCCACGAATAAATAATA-3'	Hajibabaei <i>et al.</i> , 2005
mLepF1	5'-GCTTCCCCACGAATAAATAATA-3'	Hajibabaei <i>et al.</i> , 2005
LepR1	5'-TAAACTCTGGATGTCCAAAAATCA-3'	Hebert <i>et al.</i> , 2004b
VR1-d	5'-TAGACTTCTGGTGGCCRAARAAYCA-3'	Ivanova <i>et al.</i> , 2006
C113Rdeg	5'-GGYATWACTATRAARAARATTAT-3'	Hajibabaei <i>et al.</i> 2005
CytB		
Glu14100L	5'-GAAAAACCAAAYGTTGTATTCAACTATAA-3'	Zhang, 2008
MVZ15L	5'-GAACTAATGGCCCACACA/TA/TTACGNAA-3'	Moritz <i>et al.</i> , 1992
L14841	5'-AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA-3'	Kocher <i>et al.</i> , 1989
HYD-Cytb-F1	5'-CYAACCTAAAGCWGCAAATA-3'	Matsui <i>et al.</i> , 2008
HYD-Cytb-F2	5'-AGTYATTACWAAYTTAYTWTCAAGC-3'	Matsui <i>et al.</i> , 2008
Onycho_Cytb_up70F	5'-CATAGCAAGTAAAGCTAAATAATCAT-3'	Yoshikawa, 2008
MVZ16H	5'-AAATAGGAAA/GTATCAT/CTCTGGTTA/GAT-3'	Moritz <i>et al.</i> , 1992
MVZ18H	5'-GTCTTGATGATGAGAAGTATG-3'	Moritz <i>et al.</i> , 1992
H15149	5'-AAACTGCAGCCCCCTCAGAATGATATTGTCCTCA-3'	Kocher <i>et al.</i> , 1989
CB14940H	5'-GCAAATAGGAARTAYCAYTCTGG-3'	Zhang, 2008
HYD-Cytb-R1	5'-TARRAARTGAAATGCAAARAATCG-3'	Matsui <i>et al.</i> , 2008
salamander-Cytb-RN2	5'-YTYTCAATCTKGGYTTACAAGACC-3'	Matsui <i>et al.</i> , 2008

Sequence alignment and phylogenetic analyses

Sequences were automatically aligned using program Clustal X 1.8 (Thompson *et al.*, 1997), and the alignment was reviewed visually to check for potential conflicts. The alignment of CytB and COI sequences did not show any indels or stop codons, while the 16S rRNA showed some length variation, corresponding to loop regions or single insertions in some taxa. The 13 most variable sites of 16S rRNA were excluded from the final analyses because of ambiguity in the alignment or because gaps were present in more than 50% of the taxa.

Prior to phylogenetic analysis p-distances were plotted against the number of transitions and transversions to test for saturation in ingroup-substitutions. Our data indicate that combined COI—CytB—16S rRNA alignment does not show any signs of saturation within the ingroup (not shown).

We inferred phylogenies both by a maximum likelihood (ML) and a Bayesian approach (BI). Non-parametric bootstrap ML analysis was performed with the program RaxML (Stamatakis *et al.*, 2005). One thousand bootstrap repetitions were run for the concatenated dataset. We performed partitioned Bayesian analysis using MrBayes 3.1 (Ronquist & Huelsenbeck, 2003). For those analyses, we followed two different strategies: partition by codon and gene (7 parts, 1st, 2nd and 3rd positions in COI and CytB, and 16S rRNA), and a partition by gene (3 parts, COI, CytB and 16S rRNA). In order to decide which partition is more appropriate for our data, we used Bayes factors (e.g. as in Mott & Vieites, 2009). Separated evolutionary models and parameters that best fit each partition were selected for each codon position and gene of CytB and COI, and for the complete 16S rRNA, using PAUP* 4.0b10 (Swofford, 2003) and the Akaike Information Criterion implemented in MrModeltest version 2.2 (Nylander, 2004). These models were used as priors in the Bayesian analyses in the program MrBayes 3.1. The maximum likelihood

tree for the entire dataset was used as the starting tree in the model calculations. We ran two independent analyses consisting of four Markov chains that ran for 20 million generations, sampled every 1000 generations, with default priors, and the option “prset ratepr” set as “variable”. The temperature was optimized to 0.3 after several test runs for one million generations. The two runs allowed us to test for convergence using the online application AWTY. After discarding the first 5 million generations, remaining trees from both analyses were combined and a 50% majority rule consensus tree was calculated.

For interpreting the phylogenetic trees, we considered as significant support bootstrap values of 70% and higher, in ML analyses and Bayesian posterior probabilities of 0.95 and higher. 16S rRNA and COI genetic distances between pairs of sister species of *Onychodactylus* from different populations were calculated both by using a Kimura two-parameter model (K2P) and as uncorrected *p*-distances in the program PAUP* 4.0b10 (see Table 3). These two mtDNA genes have been extensively used to evaluate genetic differentiation between species in amphibians (Vences *et al.*, 2005a,b; Vieites *et al.*, 2009; Smith *et al.*, 2008; Xia *et al.*, 2012; Che *et al.*, 2012), which may serve as comparison to the levels of divergence observed within *Onychodactylus* with other amphibian groups. Uncorrected pairwise genetic distances were calculated using PAUP* and manually transformed into percentages.

External morphological data and analyses

We examined 223 specimens from 36 populations (see Appendix 1) of *Onychodactylus* species collected mainly during the breeding season or soon after the breeding season from 1980 to 2009. For clarifying some taxonomic issues we also studied Ph. F. von Siebold’s collection of *Onychodactylus* collected in Japan between 1824 and 1829 (most probably in 1828) and stored in RMNH: RMNH-2289 (20 adults); RMNH-2290 (8 adults); RMNH-2291 (7 larvae) and RMNH-2292 (4 adults). The specimens from the last series were designated as a lectotype and paralectotypes for *Salamandra unguiculata* Temminck & Schlegel, 1838 (Hoogmoed, 1978). In our sample, we had more adult males than adult females, which may be a consequence of a higher detectability of males because of their increased activity during the breeding season, and tend to arrive at streams earlier than females (Kuzmin, 1995). They also tend to stay longer in the water, have increased locomotion, and are more easily noticed than females. Since we could not examine sufficient numbers of adult females and juveniles to assess their geographic variation, we had to combine samples collected from nearby localities into one population (see Appendix 1). In all, six groups were combined: *Onychodactylus fischeri* from Russia, *O. fischeri* from Liaoning Province, China, *O. fischeri* from Jilin Province, China, *O. fischeri* from Korea, *O. japonicus* from central Honshu and *O. japonicus* from Tohoku.

TABLE 3. Uncorrected genetic distances (*p*-distances) between 16S rRNA (above diagonal) and COI (below diagonal) gene sequences of revealed *Onychodactylus* lineages.

% uncorrected <i>p</i> -distances		A	C	H1	H2	G	F	J1	J2	I	B	E	D1	D2
1 - <i>O. fischeri</i>	A	-	5.3	6.3	6.4	6.2	6.3	6.8	6.4	5.9	6.2	5.3	6.5	6.5
2 - <i>O. zhangyapingi</i>	C	12.2	-	2.1	2.3	2.8	2.7	3.1	2.4	2.7	2.0	2.1	2.3	2.4
3 - <i>O. japonicus</i> s. str.	H1	12.3	8.5	-	0.6	3.0	3.1	3.1	2.3	2.4	2.4	2.4	2.6	2.6
4 - <i>O. japonicus</i> s. str.	H2	13.3	9.2	2.1	-	3.2	3.3	3.3	2.5	2.5	2.5	2.5	2.8	2.8
5 - <i>O. cf. japonicus</i>	G	11.1	7.9	5.1	6.2	-	2.7	3.6	3.4	3.2	2.6	2.5	2.9	3.0
6 - <i>O. cf. japonicus</i>	F	12.1	8.4	6.2	7.0	5.0	-	3.6	3.5	3.3	2.5	2.6	3.0	3.0
7 - <i>O. nipponoborealis</i>	J1	12.7	9.5	8.4	8.8	7.5	7.8	-	2.8	3.3	3.3	3.3	3.4	3.2
8 - <i>O. nipponoborealis</i>	J2	12.4	9.1	8.1	9.1	7.7	8.0	4.3	-	2.9	2.7	2.5	2.7	2.7
9 - <i>O. cf. japonicus</i>	I	12.7	9.3	8.8	9.7	8.4	7.5	4.5	4.4	-	2.9	2.9	3.2	3.2
10 - <i>O. zhaoermii</i>	B	13.4	9.0	9.1	10.2	8.4	8.3	10.8	10.5	10.7	-	1.9	2.1	2.0
11 - <i>Onychodactylus</i> sp.	E	12.4	7.5	7.8	8.7	7.6	7.5	9.5	9.6	9.4	6.0	-	1.9	1.9
12 - <i>O. koreanus</i>	D1	11.2	7.7	8.7	9.3	8.0	7.7	9.8	9.3	9.8	7.3	5.6	-	0.7
13 - <i>O. koreanus</i>	D2	11.4	7.9	8.9	9.4	8.2	7.9	10.0	9.3	9.6	7.4	5.8	1.4	-

From the salamanders collected in the field, their sex was determined directly by body dissection or using secondary sexual characters (longer tails, broader heads and well-developed claws and flaps on hind limbs in males). These determinations were made only if specimens were collected during the breeding season. Animals collected were deposited in the herpetological collections of Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, USA, Zoological Museum of Lomonosov Moscow State University (ZMMU), Moscow, Russia, Kunming Institute of Zoology C.A.S. (KIZ), Kunming, China, Ewha Women's University Natural History Museum (EWNHM), Seoul, Korea, and the herpetological collection of the National Science Museum of Tokyo (NSMT), Tokyo Japan.

We also examined specimens from the herpetological collections of the Zoological Institute of RAS (ZISP), Saint Petersburg, Russia, the Vertebrate Zoology department of Biological faculty of Moscow State University (VZMSU), Russia, and the herpetological collection of the National Museum of Natural History – Naturalis (RMNH), Leiden, the Netherlands, including the type series for *Salamandra unguiculata* Temminck & Schlegel, 1838 (RMNH-2292A-D) in order to test their affinities with studied *O. japonicus* samples from a morphological perspective.

To examine morphological variation we studied 17 morphological characters (14 of them mensural and 3 meristic) that are widely used in salamander taxonomy and species determination (eg. Good & Wake, 1992; García-París & Wake, 2000) (see Fig. 2). All measurements were taken to the nearest 0.1 mm using digital calipers, measurements of small absolute values (<10 mm) were taken under a stereoscopic binocular microscope. Measurements of bilateral morphological structures were studied for left and right body sides separately. Metric characters included: SVL—snout-vent length (measured on straightened body from snout to the anterior end of the vent); TL—tail length (measured on straightened tail from the tip of the tail to the anterior end of the vent); GA—gleno-acetabular distance (minimum distance between axilla and groin measured on a straightened body; measured separately for left and right body sides); FLL—forelimb length (length of the straightened forelimb measured from axilla to tip of the longest finger of forelimb; measured separately for left and right body sides); HLL—hindlimb length (length of the straightened hindlimb from groin to tip of the longest toe of hindlimb; measured separately for left and right body sides); HL—head length (measured from the tip of the snout to the gular fold); HW—head width (widest measurement of the head across the eyes anterior to the level of parotid glands; this does not include head broadening beyond the eyes in breeding males); EL, eye length (minimum distance from the anterior corner of the eye to the posterior corner of the eye; measured separately for left and right body sides); IN—internarial distance (minimum distance between the external nares); ON—orbitonarial distance (minimum distance between external nares and the anterior corner of the eye on the same side of the head; measured separately for left and right body sides); IO—interorbital distance (minimum distance between the upper eyelids); CW—chest width (minimum distance between left and right axillae); OR—orbitorostral distance, snout length (measured as minimum distance from tip of snout to the anterior corner of the eye; measured separately for left and right body sides); IC—intercanthal distance (measured as minimum distance between anterior corners of the eyes).

Meristic characters included: TVN—trunk vertebrae number (number of presacral vertebrae); CGN—costal grooves number (number of costal grooves between the fore- and hindlimbs, excluding axillary and inguinal grooves, following Misawa, 1989; counted separately for left and right body sides); VTN—vomerine teeth number (number of vomerine teeth; counted separately for left and right vomerine tooth series).

Body segmentation - costal grooves count and trunk vertebrae number

Various authors used different approaches for counting costal grooves (see Litvinchuk & Borkin, 2003). Dunn (1923) applied the name "costal grooves" to all lateral body grooves situated between the fore- and hindlimbs, probably, including the grooves, which touched the posterior margin of the base of the hindlimbs. According to Highton (1957), costal grooves are the grooves situated between the posterior margin of the head and the anterior margin of the hindlimb. Cope (1889) proposed to name the grooves contacting the base of forelimbs as "axillary", whereas that contacting the base of hind limbs "inguinal", respectively. Finally, Misawa (1989) in a critical review has proposed to recognize under the name "costal grooves" only lateral grooves between the fore- and hindlimbs, which do not touch the limb's posterior and anterior margins, i.e. excluding axillary and inguinal grooves. In this study, we followed Misawa's (1989) method of counting costal grooves and counted them on both sides of the body.

The number of trunk vertebrae was estimated as the number of presacral vertebrae visualized through X-ray photos using DR 3500 Plus Digital Small Animal X-Ray System. Altogether, X-ray photos were obtained for 110 animals. For additional 72 specimens, the number of presacral vertebrae was estimated from counts of the spinal processes number by means of dissection of dorsal muscles as described in Litvinchuk & Borkin (2003). Position of the sacrum was identified by feeling of the sacral ribs on the left side of the body with a preparation needle.

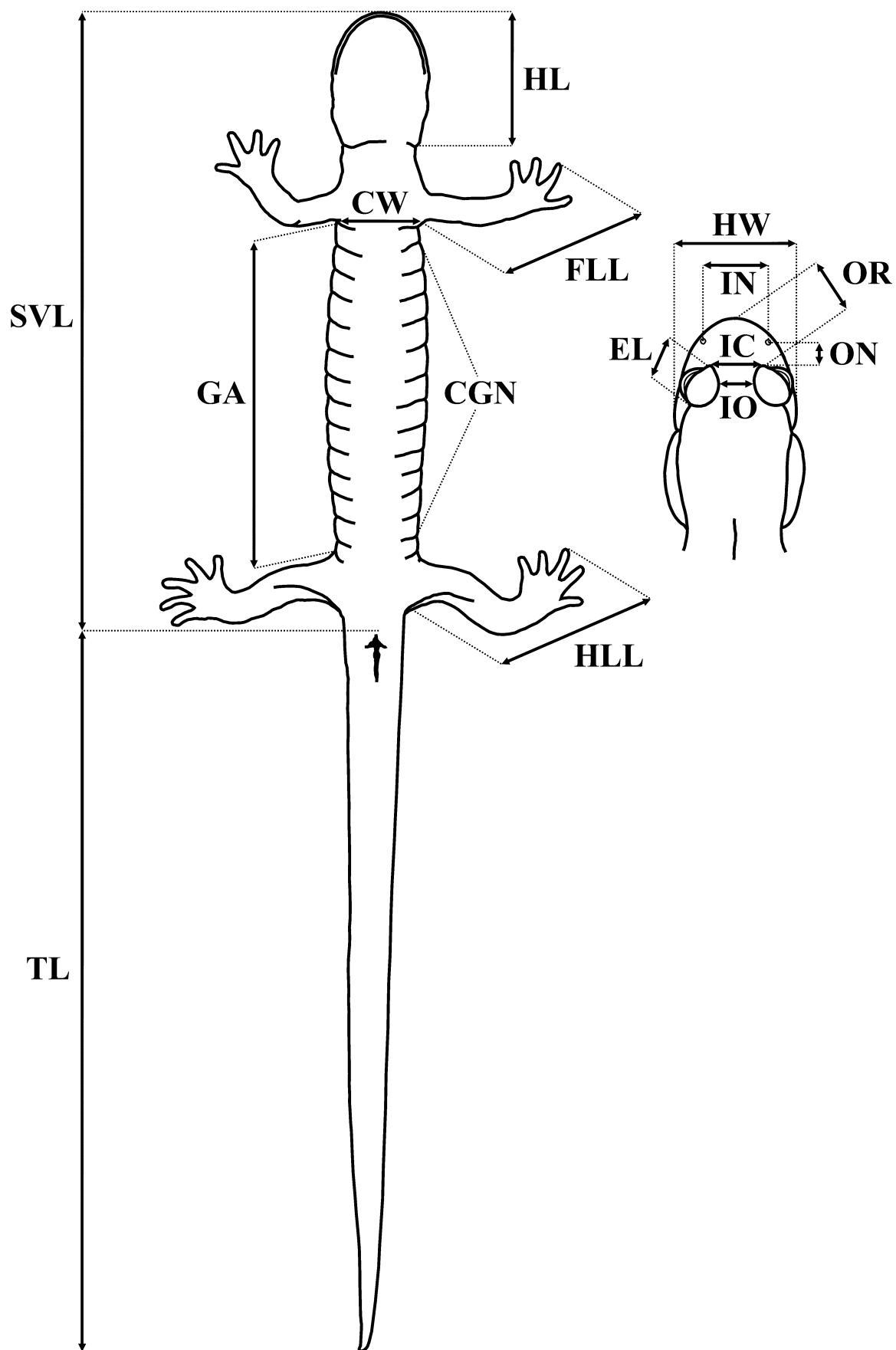


FIGURE 2. Character dimensions of *Onychodactylus* used in the study. See the character definitions and the abbreviations in Appendix 2. (A)—Ventral view of a specimen; (B)—Dorsal view of the head.

Vomerine tooth series

Number and shape of vomerine tooth series has been regarded as a key character for diagnosing closely-related species of Hynobiidae (Sato, 1934; 1943; Zhao & Adler, 1993). The shape of the series was also shown to be one of the few characters allowing distinction between *Onychodactylus japonicus* and *O. fischeri* (in *O. japonicus* right and left tooth series are in contact, whereas in *O. fischeri* there is a gap between them, see Dunn, 1923). However, comparative data on variation of this character among populations of *Onychodactylus* are absent. Thus, we studied number and morphology of vomerine tooth series of 181 *Onychodactylus* specimens under a stereoscopic binocular microscope and using Nikon D-60 digital camera with microscope adapter. The number of teeth in the inner and outer branches of the tooth series was recorded for right and left sides, and the form of the series was sketched from the digital photos.

Description of coloration

Intrapopulational variation in coloration, especially in dorsal pattern, was reported for *Onychodactylus japonicus* by Sato (1943). We attempted to describe color variation between different populations of *Onychodactylus* in principle following Tominaga *et al.* (2005) who used color variation to access population differentiation between cryptic species of the *Hynobius naevius* complex (Hynobiidae). For analysis of color variation, we studied 23 quantitative characters describing ground color, coloration pattern, markings and their color on dorsal, lateral and ventral sides of the body and tail, but not on the limbs with their character states coded. Coloration was described for 150 specimens from photos taken in the wild and museum collections. In order to access color variation among samples, the character-states were arcsine-corrected after the principal component analysis was conducted. Most typical coloration patterns were illustrated.

This coding approach is summarized as follows: 1. Dorsal ground color of trunk and head (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange). 2. Dorsal marking of trunk (0: absent; 1: small round or oval spots (size ~ SVL/40-SVL/20); 2: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5). 3. Light dorsal band (0: absent; 1: indistinct with no clear borders; 2: distinct with unclear borders, consisting of spots and variegations; 3: distinct broad band with clearly defined borders; 4: distinct discontinuous band with broken borders). 4. Dark dorsomedial stripe (0: absent; 1: present, continuous; 2: present, discontinuous). 5. Color of dorsal marking of trunk (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange). 6. Dorsal ground color of tail (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange). 7. Dorsal marking of tail (0: absent; 1: small round or oval spots (size ~ SVL/40-SVL/20); 2: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5)). 8. Light dorsal band on the tail (0: absent; 1: indistinct with no clear borders; 2: distinct with unclear borders, consisting of spots and variegations; 3: distinct broad band with clearly defined borders; 4: distinct discontinuous band with broken borders). 9. Color of dorsal marking of tail (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange). 10. Markings on dorsal and lateral surface of head (0: absent; 1: dots, or small round or oval spots (size ~ SVL/40-SVL/20); 2: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5); 4: large light confluent spots and bars (size ~ SVL/20-SVL/5)). 11. Color of head markings (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange). 12. Lateral ground color of trunk (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange; 6: plumbeous; grayish; off-white or whitish). 13. Markings on lateral surface of trunk (0: absent; 1: small dots (size < SVL/30); 2: small round or oval spots (size ~ SVL/30-SVL/20); 3: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 4: large dark variegations and spots (size ~ SVL/20-SVL/5); 5: large light confluent spots and bars (size ~ SVL/20-SVL/5)). 14. Color of lateral trunk markings (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange; 7: bluish, whitish or light-gray). 15. Lateral ground color of tail (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange; 6: plumbeous; grayish; off-white or whitish). 16. Markings on lateral surface of tail (0: absent; 1: dots, small round or oval spots (size ~ SVL/30-SVL/20); 2: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5); 5: large light confluent spots and bars (size ~ SVL/20-SVL/5); 6: continuous lines and variegations). 17. Color of lateral tail markings (0: absent

markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange; 7: bluish, whitish or light-gray). 18. Ventral ground color of trunk and head (0: dark-gray; 1: gray, plumbeous-gray; 2: brownish; 3: light reddish-purple). 19. Ventral markings on trunk and head (0: absent or faintly spotted; 2: small spots and vermiculations (size ~ SVL/40-SVL/20); 3: large variegations and spots (size ~ SVL/20-SVL/5)). 20. Color of ventral markings on trunk and head (0: absent markings; 1: black; 2: white or bluish; 3: yellowish or ochre; 4: reddish). 21. Ventral ground color of tail (0: dark-gray; 1: gray, plumbeous-gray; 2: brownish; 3: light reddish-purple; 4: reddish, orange or yellow). 22. Ventral markings on tail (0: absent or faintly spotted; 2: small spots and vermiculations (size ~ SVL/40-SVL/20); 3: large variegations and spots (size ~ SVL/20-SVL/5)). 23. Color of ventral markings on tail (0: absent markings; 1: black; 2: white or bluish; 3: yellowish or ochre; 4: reddish).

Assessment of morphological variation

For univariate analyses, we used morphometric characters, corrected by body size, and other meristic characters. Previous research (see Kuzmin, 1995) and our preliminary investigation of sexual differentiation using the set of populations from Russia showed sexual dimorphism in SVL and most ratios of the head, limbs and tail, as well as in meristic characters, assessed using nonparametric Mann-Whitney *U*-test. Therefore, sexes were separated for subsequent comparisons among the samples. For examining overall morphological variation among studied populations, we conducted multivariate statistical analyses. Whenever some characters showed high correlation between each other, in order to exclude the overweighting effect of these characters on the analysis, one of them was omitted. After metric values were log_e-transformed, we conducted a principal component analysis. To examine variation in proportions among samples we used canonical determinant analysis (CDA), and contribution of size variation was excluded using the multiple-group principle component analysis (MGPCA, Thorpe, 1988). After homogeneity of variances was assessed, we applied parametric tests (ANOVA, ANCOVA and Student's *t*-test). The significance level was set at P < 0.05. All statistical analyses were performed with Statistica 6.0 (StatSoft, Inc., 2001).

Results

Molecular differentiation and phylogenetic relationships within *Onychodactylus*

Both ML and the Bayesian analyses with a partitioning strategy by gene provided essentially similar topologies (Fig. 3). Phylogenetic analyses show significant support for twelve mtDNA lineages within *Onychodactylus*, with *O. fischeri* from Russia being the sister clade to all other populations (clade A, see Fig. 3). This lineage shows uncorrected pairwise genetic distances from other lineages between 11.1 to 13.4% in COI and of 5.3 to 6.8% in 16S rRNA (Tab. 3). All samples from the Russian localities of this species showed a surprisingly low level of genetic differentiation. All other lineages of *Onychodactylus* form a well-supported clade, with two main groups including populations that traditionally were considered as *O. fischeri* but recovered as more closely related to *O. japonicus*, and implying that *O. fischeri* is paraphyletic in its former taxonomic sense (Fig. 3 B).

A well-supported clade is constituted by Korean populations as well as specimens from Chinese populations from southern Jilin and Liaoning provinces (Fig. 3 A). In the Korean peninsula, two distinct genetic lineages are present: lineage D is found throughout the country, whereas lineage E is only restricted to the mountain area of Yangsan in the southwest region of the Peninsula. The two Korean lineages form a well-supported clade with *p*-distances among them of 5.6 to 5.8% in COI and 1.9% in 16S rRNA. These are sister to southern Jilin and Liaoning *Onychodactylus*, which show uncorrected pairwise genetic distances from all other lineages of 6.0 to 13.4% in COI and 1.9 to 6.2% in 16S rRNA (Tab. 3).

The other main clade is constituted by a mtDNA lineage from Linjiang and Tonghua, Jilin Province (lineage C), together with all Japanese populations. Lineage C from China is recovered as the sister group to *O. japonicus*, showing uncorrected pairwise genetic distances from all other lineages of 7.5 to 12.2% in COI and of 2.0 to 5.3% in 16S rRNA (Tab. 3). All populations from Japan (*O. japonicus*) constitute a well-supported monophyletic group. Within *O. japonicus*, two main clades are well supported in phylogenetic analyses. One clade (clade J) corresponds to populations from northeastern Japan (Hirosaki, Hirakawa and Yamagata from Tohoku region) being recovered as monophyletic with high statistical support in all analyses (Fig. 3). This clade shows uncorrected pairwise genetic distances from other *O. japonicus* lineages of 4.4 to 9.1% in COI and of 2.3 to 3.6% in 16S rRNA (Tab. 3). The genetic differentiation between populations from Tohoku region populations from Yamagata and Aomori (populations of Hirosaki, Hirakawa) is of 4.3% for COI and 2.8% for 16S rRNA (Tab. 3). The rest of populations of

O. japonicus cluster together forming a monophyletic group with uncorrected pairwise genetic distances among them ranging from 0.0 to 7.0% for COI and from 0.0 to 3.3% for 16S rRNA. Our analyses show several lineages with high statistical support within this group (Fig. 3). The populations from Iwaki (clade I) were recovered as the sister group to the rest of populations (BS=87%; BPP=0.95). The populations of *O. japonicus* from Shikoku Island (clade F, Ehime), from western Japan, are recovered as the sister group to the clade constituted by lineages G, H and A with pairwise genetic distances between them ranging from 5.0 to 6.2% in COI and of 2.7 to 3.3% in 16S rRNA (Tab. 3).

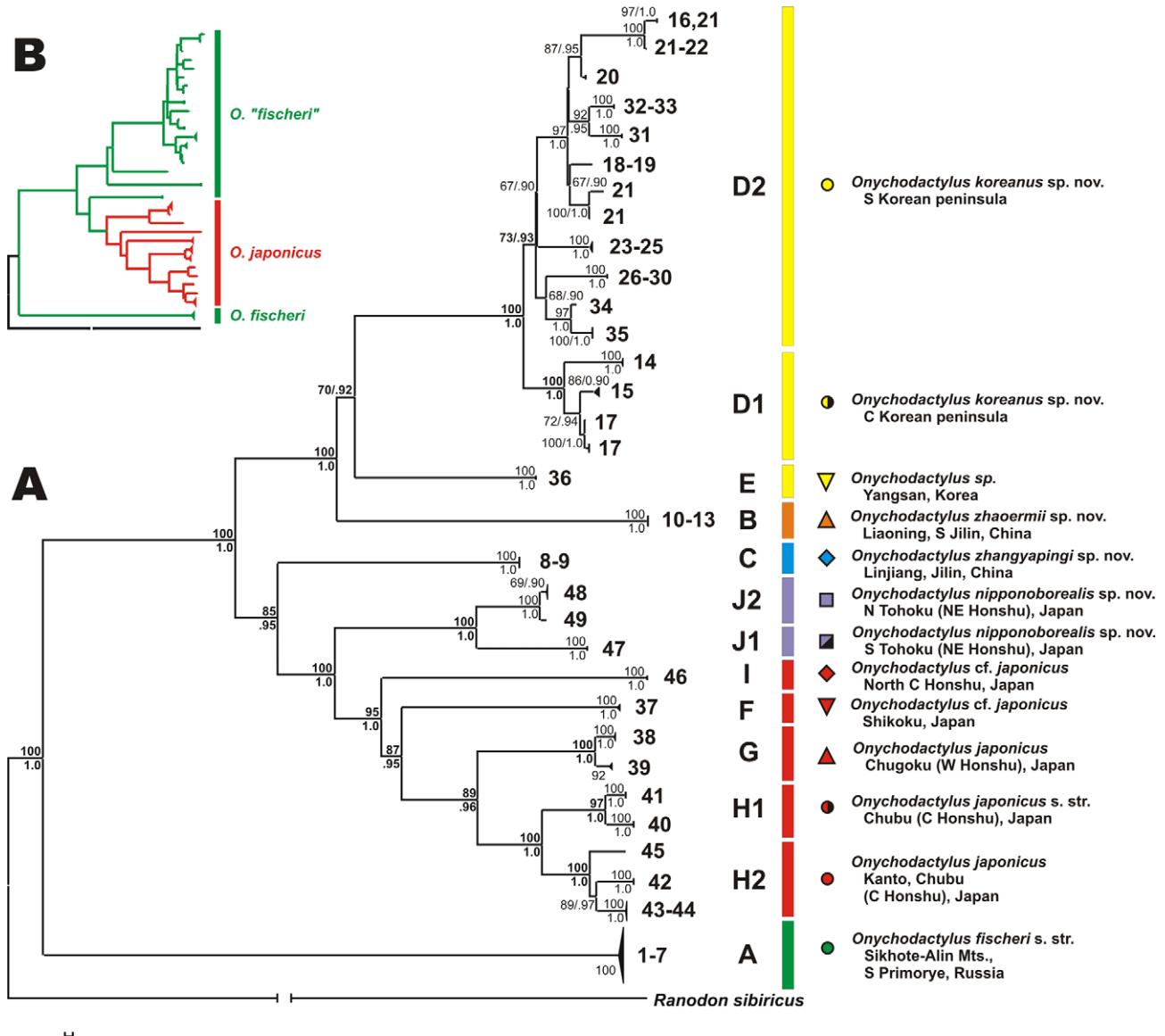


FIGURE 3. Maximum likelihood (ML) phylogenetic tree based on partial 16s rRNA, COI and CytB sequences of *Onychodactylus* species, *Ranodon sibiricus* used as an outgroup taxon (A)—Bayesian posterior probabilities (BPP) are given, and after the / sign ML bootstrap support (1000 replicates, only values higher than 70% are shown). Nodes with highest support values (BS = 100%; BPP = 1.0) are marked with an asterisk; “-” sign indicates low support. Numbers right from the branches are locality numbers as in Table 1. Clade codes are given. Color of vertical bars and icons correspond to color of species range and localities in FIGURE 1. For locality numbers, refer to FIGURE 1 and Tab. 1. (B)—Schematic representation of traditional views on taxonomy of the genus *Onychodactylus* are shown: lineages traditionally attributed to *O. fischeri* are marked with green, those of *O. japonicus*—with red.

Morphological differentiation within *Onychodactylus*

Morphometric variation

Measurement data for 14 morphometric characters in studied species of *Onychodactylus* are shown in Table 4. Comparisons of SVL measurements and percentage ratios of each character dimension to SVL are given in Table 5. Among the six samples examined, mean SVL did not vary significantly, ranging from 41.8 to 84.2 mm. The

population of *Onychodactylus* from Liaoning, China, had largest mean value of SVL in females and on average, which was significantly ($P<0.05$) larger than that in all other samples except the population of *O. fischeri* from Russia. The largest absolute SVL value in males was recorded in the sample of *Onychodactylus* from Jilin (SVL = 84.2 mm, female). Largest mean value of SVL in males was recorded in the sample of *O. japonicus* from Tohoku, northeast Japan. The sample of *O. fischeri* from Korea had significantly ($P<0.05$) smaller SVL in females, and the population of *O. japonicus* from central Honshu had significantly smaller males than in all other samples except the population of *O. fischeri* from Korea. All characters ratios proved to be informative in discriminating studied samples. IO/SVL showed the largest number of significant differences, followed by HW/SVL, EL/SVL, FLL/SVL, HLL/SVL and GA/SVL. Relatively poor impact of TL/SVL in discriminating samples examined is probably explained by the presence of specimens with regenerated tails, which we failed to distinguish from normally developed tails. Based on the analysis of examined character ratios, all six populations clearly form separated groups with regard to males and females, with many characters significantly separating them from each other. Though clearly distinct morphologically, samples of Russian *O. fischeri* and *O. japonicus* show less differences between sexes than any other clade.

Sexual variation

Many of the morphometric characters studied proved to be sexually dimorphic. In all studied populations males are characterized by significantly longer tails, and higher TL/SVL ratios ($P<0.005$). Sexual differences in character ratios in studied species of *Onychodactylus* are summarized in Table 5. In all studied samples we found significant differences ($P<0.05$) between males and females in the relative lengths of tails (TL/SVL): males always tend to have longer tails; usually their tails are ca. 2 cm longer than those of females. In the sample of *O. fischeri* from Russia sexes differed significantly ($P<0.05$) in GA/SVL and FLL/SVL. In the sample of *O. japonicus* from Tohoku sexes differed significantly ($P<0.05$) in GA/SVL, as well as in the sample of *O. japonicus* from central Honshu ($P<0.05$) in HL/SVL. In the sample of *O. fischeri* from Korea, males and females differed significantly in all characters examined, except ON/SVL, IO/SVL, and CW/SVL. These sexually dimorphic characters were often larger in males than in females, and this relationship was reversed only for ON/SVL. In the sample of Chinese *Onychodactylus* from Liaoning comparison of sexes was not possible due to the small number of males in the analysis; though males tend to have longer tails and shorter bodies (GA in females is larger than in males). In the sample of Chinese *Onychodactylus* from Jilin males tend to have significantly longer heads than females. We did not observe sexual dimorphism in most of meristic characters. However, we found sexual dimorphism in TVN and CGN with males having less trunk vertebrae and costal grooves compared to females in the sample of Korean *Onychodactylus* ($P<0.05$) and Chinese population from Liaoning (NS), but these differences were statistically non significant in the latter case possibly due to the small number of males in the analysis. In the sample of Russian *O. fischeri* sexes significantly ($P<0.05$) differed in VTN, with males having more vomerine teeth than females.

Variation of costal grooves and trunk vertebrae numbers

For meristic characters, interpopulation differences were largest in TVN and CGN. Distribution of trunk vertebrae number and costal grooves count in studied *Onychodactylus* samples are shown in Table 6. All examined samples differed very clearly in the mean number of trunk vertebrae in both males and females ($P<0.001$), this seems to be one of the most important characters to distinguish between the species identified in this paper. Our analysis confirms the revealed correlation (Litvinchuk and Borkin, 2003) between TVN and CGN in *Onychodactylus*, where $TVN \approx (CGN+5)$. The only exceptions are found in *O. japonicus* males of samples from central Honshu and Tohoku, where in a few cases males had less TVN than the expected number; this is explained by variation of the TVN in the anterior part of the body. In studied samples of *Onychodactylus* TVN varied from 16 to 22, with highest number found in *O. fischeri* from Russia (modal TVN = 21), and smallest number in *O. japonicus* from central Honshu (modal TVN = 17). In all studied populations of *Onychodactylus* TVN varied within the sample within 2-4 trunk vertebrae. Though TVN minimum and maximum values are overlapping, the six examined populations are well distinguished from each other with TVN modals decreasing gradually, from 21 in *O. fischeri* from Russia to 17 in central Honshu *O. japonicus*. Males tend to have smaller TVN than females with minimum TVN values found in males and maximum in females, though only in *O. fischeri* from the Korean sample the difference between the sexes was significant ($P<0.05$), probably due to smaller variation of this character within the sexes in this sample. Variation in CGN well reflects the pattern observed in TVN (Tab. 6); all examined samples differed clearly in the mean number of costal grooves in both males and females ($P<0.05$). CGN increases gradually from 11 to 16 with minimum values found in *O. japonicus* from central Honshu and maximum values in *O. fischeri* from

Russia. Differences in TVN and CGN values are not always significant in comparisons of Japanese and Chinese samples both for males and females, comparisons of females from North Japan and Korea and in females from Korea and Jilin, China. Also no significant differences were found between TVN and CGN numbers in Jilin and Liaoning males due to the small size of the latter sample. Significant sexual dimorphism in CGN was found in the Korean population of *O. fischeri* with males tending to have fewer costal grooves than females.

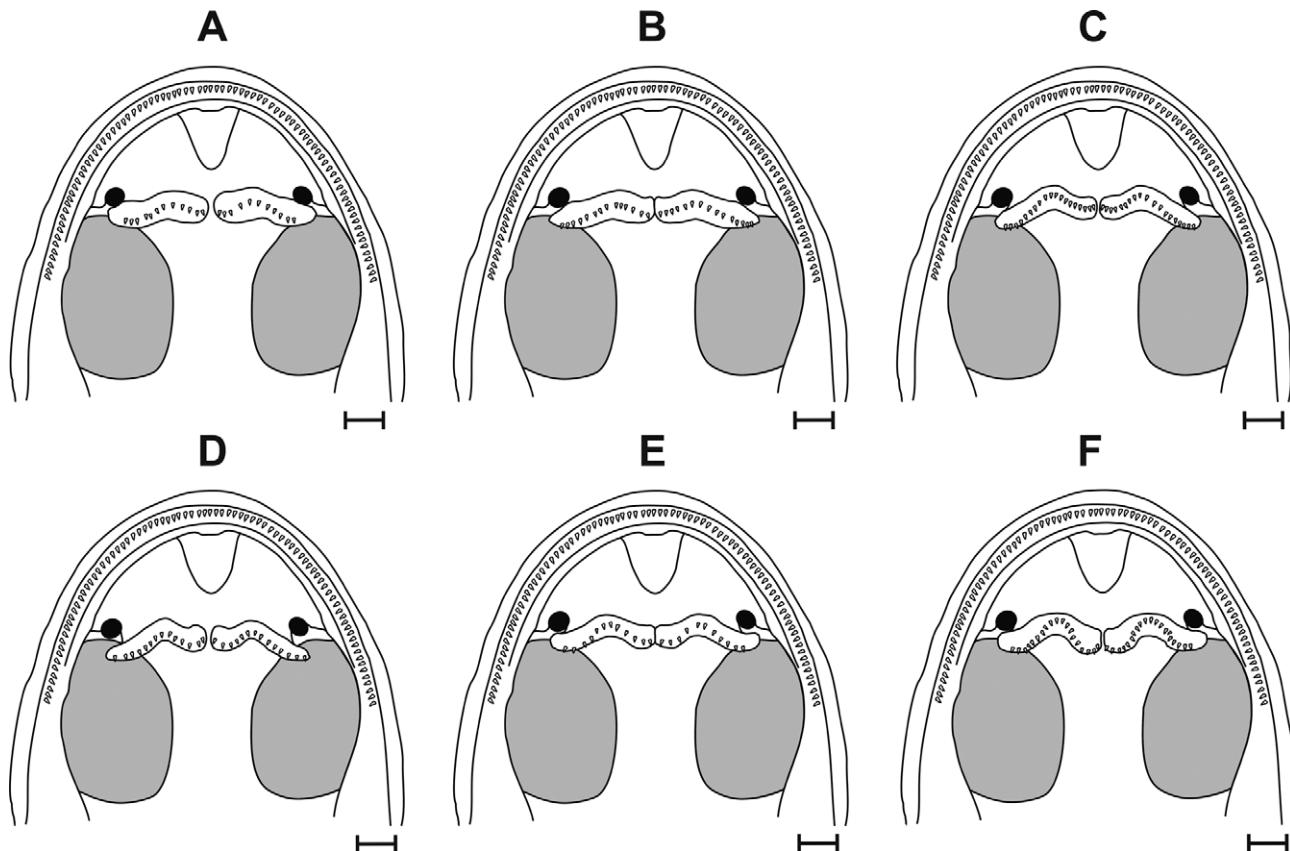


FIGURE 4. Schematic drawing of palatal view of open mouth in 5 *Onychodactylus* species showing variation in shape and number of vomerine tooth series. (A)—*O. fischeri* (Russia, Primorye); (B)—*O. zhangyapingi* (China, Jilin); (C)—*O. koreanus* (S Korea, Gangwon-do); (D)—*O. zhaoermii* (China, Liaoning); (E)—*O. japonicus* (Japan, Fukushima); (F)—*O. nipponoborealis* (Japan, Aomori). Scale bars equal to 1 mm.

Shape and teeth number variation in vomerine tooth series

We observed a significant variation of VTN and shape of vomerine tooth series among populations examined. Variation in the vomerine teeth number in studied *Onychodactylus* species is shown in Table 7. VTN is variable within the samples, number of vomerine teeth can be different in left and right tooth series, though these differences are never significant and are probably subject to stochastic variation. Though males in general tend to have higher VTN, sexual differences are significant only in the population of Russian *O. fischeri*. Intrapopulational differences in VTN proved to be significantly ($P<0.005$) informative, allowing us to distinguish all samples from each other except in comparisons of samples with lowest VTN (Russian *O. fischeri* with *O. japonicus* from central Honshu; both for males and females) and highest VTN values (Korean *O. fischeri* with *O. japonicus* from Tohoku; both for males and females; *O. fischeri* from Korea and Jilin, China, for both sexes; *O. fischeri* from Korea and Liaoning, China, for males). Shape of vomerine tooth series (VTS) also proved to be informative in distinguishing the studied samples. In general, six shape types of vomerine tooth series can be distinguished. The shape of VTS which is regarded as a diagnostic feature for many Hynobiidae species (Sato, 1943), did not differ sexually in adults; this result agrees well with data on other hynobiids (i.e. Nishikawa *et al.*, 2007). Schematic drawings of open mouths of five examined *Onychodactylus* populations showing variations in shape of vomerine tooth series are shown in Fig. 4. *O. fischeri* from Russia is characterized by having relatively short VTS, with noticeable gap between them, outer branch being slightly curved, usually of same length as inner branch, usually protruding laterally not beyond the level of the middle of the internal nares (Fig. 4, A).

TABLE 4. Mean of 14 morphometric characters (in mm), followed by ranges in parenthesis, in mm) for *Onychodactylus japonicus*, *O. fischeri*, and the type series of *O. koreanus*, *O. zhaoermii*, *O. zhangyapingi* and *O. nipponoborealis*. For character abbreviations, refer to Appendix 2 and Fig. 2 (♂ - Adult male; ♀ - Adult female; juv. - Juvenile).

Species	N	SVL	TL	GA	FLL	HLL	HL
<i>O. fischeri</i> s. str. (Primorye, Russia)							
♂	35	70.1±3.7 (60.8–80.0)	84.6±8.4 (72.2–103.6)	38.1±3.3 (30.2–46.5)	16.7±1.5 (14.4–19.4)	20.3±2.3 (16.5–28.0)	14.4±0.8 (11.5–17.3)
♀	35	66.8±5.8 (51.0–83.0)	70.0±7.9 (55.4–96.5)	36.2±5.5 (26.7–53.0)	17.0±1.9 (13.0–26.5)	19.5±1.8 (14.4–27.0)	14.7±1.3 (11.1–19.6)
Sum	70	68.4±4.9 (51.0–83.0)	76.8±8.2 (55.4–103.6)	37.1±4.2 (26.7–53.0)	16.9±1.6 (13.0–26.5)	19.9±2.0 (14.4–28.0)	14.5±1.0 (11.1–19.6)
<i>O. japonicus</i> s. str. (C Honshu, Japan)							
♂	33	62.3±5.7 (52.0–75.3)	81.2±7.7 (68.5–99.1)	34.5±3.1 (29.1–42.2)	18.9±1.6 (15.9–23.0)	20.8±1.9 (17.6–25.4)	14.3±0.9 (12.2–15.7)
♀	33	65.3±5.0 (58.2–77.3)	67.0±5.0 (59.7–79.2)	34.2±2.4 (30.5–40.5)	18.3±1.1 (16.4–20.7)	21.1±1.1 (19.0–23.2)	14.6±1.1 (13.1–17.3)
Sum	66	63.8±5.5 (52.0–77.3)	74.1±9.6 (59.7–99.1)	34.4±2.8 (29.1–42.2)	18.6±1.4 (15.9–23.0)	21.0±1.5 (17.6–25.4)	14.5±1.0 (12.2–17.3)
<i>O. koreanus</i> (Korea)							
♂	22	66.5±7.7 (36.0–77.9)	85.4±10.0 (51.2–110.3)	34.8±4.1 (24.0–41.5)	16.9±2.1 (12.2–20.1)	20.0±2.1 (14.7–23.3)	15.4±1.1 (12.3–16.6)
♀	14	58.2±8.8 (41.8–78.6)	61.1±11.0 (42.1–90.6)	30.0±5.5 (21.4–42.8)	14.8±3.0 (11.6–20.7)	17.5±1.8 (13.2–24.2)	13.8±1.1 (11.2–16.7)
juv.	13	45.0±1.4 (43.2–46.7)	45.9±1.7 (43.6–47.6)	23.1±0.3 (22.6–23.5)	12.2±0.7 (11.3–13.1)	13.8±1.1 (12.8–15.0)	10.7±0.5 (10.2–11.1)
Sum	49	60.8±8.0 (36.0–78.6)	71.9±11.6 (42.1–110.3)	31.6±5.5 (21.4–42.8)	15.5±2.8 (11.3–20.7)	18.3±2.2 (12.8–24.2)	14.2±1.2 (10.2–16.7)
<i>O. zhaoermii</i> (Liaoning, China)							
♂	2	65.3±4.0 (62.5–68.1)	89.5±9.7 (82.5–96.3)	34.5±1.5 (33.5–35.6)	18.4±1.2 (17.6–19.3)	22.6±2.2 (21.0–24.2)	15.3±0.8 (14.7–15.9)
♀	6	76.9±3.3 (71.9–81.2)	82.9±7.9 (71.4–94.9)	43.0±2.4 (39.2–45.4)	21.4±0.7 (20.5–22.4)	25.3±0.7 (24.3–26.4)	16.3±0.7 (14.9–16.8)
Sum	8	74.0±6.3 (62.5–81.2)	84.5±8.2 (71.4–96.3)	40.9±4.5 (33.5–45.4)	20.6±1.6 (17.6–22.4)	24.6±1.6 (21.0–26.4)	16.1±0.9 (14.7–16.8)
<i>O. zhangyapingi</i> (Jilin, China)							
♂	6	64.6±2.2 (61.4–67.6)	88.2±8.1 (76.9–96.4)	34.9±1.8 (32.1–36.9)	17.0±0.3 (16.5–17.4)	19.9±1.2 (18.2–21.5)	14.8±0.4 (14.4–15.3)
♀	10	73.5±6.2 (61.0–84.2)	82.7±7.2 (69.1–95.2)	41.9±4.6 (32.3–48.3)	18.5±1.2 (16.7–20.0)	22.3±1.1 (20.3–23.7)	15.1±1.0 (14.0–16.8)
Sum	16	70.0±6.6 (61.0–84.2)	84.9±7.8 (69.1–96.4)	39.1±5.1 (32.1–48.3)	17.9±1.2 (16.7–20.0)	21.3±1.6 (18.2–23.7)	15.0±0.8 (14.0–16.8)
<i>O. nipponoborealis</i> (Tohoku, Japan)							
♂	7	71.3±3.6 (66.4–75.9)	84.1±9.5 (65.5–95.5)	40.0±2.1 (37.7–43.2)	19.8±0.6 (18.9–20.5)	23.1±1.0 (21.9–24.4)	15.6±0.3 (15.3–16.2)
♀	7	67.8±5.0 (59.5–72.2)	73.8±6.1 (65.0–82.4)	38.7±3.5 (32.7–42.3)	19.2±1.1 (17.5–20.8)	22.7±1.0 (20.8–23.7)	15.4±0.5 (14.6–16.2)
Sum	14	69.6±4.5 (59.5–75.9)	79.0±9.4 (65.0–95.5)	39.3±2.9 (32.65–43.2)	19.5±0.9 (17.5–20.8)	22.9±1.0 (20.8–24.4)	15.5±0.4 (14.6–16.2)
SUM	223						

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TABLE 4. (Continued)

HW	EL	IN	ON	IO	CW	OR	IC
9.6±1.2 (7.0–11.5)	3.6±0.3 (3.0–4.3)	4.2±0.3 (3.0–5.0)	2.5±0.4 (1.9–3.2)	3.7±0.3 (2.9–4.5)	7.7±1.0 (5.8–11.0)	5.3±0.2 (4.56–6.2)	5.9±0.7 (4.8–7.2)
9.5±1.5 (7.3–12.7)	3.4±0.4 (2.6–5.1)	4.4±0.4 (3.3–6.3)	2.6±0.4 (1.6–3.9)	3.8±0.2 (2.1–5.1)	7.3±1.0 (4.8–9.4)	4.8±0.4 (3.5–6.9)	6.1±0.4 (4.16–8.2)
9.5±1.4 (7.0–12.7)	3.5±0.3 (2.6–5.1)	4.3±0.4 (3.0–6.3)	2.6±0.4 (1.6–3.9)	3.8±0.3 (2.1–5.1)	7.5±1.1 (4.8–11.0)	5.0±0.3 (3.5–6.9)	6.0±0.5 (4.2–8.2)
8.6±0.6 (7.4–9.7)	3.4±0.3 (2.8–4.1)	4.2±0.3 (3.6–4.6)	2.6±0.2 (2.2–3.0)	3.0±0.3 (2.5–3.6)	6.9±0.5 (5.9–7.5)	4.6±0.3 (3.9–4.9)	5.6±0.3 (4.8–6.0)
8.4±0.6 (7.5–9.9)	3.2±0.2 (2.9–3.6)	4.5±0.2 (4.0–4.9)	2.3±0.1 (2.0–2.6)	3.1±0.2 (2.8–3.4)	6.2±0.3 (5.6–6.8)	4.5±0.2 (4.1–4.9)	5.7±0.3 (5.7–6.1)
8.5±0.6 (7.4–9.9)	3.3±0.2 (2.8–4.1)	4.4±0.3 (3.6–4.9)	2.4±0.2 (2.0–3.0)	3.0±0.2 (2.5–3.6)	6.6±0.5 (5.6–7.5)	4.5±0.2 (3.9–4.9)	5.6±0.3 (4.8–6.1)
10.6±0.6 (9.1–11.3)	4.8±0.2 (4.0–5.4)	5.2±0.3 (4.6–5.6)	2.3±0.3 (1.9–2.9)	3.5±0.2 (3.2–3.9)	7.7±1.0 (5.4–10.8)	4.9±0.4 (4.1–5.4)	5.±90.4 (5.4–7.0)
9.9±1.9 (7.5–11.8)	4.3±0.3 (3.3–5.2)	5.0±0.7 (4.0–6.2)	2.4±0.3 (2.0–3.0)	3.5±0.3 (3.1–3.9)	7.2±1.2 (4.8–10.9)	4.7±0.5 (3.7–5.6)	5.4±0.7 (4.6–6.5)
8.2±0.1 (7.9–8.2)	3.1±0.1 (3.0–3.2)	3.9±0.1 (3.7–4.2)	1.7±0.1 (1.5–1.8)	3.2±0.1 (3.1–3.5)	5.0±0.2 (4.7–5.2)	3.6±0.2 (3.4–3.8)	5.1±0.2 (4.9–5.4)
10.0±1.4 (7.5–11.8)	4.4±0.4 (3.0–5.4)	4.9±0.6 (3.7–6.2)	2.2±0.4 (1.5–3.0)	3.5±0.2 (3.1–3.9)	7.2±1.1 (4.7–10.9)	4.7±0.4 (3.4–5.6)	5.6±0.6 (4.6–7.0)
10.0±0.2 (9.8–10.1)	3.8±0.3 (3.6–4.0)	4.6±0.2 (4.4–4.7)	2.2±0.0 (2.2–2.3)	3.7±0.3 (3.5–4.0)	9.7±0.5 (9.3–10.0)	4.6±0.2 (4.5–4.8)	6.2±0.0 (6.2–6.2)
11.2±0.4 (10.5–11.6)	4.6±0.3 (4.1–5.0)	5.1±0.4 (4.6–5.7)	2.5±0.2 (2.3–2.8)	4.0±0.4 (3.4–4.4)	10.4±2.0 (8.7–14.0)	5.1±0.2 (4.8–5.4)	6.6±0.3 (6.2–7.0)
10.9±0.7 (9.8–11.6)	4.4±0.5 (3.6–5.0)	4.9±0.4 (4.4–5.7)	2.5±0.2 (2.2–2.8)	2.9±0.3 (3.4–4.4)	10.2±1.7 (8.7–14.0)	5.0±0.3 (4.5–5.4)	6.5±0.3 (6.2–7.0)
10.0±0.3 (9.0–9.8)	4.0±0.4 (3.5–4.4)	4.2±0.4 (3.8–5.0)	2.2±0.2 (1.8–2.5)	3.3±0.3 (3.0–3.7)	8.9±0.8 (7.9–10.0)	4.8±0.2 (4.5–5.0)	5.7±0.3 (5.2–6.1)
10.5±0.8 (9.4–11.9)	4.2±0.4 (3.7–4.8)	4.6±0.3 (4.0–4.9)	2.3±0.2 (2.0–2.5)	3.7±0.3 (3.5–4.2)	9.0±1.2 (7.1–11.1)	5.3±0.5 (4.4–6.0)	6.4±0.4 (5.6–7.1)
10.2±0.8 (9.0–11.9)	4.1±0.4 (3.5–4.8)	4.4±0.4 (3.8–5.0)	2.2±0.2 (1.8–2.5)	3.6±0.4 (3.0–4.2)	9.0±1.0 (7.1–11.1)	5.1±0.5 (4.4–6.0)	6.2±0.5 (5.2–7.1)
11.9±0.7 (10.9–13.0)	4.3±0.3 (3.9–4.8)	5.4±0.3 (5.1–5.9)	2.2±0.4 (1.7–2.7)	5.7±0.3 (4.7–6.5)	7.8±0.7 (6.9–8.7)	4.6±0.2 (4.3–4.8)	6.2±0.2 (5.8–6.5)
11.7±0.9 (10.8–12.9)	4.0±0.2 (3.7–4.3)	5.1±0.3 (4.7–5.6)	2.3±0.4 (1.7–3.0)	5.5±0.4 (4.2–6.1)	7.2±0.4 (6.6–7.7)	4.7±0.4 (4.1–5.4)	5.6±0.3 (5.2–6.2)
11.8±0.7 (10.8–13.0)	4.1±0.3 (3.7–4.8)	5.3±0.3 (4.7–5.9)	2.2±0.4 (1.7–3.0)	5.6±0.3 (4.2–6.5)	7.5±0.6 (6.6–8.7)	4.6±0.3 (4.1–5.4)	5.9±0.4 (5.2–6.5)

O. fischeri from Jilin, China has very straight “^” formed VTS, with no noticeable gap between them, and outer branch of VTS being slightly longer than the inner branch and usually reaching the level of outer edge of the internal nares (Fig. 4, B). *O. fischeri* from Korea is distinguished by having longer and deeper VTS, with both inner and outer branches always being slightly curved, usually with a little gap between the VTS (Fig. 4, C). In this group, the outer VTS branch is longer, and the inner ends of the VTS are situated more anteriorly than the outer ends. *O. fischeri* from Liaoning, China, have a VTS shape similar to that of the Korean sample with the inner branches being much more strongly curved and a gap between the series which is wider and always visible (Fig. 4, D). In *O. japonicus* from central Honshu the VTS are usually relatively deep compared with those of *O. fischeri* with no gap between them and both branches are slightly curved (Fig. 4, E). However, in *O. japonicus* from Tohoku the VTS are the deepest and highest compared with any other sample, both VTS branches are greatly curved usually with a small gap between them (Fig. 4, F). In this form the inner ends of the VTS are situated on the same level or even sometimes more posteriorly than the outer ends.

Color variation.

Male-female comparisons for all studied samples failed to detect sexual dimorphism in any of the 23 coloration characteristics (Fischer's exact test, $P>0.05$). Analysis of color characters among samples examined revealed the presence of several clearly different coloration types, in general corresponding well to the selected geographic populations of *Onychodactylus*. Most typical color variants are shown in Fig. 5. All four lineages within *O. fischeri* (sensu lato) are clearly distinguished by coloration. Russian *O. fischeri* (Fig. 5, A) specimens differ in light ground colors of the back, head, tail, and trunk (brownish, ochre, golden), absences of small light spots on dorsal and lateral surfaces of the back and head, presence of a very indistinct light dorsal band with unclear borders in juveniles which can completely disappear in adults, but sometimes is noticeable. The dorsal side of the body is covered with numerous black variegations, blotches and spots and mottling of different sizes; the lateral sides of the trunk are lighter. The Chinese form of *O. fischeri* from Jilin (Fig. 5, B) has a darker coloration; the ground color of the back and lateral sides of the body is black, brownish or gray-brown. The light dorsal band is always absent. Lateral and dorsal surfaces of head, trunk and tail are covered with numerous light (pinkish, yellowish or ochre) vermiculations and confluent lines, forming a dense reticulated pattern, and large dark or light blotches are absent. The Liaoning form of *O. fischeri* (China) shows a somewhat similar pattern with numerous bright (orange, copper) blotches of irregular shape forming a dense reticulated pattern (Fig. 5, C). This pattern however is clearly distinguishable from the pattern typical for the Jilin population since the light blotches are much more numerous which creates an overall effect of light coloration, whereas the Jilin *O. fischeri* are dark. The Korean form of *O. fischeri* (Fig. 5, D) is characterized by extremely contrasting coloration in juveniles with the ground color of dorsal and lateral surfaces of trunk and tail being almost black, or dark-brown with numerous round or oval shaped small bright (yellow, golden, orange) spots. Occasionally, the spots form small ocelli with tiny dark spots in the center. This juvenile coloration is often retained in adults, and sometimes (presumably in older specimens) these small yellow spots fade away and the animal acquires a darker coloration with a dark-brown ground color and indistinct lighter mottling on the dorsal surfaces of head, trunk and tail. *O. japonicus* showed the highest variation in color characters. Generally in this species several color forms can be distinguished, grouping into two main clusters—*O. japonicus* from western Japan (western Honshu and Shikoku) and *O. japonicus* from Northeastern Honshu (Sato, 1943). We did not analyze samples of western *O. japonicus* for morphology, although the specimens examined allow us to distinguish a clearly different coloration type (Fig. 5, F, Ishizuchi-San, Shikoku, 4 males, 2 females and literature data, morphological data not included in the analysis). These specimens are very dark with an almost black or dark-brown ground color of the dorsal and lateral sides of head, trunk and body, and with a relatively dark belly coloration. On the dorsal surfaces, a light dorsal band has distinct borders but it is interrupted and forms numerous contrasting (almost red or bright-orange) blotches, stripes and confluent spots. On the dorsolateral sides of the head, the light dorsal band usually forms a bifurcation. Animals from Tohoku (Fig. 5, E) and central Honshu (Fig. 5, G) are characterized by having much lighter coloration and the presence of a clear, uninterrupted dorsal band with an almost straight (normal for central Honshu) or meandering borders (normal for Tohoku, also found in central Honshu). In many specimens from Tohoku (Fig. 5, E) the light dorsal band is indistinct, has no clear borders and the light ground color of dorsal surfaces of head, trunk and tail are covered with numerous indistinct dark blotches and mottling. The same pattern is found, however, in the central Honshu sample, assuming dorsal coloration in *O. japonicus* is likely subject to an animals' age or environmental characteristics. In general, coloration does not allow us to distinguish effectively between central Honshu and Tohoku samples effectively.

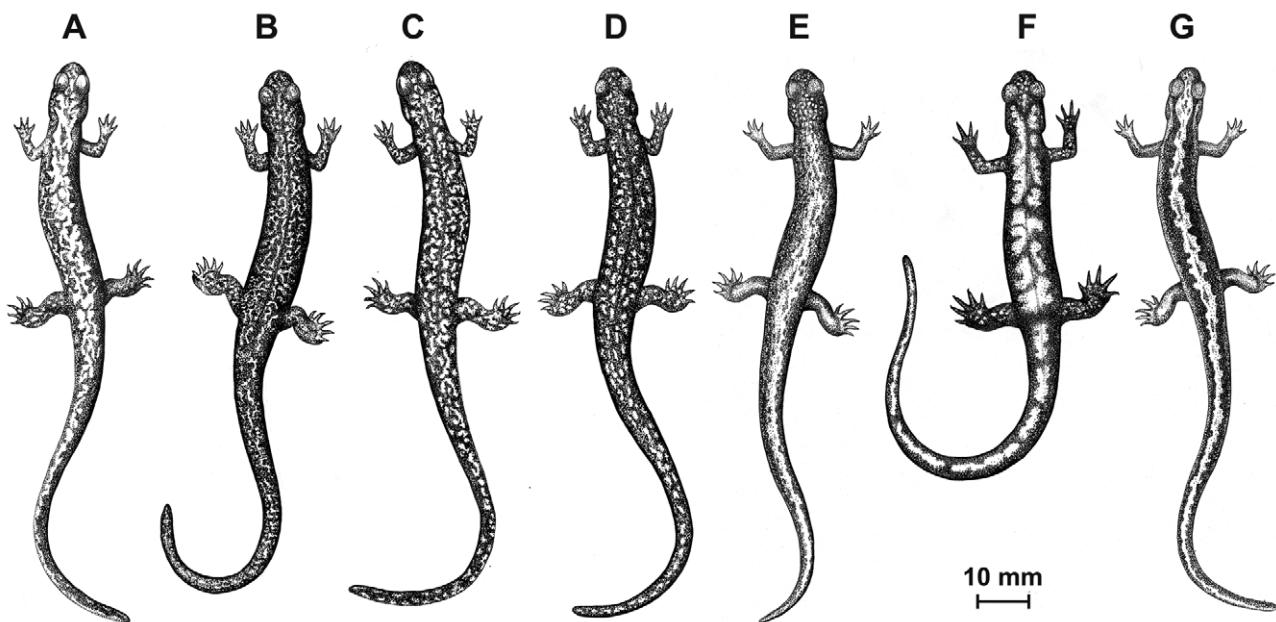


FIGURE 5. Most typical color variants in males of 5 *Onychodactylus* species. (A)—*O. fischeri* (Russia, Primorye); (B)—*O. zhangyapingi* (China, Jilin); (C)—*O. zhaoermii* (China, Liaoning); (D)—*O. koreanus* (Korea, Gangwon-do); (E)—*O. nipponoborealis* (Japan, Aomori); (F)—*O. cf. japonicus* (Japan, Shikoku); (G)—*O. japonicus* s. str. (Japan, Hakone).

Principal Component Analysis

We found a significant correlation between SVL and GA ($P<0.005$), and TVN and CGN ($P<0.0001$). For each of these characteristic sets, we omitted the variable with the highest variation coefficient in the multivariate analysis. Multivariate analysis of coloration characters was based on arcsine-corrected frequencies of color character states for each sample. PCA using 35 characters resulted in the dominant eigenvector indicating positive values of similar magnitudes for all characters examined. Two-dimensional plots of the first two and the first and third factors of PCA are shown in Fig. 6 for males (Fig. 6, A, B) and females (Fig. 6, C, D).

Two-dimensional plots of the first two principle components (PRIN1 and PRIN2; Fig. 6, A) for males completely discriminated the following three groups: (I) *O. fischeri* from Liaoning Province, China, (II) *O. japonicus* from central Honshu and (III) *O. fischeri* from Russia. Male *O. japonicus* from Tohoku and Korea were also differentiated from each other in general, though they partially overlapped. PCA analysis did not sufficiently distinguish samples of males from Korea and Jilin Province, China. Plots of the third variable against the first variable (PRIN1 and PRIN3; Fig. 6, B) for males resulted in complete separation of Russian *O. fischeri* and Liaoning *O. fischeri* from all other populations, whereas scores for the rest of the samples largely overlapped. However, compared with the plots of the first two principal components, the population of Liaoning *O. fischeri* was not as clearly separated from *O. japonicus* from Tohoku, with their ranges partially overlapping in the third and first axis.

Two-dimensional plots of the first two principle components (PRIN1 and PRIN2; Fig. 6, C) for females allowed us to sufficiently discriminate the following samples: (I) *O. fischeri* from Russia, (II) *O. fischeri* from Korea, (III) Chinese *O. fischeri* from Jilin Province and (IV) north-Japanese *O. japonicus* from Tohoku. There were no significant differences found between females of *O. japonicus* from central Honshu and Chinese *O. fischeri* from Liaoning Province, however these two samples formed a group significantly distant from all other *Onychodactylus*. Plots of the third variable against the first variable for females (PRIN1 and PRIN2; Fig. 6, D) resulted in complete discrimination of *O. fischeri* from Liaoning Province and *O. japonicus* from central Honshu.

In summary, both in character ratios, meristic and coloration characters, all six examined geographic lineages form clearly separated morphological groups, with many characters significantly separating them from each other. The paralectotypes of *Salamandra unguiculata* Temminck & Schlegel, 1838 (RMNH-2292: 4 adults, 2 males and 2 females) in all analyses were not significantly different from the central Honshu group of *O. japonicus* (see Fig. 6), which confirms the assumption of Iizuka *et al.* (2011) (see discussion in the taxonomic account on *O. japonicus* below).

TABLE 5. Comparisons of SVL measurements (means \pm SD, followed by ranges in parenthesis, in mm) and percentage ratios of each character dimension to SVL (medians, followed by ranges in parenthesis, in %) in *Onychodactylus japonicus*, *O. fischeri*, and the type series of *O. koreanus*, *O. zhaoermii*, *O. zhangyapingi* and *O. nipponoborealis*. For character abbreviations, refer to Appendix 2 and Fig. 2 (δ —Adult male; φ —Adult female; juv.—Juvenile).

Species	N	SVL	TL/SVL	GA/SVL	FLL/SVL	HLL/SVL	HL/SVL	HW/SVL
<i>O. fischeri</i> s. str. (Sikhote-Alin Mts.)								
δ	35	70.1 \pm 3.7 (60.8–80.0)	120.7 (109–132)	61.0 (48–75)	26.7 (23–31)	32.6 (27–45)	23.0 (18–28)	15.4 (11–18)
φ	35	66.8 \pm 5.8 (51.0–83.0)	105.1* (93–121)	57.9* (43–85)	27.3* (21–43)	31.2 (23–43)	23.5 (18–31)	15.2 (12–20)
Sum	70	68.4 \pm 4.9 (51.0–83.0)	112.3 (93–132)	59.4 (43–85)	27.0 (21–43)	31.8 (23–45)	23.3 (18–31)	15.3 (11–20)
<i>O. japonicus</i> s. str. (C Honshu, Japan)								
δ	33	62.3 \pm 5.7 (52.0–75.3)	130.4 (118–147)	55.4 (47–68)	30.3 (26–37)	33.4 (28–41)	22.9 (20–25)	13.8 (12–15)
φ	33	65.3 \pm 5.0 (58.2–77.3)	102.6* (101–103)	54.7 (49–65)	29.3 (26–33)	33.8 (30–37)	23.5* (21–28)	13.4 (12–16)
Sum	66	63.8 \pm 5.5 (52.0–77.3)	116.5 (101–147)	55.0 (47–68)	29.8 (26–37)	33.6 (28–41)	23.2 (20–28)	13.6 (12–16)
<i>O. koreanus</i> (Korea)								
δ	22	66.5 \pm 7.7 (36.0–77.9)	128.7 (118–154)	55.7 (38–66)	27.1 (20–33)	32.0 (24–38)	24.6 (20–27)	16.9 (15–18)
φ	14	58.2 \pm 8.8* (41.8–78.6)	104.0* (93–115)	48.1* (34–68)	23.7* (18–33)	28.1* (21–39)	22.1* (18–27)	15.8* (12–19)
juv.	13	45.0 \pm 1.4 (43.2–46.7)	102.0 (101–103)	37.4 (36–38)	19.5 (18–21)	22.1 (20–24)	17.1 (16–18)	13.1 (13–13)
Sum	49	60.8 \pm 8.0 (36.0–78.6)	117.0 (93–154)	50.6 (34–68)	24.8 (18–33)	29.3 (20–39)	22.7 (16–27)	16.0 (12–19)
<i>O. zhaoermii</i> (Liaoning, China)								
δ	2	65.3 \pm 4.0 (62.5–68.1)	136.8 (132–141)	52.9 (52–54)	28.2 (28–28)	34.6 (34–35)	23.4 (23–24)	15.3 (15–16)
φ	6	76.9 \pm 3.3 (71.9–81.2)	107.5* (99–117)	55.9* (55–57)	27.8 (27–29)	34.9 (32–35)	21.3 (19–23)	14.5 (14–15)
Sum	8	74.0 \pm 6.3 (62.581.2)	114.9 (99–141)	55.2 (52–57)	27.9 (27–29)	33.3 (32–35)	21.8 (19–24)	14.7 (14–16)
<i>O. zhangyapingi</i> (Jilin, China)								
δ	6	64.6 \pm 2.2 (61.4–67.6)	136.6 (118–146)	54.0 (52–59)	26.4 (26–28)	30.8 (28–32)	23.0 (21–24)	14.9 (14–16)
φ	10	73.5 \pm 6.2 (61.0–84.2)	110.9* (96–123)	56.5 (53–60)	25.5 (23–28)	30.6 (28–33)	20.8* (19–23)	14.5 (13–16)
Sum	16	69.9 \pm 6.6 (61.0–84.2)	120.5 (96–146)	55.6 (52–60)	25.8 (23–28)	30.7 (28–33)	21.6 (19–24)	14.6 (13–16)
<i>O. nipponoborealis</i> (Tohoku, Japan)								
δ	7	71.3 \pm 3.6 (66.4–75.9)	118.1 (99–136)	64.0 (60–70)	31.7 (31–32)	37.0 (35–39)	25.1 (25–26)	19.1 (17–21)
φ	7	67.8 \pm 5.0 (59.5–72.2)	109.0* (97–118)	62.0* (53–68)	31.1 (29–33)	36.6 (34–38)	24.7 (23–26)	18.7 (17–21)
Sum	14	69.6 \pm 4.5 (59.5–75.9)	113.5 (97–136)	63.0 (53–70)	31.4 (29–33)	36.8 (34–39)	24.9 (23–26)	18.9 (17–21)
SUM	223							

Note:

* - significantly different from the conspecific male.

TABLE 6. Distribution of trunk vertebrae number and costal grooves count in studied *Onychodactylus* species, including *Onychodactylus japonicus*, *O. fischeri*, and the type series of *O. koreanus*, *O. zhaoermii*, *O. zhangyapingi* and *O. nipponoborealis* (♂—Adult male; ♀—Adult female).

Species	Sex	N	Trunk vertebrae (%)						Costal grooves (%)						
			16	17	18	19	20	21	22	11	12	13	14	15	16
<i>O. fischeri</i> s. str.	♂	31				6	43	51			6	43	51		
	♀	31				43	53	4			43	53	4		
<i>O. koreanus</i>	♂	22		5	18	77				5	18	77			
	♀	14			21	72	7			21	72	7			
<i>O. zhangyapingi</i>	♂	6		33	50	17				33	50	17			
	♀	10			50	50				50	50				
<i>O. nipponoborealis</i>	♂	7		14	43	43				14	72	14			
	♀	7			72	14	14			72	14	14			
<i>O. zhaoermii</i>	♂	2		100						100					
	♀	6		33	67					33	67				
<i>O. japonicus</i> s. str.	♂	23	15	54	31					69	31				
	♀	23		86	14					86	14				
Sum		182													

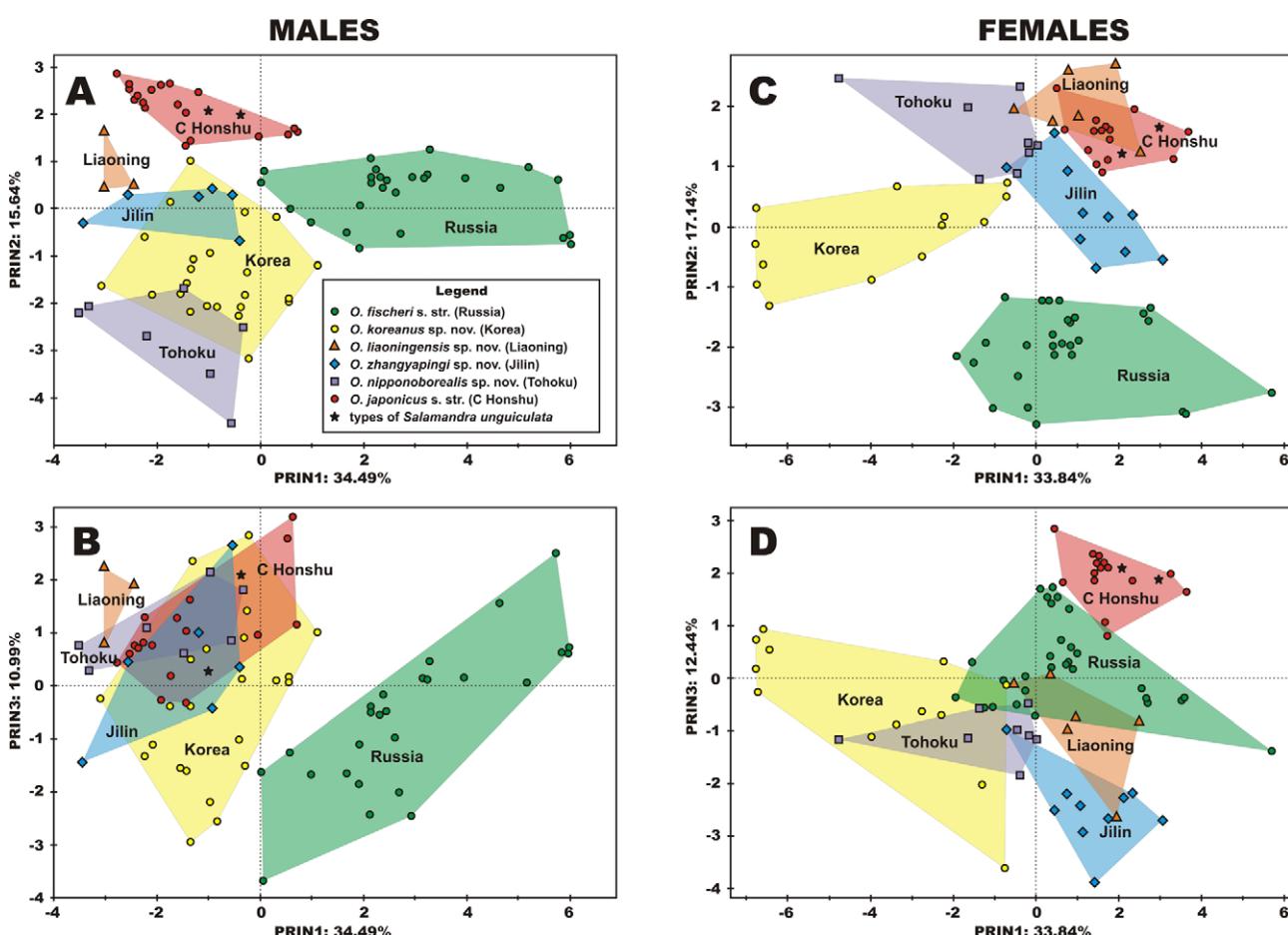


FIGURE 6. Two-dimensional plots of (A, C) the first two factors of PCA and (B, D) the first and third factors of morphological characters for the samples examined. Data are given separately for males (A, B) and females (C, D). Green circles, yellow circles, orange triangles, blue diamonds, violet squares and red circles indicate scores of Russian *O. fischeri*, Korean *O. fischeri* (*O. koreanus*), Chinese *O. fischeri* from Liaoning (*O. zhaoermii*), Chinese *O. fischeri* from Jilin (*O. zhangyapingi*), *O. japonicus* from Tohoku (*O. nipponoborealis*) and *O. japonicus* s. str. from central Honshu respectively (see Legend). Stars indicate scores of 4 lectotypes of *Salamandra unguiculata* Temminck & Schlegel, 1838 (RMNH 2292A–D).

TABLE 7. Variation in the vomerine teeth number in studied *Onychodactylus* species, including *O. fischeri*, *O. japonicus*, and the type series of *O. koreanus*, *O. zhaoermii*, *O. zhangyapingi* and *O. nipponoborealis*. Means \pm SD for right and left vomerine tooth series and average values are given. Figures in parenthesis indicate variation range (δ —Adult male; ♀—Adult female; juv.—Juvenile).

Species	N	VTN L	VTN R	VTN средн.
<i>O. fischeri</i> s. str. (Primorye, Russia)				
♂	32	12.1 \pm 0.79 (10–13)	12.2 \pm 1.08 (10–14)	12.2 \pm 0.78 (10.5–13.5)
♀	35	10.3* \pm 1.17 (8–12)	10.6* \pm 1.13 (9–13)	10.8* \pm 1.23 (8.5–12.5)
Sum	67	11.2 \pm 1.35 (8–13)	11.4 \pm 1.35 (9–14)	11.5 \pm 1.23 (8.5–13.5)
<i>O. japonicus</i> s. str. (C Honshu, Japan)				
♂	23	11.9 \pm 1.21 (10–14)	11.7 \pm 1.44 (9–14)	12.1 \pm 1.24 (9.5–13.5)
♀	25	10.8 \pm 1.36 (9–13)	11.3 \pm 1.25 (9–13)	11.0 \pm 0.99 (9.5–12.5)
Sum	48	11.3 \pm 1.38 (9–14)	11.5 \pm 1.33 (9–14)	11.4 \pm 1.16 (9.5–13.5)
<i>O. koreanus</i> (Korea)				
♂	12	17.3 \pm 2.10 (13–22)	17.2 \pm 2.75 (11–25)	17.2 \pm 2.24 (11.5–23.5)
♀	12	17.4 \pm 2.55 (13–19)	16.9 \pm 2.32 (13–22)	17.1 \pm 2.26 (13–19.5)
juv.	4	16.7 \pm 2.16 (14–19)	16.8 \pm 1.71 (15–19)	16.7 \pm 1.65 (14.5–18.5)
Sum	28	17.1 \pm 2.19 (13–22)	17.0 \pm 2.41 (11–25)	17.1 \pm 2.11 (11.5–23.5)
<i>O. zhaoermii</i> (Liaoning, China)				
♂	2	14.0 \pm 0.0 (14–14)	14.5 \pm 0.71 (14–15)	14.3 \pm 0.35 (14.0–14.5)
♀	6	13.3 \pm 1.75 (11–16)	13.8 \pm 1.33 (13–16)	13.6 \pm 1.46 (12.0–16.0)
Sum	8	13.5 \pm 1.51 (11–16)	14.0 \pm 1.20 (13–16)	13.8 \pm 1.3 (12.0–16.0)
<i>O. zhangyapingi</i> (Jilin, China)				
♂	6	17.2 \pm 0.75 (16–18)	16.7 \pm 1.21 (15–18)	16.9 \pm 0.92 (16.0–18.0)
♀	10	16.1 \pm 1.29 (14–18)	16.2 \pm 1.03 (15–18)	16.2 \pm 1.03 (14.5–18.0)
Sum	16	16.5 \pm 1.21 (14–18)	16.4 \pm 1.09 (15–18)	16.4 \pm 1.03 (14.5–18.0)
<i>O. nipponoborealis</i> (Tohoku, Japan)				
♂	7	17.1 \pm 0.69 (16–18)	17.0 \pm 1.15 (15–18)	17.1 \pm 0.79 (16.0–18.0)
♀	7	17.6 \pm 1.72 (15–20)	17.3 \pm 2.36 (14–20)	17.4 \pm 2.03 (14.5–20)
Sum	14	17.4 \pm 1.28 (15–20)	17.1 \pm 1.79 (14–20)	17.3 \pm 1.49 (14.5–20.0)
Sum	181			

Note:

*—significantly different from the conspecific male.

Discussion

Taxonomic remarks

The present-day taxonomy of the genus *Onychodactylus* does not reflect the actual genetic and morphological diversity observed on this ancient salamander group. Genetic analyses recover nine well-supported clades (Fig. 3), showing uncorrected genetic *p*-distances over 5% in COI gene among them. According to the current two-species taxonomy, four of these lineages correspond to *O. japonicus* whereas five belong to *O. fischeri* which however in its current definition is highly paraphyletic. The integration of morphological data shows that six of these genetic lineages present both diagnostic morphological traits, being easily distinguished from each other in the field, as well as high genetic differentiation in mtDNA. Although the genetic differentiation in 16S between some of these lineages is below the threshold commonly used in neobatrachians (e.g. Fouquet et al., 2007; Vieites et al., 2009), the substitution rates in salamanders are much lower and the thresholds for candidate species recognition should be lower too. However, the concordance of clear morphological differentiation with genetic differentiation between these clades is key to support the consideration of four of them as confirmed candidate species, which we formally describe below as new species.

The taxonomic status of the divergent South Korean (clade E, Fig. 3) and Japanese lineages (clades I, F, G) is unclear. Based only on mtDNA divergence, the lack of morphological data and lack of nuclear genetic data (which could show if there is admixture with other lineages), we treat them here as unconfirmed candidate species pending further investigation (see Vieites et al. 2009). The summary of our results and taxonomic conclusions is given below.

- (I) Within the genus *Onychodactylus*, at least nine highly divergent mtDNA lineages have been identified, and six of them show diagnostic morphological differences in a number of morphological characters. This allows us to consider them taxonomically defined groups on the base of genetic and morphological differences, and to describe four of them as new species.
- (II) Mitochondrial DNA suggests that *O. fischeri* is paraphyletic with respect to *O. japonicus*, consisting on five distantly related mtDNA lineages, found in northeastern Asia (Russia, Japan and Korea) region.
- (III) The name *Geomolge fischeri* Boulenger, 1886 should be applied exclusively to *Onychodactylus* populations from the Primorye Territory of Russia. This species is endemic to Russia and so far is only found in the southern slopes of Sikhote-Alin Mts. *O. fischeri* shows a large degree of genetic differentiation from the rest of clades, being sister to all of them. Nevertheless, to date there are no reasons to consider the genus *Geomolge* as a valid genus.
- (IV) Our mtDNA topology suggests two main well-supported groups apart from *O. fischeri* from the Primorye Territory of Russia: one is constituted by three well-supported lineages found in the Korean peninsula, mountain areas of Liaoning Province and, possibly the southern part of Jilin Province in China. The second group shows a distinct mtDNA lineage from the mountains of Jilin Province of China as well as a clade constituted by all the populations from the Japanese archipelago.
- (V) In the southern part of the Korean peninsula two geographically isolated mtDNA clades are found, one of them is restricted to the mountain area of Yangsan in the southeast, and the other one inhabits mountains throughout the country. The taxonomic status of the Yangsan population remains unclear because of the absence of morphological data on adult specimens; hence, we treat it here as an unconfirmed candidate species based only on the high degree of genetic differentiation from the rest. The other clade from Korea, as well as the distinct ones from China (Jilin and Liaoning), show diagnostic morphological traits and genetic differences at a level that allows us to describe them as new species. Whether these clades occur in North Korea is unknown and requires further investigation.
- (VI) Two main clades are supported within Japanese populations, one corresponding to the populations from Honshu and Shikoku, and the other to the rest of Japanese populations of *O. japonicus*. The *Onychodactylus* form inhabiting Tohoku region in the northeast of Honshu is morphologically distinct and different from the rest of Japanese *Onychodactylus*, being well supported also in phylogenetic analyses as sister to the rest of Japanese populations. This degree of genetic and morphological differentiation in a number of diagnostic characters, supports its consideration as a new species which we describe below. The southernmost known localities of this form are located in Yamagata and Fukushima prefectures.
- (VII) The rest of Japanese populations show a high degree of genetic variation in mtDNA, with at least seven highly divergent mtDNA lineages. For many of those, significant differentiation was shown by means of allozyme analyses (Yoshikawa et al., 2008; 2010a; 2010b), and two of these forms have reproductive isolation in sympatry (Yoshikawa et al., 2010a; 2010b). Considering the significant morphological variation across the *O. japonicus* range, its fragmented distribution and the existence of several

divergent mtDNA lineages, further taxonomic reassessment of *O. japonicus* populations is required, and the description of new taxa especially from the western part of *O. japonicus* range is expected.

Taxonomic accounts and description of new species

Note: the square brackets in synonymy indicate the quotation is not a nomenclatural act.

Genus *Onychodactylus* Tschudi, 1838

Onychodactylus Tschudi, 1838: 57, 92. **Type species:** *Onychodactylus schlegeli* Tschudi, 1838 (= *Salamandra japonica* Houttuyn, 1782), by monotypy.

Dactyloyx Bibron in Bonaparte, 1839: fasc. 26; pages unnumbered. Treated as substitute name for *Onychodactylus* Tschudi, 1838 by Frost (2009, 2011).

Onycopus Duméril & Bibron, 1841: 4. Substitute name for *Onychodactylus* Tschudi, 1838. Dunn (1923: 507) proposed that it is a *lapsus calami*.

Onychopus Duméril, Bibron, & Duméril, 1854: 113. Substitute name for *Onychodactylus* Tschudi, 1838.

Geomolge Boulenger, 1886: 416. **Type species:** *Geomolge fischeri* Boulenger, 1886, by monotypy. Synonymy with *Onychodactylus* Tschudi, 1838 given by Dunn, 1918: 454.

Onychodactylus—Tago, 1904: pp. 41. Unjustified emendation of the original spelling.

Ouychodactylus—Tago, 1904: pp. 43 (*ex errore*).

Ornychodactylus—Hashimoto, 1910: p. 499 (*ex errore*).

Geemolge—Emelianov, 1923: p. 139 (*ex errore*).

Nychodactylus—Dunn, 1923: p. 513, (*ex errore*) typographical error.

Onichodactylus—Okhotina, 1959: p. 143 (*ex errore*).

Geomolgo—Ji, Liu, Liu, Zhou, Huang, Wen, & Zou, 1987: p. 21 (*ex errore*).

Diagnosis. Hynobiid salamanders of medium size with distinct, acute blackish horny claws in larvae and in some adults (at least during the breeding season in males); body slender; lungs absent; ypsiloid cartilage present; premaxillary fontanelle very large, fully separating nasals; frontoparietal fontanelle absent; 16–22 presacral vertebrae, of those 5 in the anterior part of the trunk; caudal ribs numerous, normally from 9 to 12; gills of larvae short without filament rachii; vomerine teeth in a nearly transverse arc-shaped or slightly bended, almost continuous series; tail longer than the body and head length and nearly cylindrical over the whole length, slightly compressed at the end; toes 5; in larvae fore- and hindlimbs with skin folds on posterior side, similar folds are developed on hindlimbs in breeding males; paired egg sac with very thick envelope with no obvious texture; few eggs in egg sacs (usually 11–24 eggs per clutch, from 2 to 13 per egg sac); eggs large (diameter 4.5–5.5 mm); larval balancer absent; large genome size (>100 pg per diploid nucleus) and chromosome number ($2n = 78$ chromosomes, of which 38 are microchromosomes).

Taxonomy. Before the description as a separate genus by Tschudi (1838), the representatives of the genus *Onychodactylus* were regarded as members of the following genera: *Salamandra* (Houttuyn, 1782: 329), *Lacerta* (Thunberg, 1787: 124) and *Molge* (Merrem, 1820: 185).

The relationship of *Onychodactylus* with respect to other hynobiids was investigated by numerous authors based on studies of their morphology, karyology and reproductive biology (see a review in Kuzmin, 1995). Several phylogenetic reconstructions based on mtDNA analyses (i.e. Larson *et al.*, 2003; Zhang *et al.*, 2006), indicated this genus to be a sister-clade to all other living hynobiids. The description of the genus *Geomolge* by Boulenger (1886) was based on the first known record of *Onychodactylus* from Continental Asia and the main diagnostic feature was supposed to be the absence of claws. Later it was shown that the continental species also posses claws and the genus was synonymized with *Onychodactylus* by Dunn, 1918. Historically, the genus included two species—*O. japonicus* on the Japanese islands, and the name *O. fischeri* was applied to all continental populations. Recent molecular studies reported the possible presence of cryptic species in Japanese *Onychodactylus* (e.g. Yoshikawa *et al.*, 2008; 2010a; 2010b). Here, we describe four new species within this genus: *O. koreanus* sp. nov., *O. zhangyapingi* sp. nov., *O. zhaoermii* sp. nov. and *O. nipponoborealis* sp. nov. from the Korean peninsula, Jilin and Liaoning provinces of northeast of China and northeast of Honshu Island, Japan, respectively.

Etymology. The genus is named from the Greek “*onychos*”—claw, and “*dactylos*”—digit.

Distribution. Temperate areas in northeastern Asia, found in the mountainous forest regions of the southern slopes of the Sikhote-Alin Mts. (Primorye Territory, Russia); Changbaishan mountain area in Jilin Province of China, DaLing Mts. and LiaoDong peninsula in Liaoning Province of China, in mountainous areas of North and South Korea southwards as far as Jiri-san Mt. and Yang-san. The genus is absent on small islands of the Korean strait and Kyushu but inhabits mountainous areas of the Japanese islands Honshu and Shikoku, not reaching Hokkaido, forming a number of isolated populations in solitary mountains of Chugoku, Kanto and Tohoku regions.

Phylogenetic position. Recent studies on salamander phylogenetic relationships based on analyses of complete mitochondrial genomes have recovered *Onychodactylus* as a basal and highly divergent lineage in respect to other Hynobiids, being the sister clade to all of them (Zhang *et al.*, 2006; Zhang & Wake, 2009; Peng *et al.*, 2010). The split between *Onychodactylus* and the rest of hynobiids happened in the Middle Cretaceous ca. 110.7 MYA (Zhang *et al.*, 2006).

Onychodactylus fischeri (Boulenger, 1886)

Geomolge fischeri Boulenger, 1886: 416; pl. XXXIX, f. 2c. **Syntypes:** BMNH Nr 1886.5.15.11-12, male and female, according to Kuzmin and Maslova (2005: pp. 88-90); stated as BM 1947.9.7.70-71 by Kuzmin (1995: 57-95), see also Fei, Hu, Ye, & Huang, (2006: p. 201). **Type locality:** «Chaborowska [now Khabarovsk], on the River Ussuri, Manchuria», Russia, collected by Mr. Doerries from Hamburg. The indication of type locality is erroneous according to Kuzmin (1995) and Kuzmin and Maslova (2005) (see taxonomic comment below). See also Nikolsky, 1896: 77, who reports on two specimens collected by N.A. Palchevsky in Suchan River Valley, Ussuri (ZISP 1904?, Th. Busse, 19.VII.1893). See also Boulenger, 1890: 144; Nikolsky, 1906 ("1905"): 440; Stejneger, 1907: 47; Nikolsky, 1918: 242 (f. 45) (report for Russia). Following authors: Mori, 1916: 119 (cit. from Sato, 1943); Doi, 1920: 123; Abe, 1922 ("1921"): 328 report this species for Korea (see taxonomic comment for *O. koreanus*).

Onychodactylus rossicus Nikolskii, 1914 "1912": 28. **Syntypes:** 4 specimens, place of deposition not stated. Kuzmin and Maslova (2005: pp. 88-90) considered the types to include ZISP 2440 (1 specimen), one adult specimen in the Zoological Museum of Kharkov University and two specimens in the former Museum of Troitskosavsk-Kyakhta Branch of Russian Geographic Society. Fei, Hu, Ye, & Huang (2006: p. 201) indicate, that types include ZMAL (= ZISP) 2440 (1) (designated as larva), ZDKU (1 adult) and Museum of Troitskosavsk-Kyakhta Branch of Russian Geographic Society (2 specimens). **Type locality:** "Primorskaya oblast" [= Maritime Province, or Primorye], Russia. Later designated as "*prope sinus Ussuriensem Sibiriae orientalis*" (nearby Ussuri River Valley in Eastern Siberia) by Nikolskii, 1914 "1913": 260. Kuzmin and Maslova (2005: pp. 88-90) assigned the type locality to "small mountain river approximately in 21-32 km (20-30 versts) from Kangauz bay, Primorskiy territory, Russia". Terentjev & Chernov, 1949: 58 noted this as the original description and not that of Nikolsky, 1914 "1913": 260, as was proposed by Dunn, 1923: 513 (indicated "Ussuri" as type locality). Nikolsky gives a species account under the name in his monograph on Russian Amphibians: Nikolsky, 1918: 259 (f. 57-58, pl. IV, f. 5). **Synonymy** by Dunn, 1918: 455; Terentjev, 1938; Thorn, 1968: 99. Treated as a separate species in Jiang, 1998: 139.

Onychodactylus fischeri—Dunn, 1918: 454; Dunn, 1923: 513-514; Emelianov, 1934: p. 130; Okada, 1934: 19; Terentjev & Chernov, 1936: p. 13; Terentjev & Chernov, 1940: p. 17; Terentjev & Chernov, 1949: p. 54, 58-59; and many other authors.

Onychodactylus russicus—Dunn, 1918: 455. Unjustified emendation of the original spelling.

Geemolge fischeri—Emelianov, 1923: p. 139 (*ex errore*). Unjustified change of the original spelling.

Nychodactylus fischeri—Dunn, 1923: 513 (*ex errore*). Typographical error.

Onichodactylus fischeri—Okhotina, 1959: p. 143 (*ex errore*). Unjustified emendation of the original spelling.

Onychodactylus sischeni—Won, 1971: p. 30 (*ex errore*). Unjustified change of the original spelling.

Geomolgo fischeri—Ji, Liu, Liu, Zhou, Huang, Wen, & Zou, 1987: p. 21 (*ex errore*).

Onychodactylus fisheri—Ji, Liu, Liu, Zhou, Huang, Wen, & Zou, 1987: p. 21; Shim, 2001: p. 143; Uchiyama, Maeda, Numata & Seki, 2002: p. 55. Unjustified emendation of the original spelling.

Onychodactylus fischery—Maslova, 1999: p. 70 (*ex errore*).

Vernacular and trivial names:

Chinese name: Wusuli Zhaoni (乌苏里爪鲵); Feixier Zhaoni (費希爾爪鲵).

English name: Russian Clawed Salamander, Fischer's Clawed Salamander.

Japanese name: Hakone-Sansyouo-modoki.

Korean name: Reosia Ggorichire Dorongnyong.

Russian name: Ussuriyskiy [dalnevostochnyi] kogtistyi (bezlegochnyi) triton.

Syntypes. Two specimens: BMNH Nr 1886.5.15.11-12, male and female, according to Kuzmin and Maslova (2005: pp. 88-90); stated as BM 1947.9.7.70-71 by Kuzmin (1995: 57-95), see also Fei, Hu, Ye, & Huang, (2006: p. 201).

Type locality. «Chaborowska [now Khabarovsk], on the River Ussuri, Manchuria» (Boulenger, 1886), Russia, collected by Mr. Doerries from Hamburg.

Taxonomic comment. There are two names available within *O. fischeri*: *Geomolge fischeri* Boulenger, 1886 and *Onychodactylus rossicus* Nikolskii, 1914 "1912". Kuzmin (1995) as well as Kuzmin & Maslova (2005) pointed out that the type locality is wrong, since the nearest known localities of the species are found only 450 km southwards or south-eastwards from Khabarovsk (the same is true for *Bombina orientalis*, also described by Boulenger from Khabarovsk, but in fact found only 300 km to the south from the type locality). All further

attempts to find *Onychodactylus* in Khabarovsk Territory were not successful, though some contradictory information on a dubious record from an area north from Khabarovsk was published (Tagirova, 1977). Kuzmin & Maslova (2005) assume that the stated type locality corresponds to the place where materials were bought or to the only noticeable settlement in the area which was available on English maps. They suggest that most likely the collector – Mr. Doerries – received the specimens from unfamiliar hands and that the species is described from somewhere in the upper part of the Ussuri River basin, but undoubtedly from Sikhote-Alin Mts., i.e. from a Russian territory. Morphological analysis of the type specimens and original species description confirm this conclusion, thus the name *Geomolge fischeri* Boulenger, 1886 corresponds to the Russian population from Sikhote-Alin Mts. in the upper part of Ussuri River basin. The description of *Onychodactylus rossicus* was based on juvenile specimens of *Onychodactylus fischeri* (Dunn, 1918; Terentjev, 1938; Kuzmin, Maslova, 2005). The type specimens of *Onychodactylus rossicus* Nikolskii, 1914 "1912" collected by V. Shustov (Nikolsky, 1918) are kept in ZISP, Russia, and in the Zoological museum of Kharkov University, Ukraine, and were studied by Kuzmin & Maslova (2005), who restrict the type locality for this species to a "small mountain river approximately in 21-32 km (20-30 versts) from Kangauz Bay, Primorskiy territory, Russia". Thus, undoubtedly both available names correspond to the Russian form of *Onychodactylus*.

Diagnosis. A slender relatively medium-sized hynobiid salamander, member of the genus *Onychodactylus* on the basis of the following combination of features: absence of lungs, presence of black claw-like horny structures on both fore- and hindlimbs in larvae and breeding adults, tail longer than the sum of head and body lengths, tail almost cylindrical, slightly compressed at the end, vomerine teeth in transverse short arch-shaped series almost in contact with each other, presence of large premaxillary fontanelle completely separating the nasals, presence of more than 9 caudal ribs, presence of skinfolds in larvae on the posterior edges of both fore- and hindlimbs and dermal flaps in males being developed during the breeding season, with diploid chromosome number $2n = 78$ and other typical features of the genus. From the other members of the genus this species differs in a combination of the following attributes. In meristic characters the species is different by having 20-21 (19-22)¹ presacral trunk vertebrae, 14-15 (13-16) costal grooves (see Tab. 6), 11-12 (8-14) vomerine teeth in each vomerine tooth series (see Tab. 7), shallow slightly curved vomerine tooth series with a distinct gap between them and the inner and outer branches being of nearly the same length (see Fig. 4, A). In body proportions, the species is different in a relatively shorter tail in males, relatively narrower heads in both sexes and relatively greater distance between the eyes (see Tab. 4, Tab. 5) than in the other species. Black acute claws usually appear on hindlimbs in males during the breeding season and often are absent in both sexes out of the reproductive season, and sometimes can also be absent in females during breeding. In coloration this species is different in having a normally light dorsum (brownish, ochre and yellowish) with numerous black mottling, variegations and spots, most occurring on the sides, which also bear some whitish spots; with a light dorsal band absent or rather obscure (Fig. 5, A; Fig. 7, A). Juveniles are characterized with the presence of a light ground color of the trunk sometimes with relatively distinct light dorsal band but with irregular edge shape. Larvae normally do not have an obvious dorsal band (Fig. 7, B).

Description and variation.

Type specimens. Syntypes kept in the BM have the following measurements (following Boulenger, 1886): BM 1947.9.7.70 (male) has total length 163 mm, head length 12 mm, body 58 mm and tail length 93 mm; BM 1947.9.7.71 (female) has head length of 14 mm and a body length of 66 mm (no other measurements available). Dunn (1923) notes that "these Ussuri specimens have shorter heads than the ones I have seen from Korea". According to the illustration in the original description (Boulenger, 1886: pl. XXXIX, f. 2c) the male type depicted shows a pattern quite typical for this species: the ground color is light with a dorsal band that is not prominent – on the dorsolateral edges of the body a number of black spots and variegations form a dotted edge line, becoming more solid and prominent at the base of the tail, in the second half of the tail the light band on the dorsal surface is interrupted several times by black blotches and lines. Smaller dark spots and variegations are found on the dorsal surface of the head, limbs and in the middle of the back, tending to form an unclear clouded pattern. The male syntype has vomerine teeth arranged into two short slightly curved series with equal lengths of outer and inner branches and a slight gap between them. Both syntypes kept in the BM lack black horny claw-like structures on fore- and hindlimbs, which indicate that most likely they were collected out of the breeding season. This feature, in addition to the broken tooth series with a distinct gap between them, were the main reasons for the establishment of the monotypic genus *Geomolge* Boulenger, 1886.

1. Here and later on after modal values we give character ranges in brackets.

Variation.

Morphometrics. Morphological measurements of *O. fischeri* are shown in Tables 4 and 5. The species is in general characterized by the following morphometric parameters (ranges for males / females, 86 specimens): snout-vent length (SVL): 60.8–80.0 / 51.0–83.0; tail length (TL): 72.2–103.6 / 55.4–96.5; gleno-acetabular distance (GA): 30.2–46.5 / 26.7–53.0; forelimb length (FLL): 14.4–19.4 / 13.0–26.5; hindlimb length (HLL): 16.5–28.0 / 14.4–27.0; head length (HL): 11.5–17.3 / 11.1–19.6; head width (HW): 7.0–11.5 / 7.3–12.7; eye length (EL): 3.0–4.3 / 2.6–5.1; internarial distance (IN): 3.0–5.0 / 3.3–6.3; orbitonarial distance (ON): 1.9–3.2 / 1.6–3.9; interorbital distance (IO): 2.9–4.5 / 2.1–5.1; chest width (CW): 5.8–11.0 / 4.8–9.4; snout length (OR): 4.6–6.2 / 3.5–6.9; intercanthal distance (IC): 4.8–7.2 / 4.16–8.2 (measured on the preserved specimens). From a morphometric perspective, Russian populations of *O. fischeri* are morphologically most distant from all other *Onychodactylus* species and are clearly discriminated by PCA analysis (see Fig. 6; Results and Comparisons).

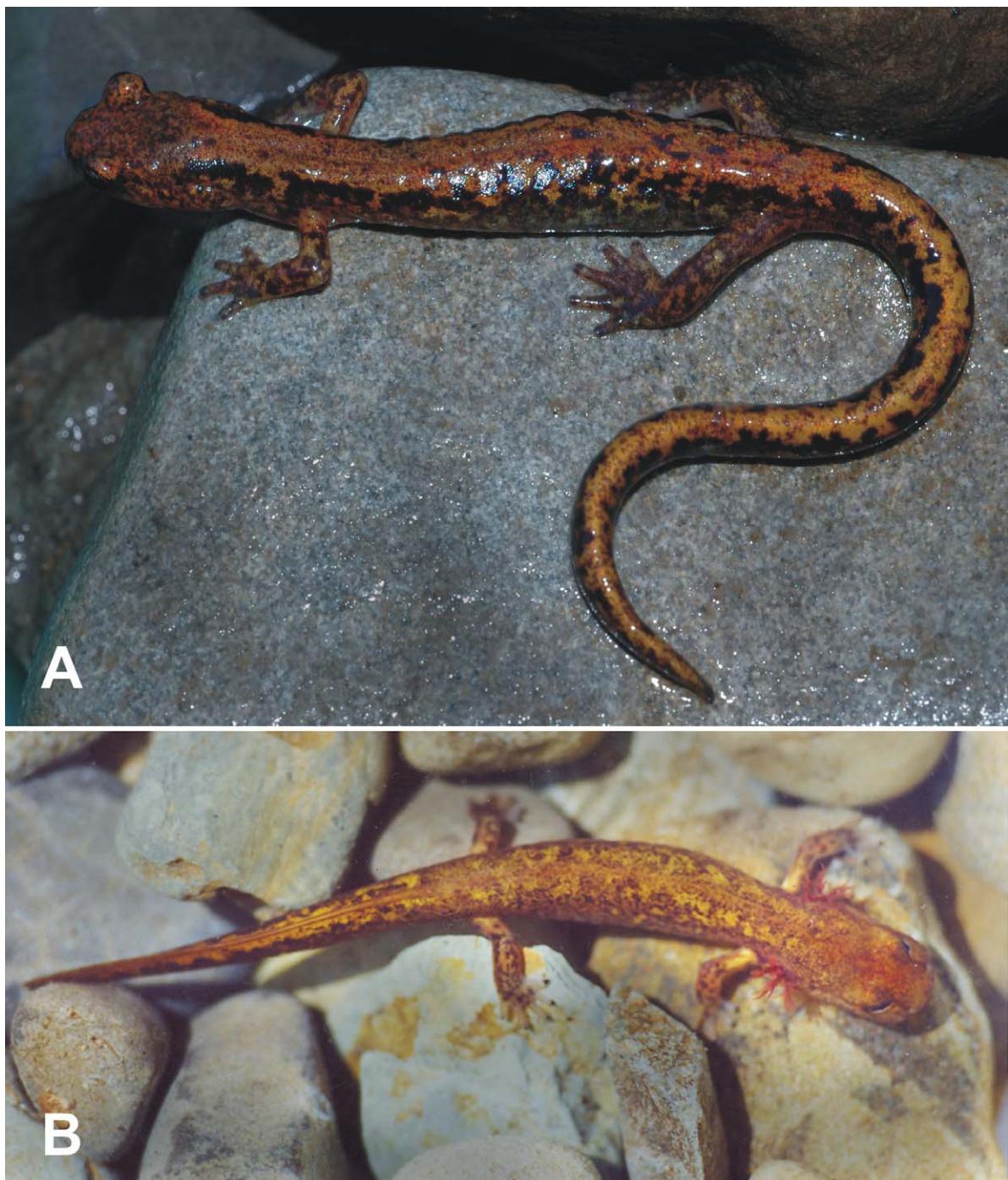


FIGURE 7. *Onychodactylus fischeri* s. str.: (A)—Adult male from Tigrovoi environs, Partizansk district, Primorye territory, Russia; (B)—Premetamorphic larva from the same locality. Photos by E.A. Dunayev.

Sexual variation. Sexual dimorphism in morphometric features within *O. fischeri* is found in several measurements (see Results, Tab. 5), and our results are concordant with previously published data (see Kuzmin, 1995). Among the most prominent are the differences in tail length (TL: significantly longer in males) and glenoacetabular distance (GA: larger in males) and forelimb length (FLL: longer in males), though no significant differences in hindlimb length were found despite the observed secondary sexual differences (see below). During the reproductive season females have obviously swollen abdomens due to the presence of large eggs in the oviducts and female body mass is significantly larger than those of males (Kuzmin, 1995). Here, we report on significant sexual differences in vomerine teeth numbers in *O. fischeri* (see below).

Secondary sexual characters. Kuzmin (1995) noticed that the degree of differentiation among sexes in *O. fischeri* is weak in comparison with *O. japonicus*. During the breeding season the males develop a prominent lateral skin flap from the fifth toe to the tibia, which is the only clear secondary sexual character in this species. The fold is most likely used in clutch grasping male behavior (Serbinova & Solkin, 1992; Griffin & Solkin, 1995), which is why even outside the breeding season male *Onychodactylus* have noticeably crooked and broadened hindlimbs with feet orientated to a specific angle to the tibia. Males also have more swollen vents during the breeding season than females, though no significant differences in vent structure was reported (Kuzmin, 1995: 60), and males tend to have longer cloacal slits than females. Males have a more noticeably enlarged, flattened and gently rounded tail tip, whereas it is narrower and pointed in females, though tail height is not different in both sexes even during the reproductive season (Kuzmin, 1995). Black, claw-like horny structures in *O. fischeri* develop during the breeding season mostly in males and normally are absent in both sexes during the land-stage in this species (see Fig. 7, A). This is one of the main reasons why *O. fischeri* was initially treated as a member of separate genus *Geomolge* Boulenger, 1886. During the reproductive season almost all males develop claws, though clawed females are also known. In *O. fischeri*, the reduction of the hindlimb folds actually takes more than two months (Solkin, 1993), whereas the black claws seem to disappear immediately after breeding.

Color in life. Normal coloration pattern of *O. fischeri* adults is shown in Fig. 5, A and Fig. 7, A. Typical background color on the dorsal and lateral surfaces of the head, body and tail is light brown of various shades: from light-golden, yellowish and light-ochre in metamorphs and juvenile specimens to dark-bronze, dark-orange, tan and brown in adults (Fig. 7, A). Old specimens can have copper-brown, dark-brown or an almost gray-brown background color. Lateral sides of the body are sometimes noticeably lighter and often have grayish or bluish shades; this color gradually turns to a lighter color of the belly and other ventral surfaces, which are usually pinkish or light gray-purple. In older specimens the sides of the body can be very dark. The pattern in this species seems to be dependent on age. In adults, normally irregular, dark (brown to dark-gray and black) blotches on the sides of the body form two unclear, interrupted dorsolateral series. These series continue all the way to the lateral sides of the tail, where they usually more prominent and form a confluent irregular pattern. These blotches continue to the sides of the head, where in contrast they become less pronounced, draw closer to each other on the head and usually end in a thin dark line or a series of dark spots continuing along the parotid to the posterior corner of the eye (Fig. 7, A). Often the dark line continues on the snout from the anterior corner of the eye through the nostril area. Smaller dark spots and blotches are present on the dorsal surface of the head where they usually form an irregular mottled-pattern. Black spots on the dorsal side of body tend to form irregular variegations, and occasionally there is a slightly pronounced dark middorsal stripe or a line of elongated black spots. Dark blotches on dorsal surface of the tail tend to form dark irregular bars in older specimens. Dorsal surfaces of fore- and hindlimbs are usually covered with irregular light and dark mottling or small blotches.

There is a certain degree of intrapopulational color variation within this species. Griffin and Solkin (1995: f. 2) designated several typical color patterns for individuals according to a categorization of light-colored spot placement on the neck, back and tail: A is a light-colored type with almost no dark pattern on dorsal surface (1%—here and further in brackets we give the percentage of patterns from 351 specimens studied by Griffin & Solkin, 1995); B—specimens with a light back and unclear dorsolateral series of dark spots and with or without (B²) dark bars on the tail (36.4%); C—similar to B, but the dorsal surface is covered with numerous black spots and blotches (46.7%, similar to Fig. 5, A; Fig. 7, A); D—specimens with dark sides and obscure light dorsal band with unclear edges continuing to the tail (5%); F—pattern similar to D, but the light dorsal band has variegated edges and is covered with black mottling, light dorsal stripe on the tail is greatly interrupted (4.8%); and L—light-colored type, similar to A, but with numerous irregular leopard-like dark spots across the dorsal surface of the body (0.3%). From these data it is clear that the typical coloration pattern is similar to those of the type specimens of *O. fischeri*.

(Fig. 5, A; Boulenger, 1886: pl. XXXIX, f. 2c) and is found in 80–85% of studied specimens and, we believe, can be used for species identification. Intrapopulational geographic variation in coloration patterns across the range of *O. fischeri* in Russia has never been studied; most likely due to the small distribution area of the species which is restricted to the south slopes of the Sikhote-Alin mountains and there is little or no geographic variation within this species. No information on differences in coloration between the sexes has been reported thus far, and we failed to find any differences in them as well.

Color in preservative. When preserved in alcohol, bright and light colors fade first, starting with the pinkish and purplish coloration of the ventral side and after two years in preservative the yellow and orange coloration also disappears. If preserved for more than 25 years, the general coloration becomes lighter and blackish or brownish parts of skin turn a dark-grayish color. However, body patterns do not change and in principle they correspond well to those in life.

Osteology and anatomy. Preliminary reports on axial and rib morphology of *O. fischeri* were given by Antipenkova (1982). Trunk and sacral vertebrae of this species were described in detail by Ratnikov & Litvinchuk (2007) (based on one specimen from Primorye Territory, Russia), and they are characterized by the following features: anterior margin of neural arch is concave or straight, at the level of the posterior third or, rarely, middle part of prezygapophyseal articular facets; posterior margin of neural arch straight or salient, at the level prior to the posterior edges of postzygapophyseal articular facets; subcentral foramina and neurapophysis are lacking (Ratnikov & Litvinchuk, 2007: 180). Atlantal vertebrae were described by the authors and are characterized by the following parameters: processus odontoideus slightly narrower than cotylus and much narrower than neural canal; in dorsal view, anterior edge of neural arch slightly uneven with the wide median lobe; in both anterior and posterior views, neural canal rounded with slight dorsal narrowing. In dorsal view, bulge on neural arch is clearly widened near the posterior edge (T-shaped) (Ratnikov & Litvinchuk, 2009: 58). Normally, *O. fischeri* has a large number of trunk vertebrae—modal TVN-number is 21 for both sexes, though the ranges vary (19–21 in males, mean value is 20.6 ± 0.51 ; and 20–22 in females, mean value is 20.7 ± 0.53), this is the largest TVN-number known for hynobiid salamanders (see Litvinchuk & Borkin, 2003). These trunk-vertebrae numbers result in the respective costal groove counts: 15 (13–15) for males and 15 (14–16) for females (based on 62 specimens, see Tab. 6). Dermal ossifications and cranial morphology of *O. fischeri* were described by Lebedkina (1981); peculiarities of chondrocranial morphology were given by Regel (1970, 1979). Features of internal anatomy of the Russian species were described by various authors, such as circulatory system (Regel, 1981), seismosensory system and nasal organ (Medvedeva, 1975), nasal muscles (Nikitin, 1986), and sound-conducting apparatus (Smirnov, 1987; Smirnov & Vorobyeva, 1988). A detailed description of skeletal and dental ontogeny of *O. fischeri* (based on ontogenetic series from the Suputinsky Reserve, Primorye Territory, Russia) was presented in a study by Smirnov & Vassilieva (2002) showing unique developmental patterns and combination of paedomorphic and derived character states with a high level of embryonization in this species, in particular in dentition ontogeny patterns.

Vomerine teeth morphology. In adult specimens of *O. fischeri* vomerine teeth are arranged into two arch-shaped series with equal lengths of inner and outer branches and a noticeable gap between them. Both outer and inner branches are normally nearly straight in this species, the outer branch can be slightly curved at the end (see Fig. 4, A). The presence of a gap even in adults and old specimens of *O. fischeri* was reported by previous researchers (e.g. Dunn, 1923), and since has been compared with *O. japonicus* where the two vomerine tooth series are in contact. This character state resembles a condition found in metamorphic and juvenile *O. japonicus* specimens, and is believed to be a paedomorphic feature (Kuzmin, 1995). Lebedkina (1981) reported an interval between vomers found even in 10 year old specimens. We observed a distinct gap between tooth series in all studied specimens of *O. fischeri* (see Fig. 4, A); gap width was approximately half the width of the naris. The number of vomerine teeth in this species is comparatively small: 10–14 (mean 12.2 ± 0.78) teeth per each branch in males and 8–13 (mean 10.8 ± 1.23) for females (based on 67 specimens, see Tab. 7). We found sexual differences in vomerine teeth numbers between males and females, with males having significantly larger number of vomerine teeth. There has been information reported on sexual dimorphic dentition features in other Hynobiidae representatives, such as in the genus *Pachyhynobius* (Clemen & Greven, 2009), which possibly is explained by reproductive biology of the species. Though tail wounds have been reported for *O. fischeri* populations (Griffin & Solkin, 1995), the possible reasons for these differences in *Onychodactylus* are not clear. However, we consider vomerine tooth series morphology and vomerine teeth number to be an important feature in interspecific taxonomy of *Onychodactylus*, as it was previously shown for other Hynobiidae salamanders (Inukai, 1932; Sato, 1934a; Sato, 1934b; Sato, 1943; Zhao & Hu, 1988 etc.).

Eggs and clutch. Observations on the reproductive biology of Russian populations of *O. fischeri* are scarce. The only observation of egg clutches found in the wild are by Kozik (1991) and Kozik & Truberg (1991). The authors report on a clutch they found in a rapid mountain stream that was attached to a stone (Lazovsky Nature Reserve), which is probably an abnormal situation since eggs were not developing and no other such clutches have been found or recorded. Two small, paired egg sacs, elliptical in shape and joined together at the distal end are attached to a stone by a mucous stalk; each sac has a total length of 45 mm (including the stalk). Eggs are very large, 5–6 mm in diameter, and completely without pigment (whitish). Paired egg sacs contain 3–7 eggs each and have gelatinous stalks. Artificial stimulation of spawning (Serbinova & Solkin, 1992) encouraged *O. fischeri* females to lay egg sacs which correspond similarly to the clutches described by Kozik (1995) and Kozik & Truberg (1991); egg diameter varied between 5 and 6 mm, egg number varied from 1 to 8 eggs per egg sac. Griffin & Solkin (1995) reported five to ten eggs in each sac, with egg diameter of 6 to 8 mm. Most likely, breeding in this species normally takes place secretly several meters underground between rocks in the stream-bed near the springs or torrents.

Larval morphology and metamorphosis. The first descriptions of *O. fischeri* larvae are found in the works by Emelianov (1940, 1947), who described five developmental stages. Morphological and ecological data on *O. fischeri* larvae are also given by Thiesmeier (1996). Peculiarities of reproductive biology and a preliminary description of larval morphology of *O. fischeri* was presented by Regel & Epshtein (1975), this work was followed by a more detailed description of external larval morphology up until metamorphosis by the same authors (Regel & Epshtein, 1977). Larvae at the age of active feeding (stages 1–3 according to Regel & Epshtein, 1977) appear in streams with body lengths between 35–40 mm and are characterized by a square-shaped head which is wider than the body, rounded snout, slightly prominent eyes, forelimbs with four digits and hindlimbs with five digits, with each of them possessing a black, cone-shaped sharp, horny claw (see Fig. 7, B). The back surfaces of the fore- and hindlimbs posses a dermal flap, which slowly disappears as the larvae begin to metamorphose. They also possess very short gills, the base of which is covered with an opercular skin fold, which does not reach the branchial septa. The tail fin is presented by a low caudal fold starting on the back surface of the tail in the first third of its length and not reaching the cloaca on the ventral side of the tail; the dorsal tail fin is slightly higher than the ventral fin. Metamorphosis is usually accomplished when a total length of 75–85 mm is reached, and may take up to 3 or 4 years, and sometimes even longer (Griffin & Solkin, 1995). Normally, background coloration in larvae is often light-brownish and occasionally yellowish; they develop dark pigment at lengths of 40–45 mm; this coloration will appear as dispersed dots and spots along the dorsal body surface. The belly is lighter than other body surfaces and lack black spots. Closer to metamorphosis (55–75 mm) the dark pigment will develop complex variegated patterns on the tail and back, at the same time the skin coloration on the back surface becomes much brighter (yellowish to orange). The newly metamorphed salamanders lack horny claws and after shedding they show much brighter coloration than the larvae—normally exhibiting contrast dark (brownish, blackish) variegations on a yellowish or ochre background. As the larvae age the yellowish color changes to dark-brown, the black spots become larger, and as a consequence the larger specimens become darker and show a less contrasting pattern (Kuzmin, 1995). The lifespan of this species in the wild has been documented to be up to 18 years (Smirina *et al.*, 1994; Griffin & Solkin, 1995).

Etymology. The specific name “*fischeri*” is a patronymic noun in the genitive singular; the name was given in honor of Dr. Johann Gustav Fischer (1819–1889), a well-known herpetologist from Hamburg, who passed the type specimens to G.A. Boulenger.

Distribution. A species endemic to the Russian Far East (see Fig. 1). Its distribution is described in detail and analyzed in Kuzmin (1995) and Kuzmin & Maslova (2005). *O. fischeri* is found in the mountainous forest regions of the Sikhote-Alin Mts. (Primorye Territory, Russia), southwards from the Zerkalnaya River Valley (Lazovskiy, Partizanskiy, Shkotovskiy, Chuguyevskiy, Olginskiy, Nadezhdinskiy, Ussuriyskiy, Anuchinskiy and Kavalerovskiy districts). Records from environs of the type locality (Khabarovsk), Sikhote-Alin Nature Reserve, and the westernmost region of the Primorye Territory along the border with China (Kedrovaya Pad Nature Reserve, Khasan district, Partizansky mountain ridge and environs of Khanka Lake) were not confirmed by subsequent surveys and seem to be erroneous (Kuzmin & Maslova, 2005).

Comparisons. Since originally only two species were recognized in the genus *Onychodactylus*, the amount of published data on interspecific comparisons between the forms of the genus is scarce. Other reasons preventing comparative studies in this field is the transboundary distribution of *O. fischeri* sensu lato, found in Korea, China and Russia and isolated distributional records of *O. japonicus* in the Japanese archipelago, as well as different

approaches to counting costal grooves and measuring salamanders. Dunn (1923) had the opportunity to examine large collections from Japan and Korea, but was not able to obtain material from Russia and had to use original the description of *Geomolge fischeri* by Boulenger (1886) and descriptions by Nikolsky (1905, 1918) which did not contain many morphological data to compare. Thus, based on the comparison of Japanese and Korean materials Dunn (1923: 511) concluded that the Japanese form "...is extremely close to the Korean species. Far from being generically distinct it is doubtful if any constant character separates the two species." However, he noticed that the mainland form is different from the island one in having a gap between the vomerine tooth series, having one more costal groove and lacking the light dorsal band. In addition he noticed morphometric differences between the Korean material and original description of *O. fischeri* by Boulenger (1886), pointing out that the Ussuri specimens have shorter heads. This position was widely adopted, and in his monograph on the genus Kuzmin (1995) repeats Dunn's opinion on similarity between *O. fischeri* and *O. japonicus*. However, some data, such as unique character states in sound-conducting apparatus morphology in *O. fischeri* (Smirnov, 1987; Smirnov & Vorobyeva, 1988) is not shared with other hynobiids including *O. japonicus* (Cloete, 1961) which would indicate more distant relationships between *O. fischeri* and its congeners.

Our data show that *O. fischeri* is different from all other congeners in the highest number of trunk vertebrae (20–21), as well as the number of costal grooves (14–15) (Tab. 6). Members of the *O. japonicus* species complex (*O. japonicus* (Houttuyn, 1782) and *O. nipponoborealis*) are geographically isolated from continental forms and populations of this species have the smaller number of trunk vertebrae (less than 19, versus 20–21 in *O. fischeri*) and costal grooves (less than 13, versus 14–15 in *O. fischeri*) (Tab. 6), notably curved rows of vomerine teeth with no or little gap between them (versus slightly bended series of vomerine teeth with a distinct gap between them in *O. fischeri*, Fig. 4, A), light dorsal stripe normally distinct (versus dorsal stripe indistinct, light dorsum with clouded dark variegations in *O. fischeri*, Fig. 5, A), so it is unlikely that they can be confused with *O. fischeri*. A more detailed comparison of *O. fischeri* (Boulenger, 1886) with the members of the *O. japonicus* species complex (*O. japonicus* (Houttuyn, 1782) and a new species, *O. nipponoborealis*) is provided in "Comparisons" section in species taxonomic accounts given below.

From other continental species of *Onychodactylus* (*O. koreanus*, *O. zhaoermii* and *O. zhangyapingi*, see below), *O. fischeri* is very distinct in the combination of the following features: typical coloration of this form - light dorsum with black variegations and blotches and an indistinct dorsal band (Fig. 5, A) is almost never found in Korean and Chinese populations. According to our data, Russian *O. fischeri* is also different from rest of continental *Onychodactylus* in the absence of contrast spotted coloration in juveniles and adults, the light ground color of the dorsum, slightly bended vomerine tooth series with smaller number of teeth (8–14) and a distinct gap between the series, relatively shorter tail in males, and a relatively narrower head in both sexes as well as a relatively greater distance between the eyes (Figs. 5, A; 4, A; Tabs. 4; 5; 7). For a more detailed comparison of *O. fischeri* (Boulenger, 1886) with the new species described from the mainland Northeast Asia see "Comparisons" in taxonomic accounts for *O. koreanus*, *O. zhaoermii* and *O. zhangyapingi* given below.

Karyotype. Reported as $2n = 78$ by Kuzmin (1999). However, to date publications on the karyology of Russian *O. fischeri* populations are absent and this information is based on the karyotypes of Korean *Onychodactylus*. Thus, the karyotype of *O. fischeri* sensu stricto remains unknown.

Genome size. Genome size is estimated using Feulgen densitometry reported as 45.5 pg per diploid nucleus by Mazin (1978). Genome size estimated using DNA-flow cytometry reported as 95.08 by Vinogradov (1998); as 106.7–109.0 pg per diploid nucleus; CV = 53.4–54.5 (Litvinchuk *et al.*, 2004). Our estimate of *O. fischeri* genome size is 107.8–110.1 pg per diploid nucleus; CV = 53.9–55.1 (DNA flow cytometry; five specimens from Shkotovskiy district, Primorye Territory, Russia; N.A. Poyarkov, pers. obs.; peripheral red blood cells of the Ribbed Newt, *Pleurodeles waltl*, and the Southern Crested Newt, *Triturus karelinii karelinii* (Salamandridae), were used as a reference standard for genome size measurements).

Phylogenetic position. This species is recovered as the sister taxon to the rest of *Onychodactylus* species (Fig. 3), showing uncorrected genetic distances from all other mtDNA lineages of 11.1 to 13.4% in COI and of 5.3 to 6.8% in 16S rRNA (Tab. 3).

Habitats and natural history. The first data on the natural history of the species was provided by A.A. Emelianov (1940; 1947). For detailed ecological and natural history data on *O. fischeri* with complete bibliography see Solkin (1993) and extensive monographs by Kuzmin (1995; 1999) and Kuzmin & Maslova (2004, 2005). In the mountainous regions of Sikhote-Alin Mts. *O. fischeri* inhabits coniferous and mixed cedric pine - broad leafed forest. This species is highly specialised with respect to habitat: here it is usually found near the springs of clean

mountain streams from 100 to 1,700 m above sea level (Kuzmin & Maslova, 2004, 2005). It is associated with the upper current of small mountain streams, overgrown by mixed forests of broad-leaved trees and cedar pines. Preferred streambeds have a thick layer of pebbles and moss-covered rocks, with abundant hiding places, a high humidity and water temperature ranging from 6°C to 11°C (Solkın, 1993; Sparreboom, 2012). Stream banks are very moist: aerial humidity ranges from 75%–92%. The animals remain close to springs, permanent stream pools and waterfalls and are found under rocks, stones, fallen trees and logs (Kuzmin, 1995). Sometimes *O. fischeri* may be observed in mountain lakes (Kuzmin, 1999). Homing behavior was also observed in adult salamanders (Griffin & Solkin, 1995). *O. fischeri* feeds on a variable diet of aquatic, but mainly terrestrial insects, millipedes, etc. (Kuzmin, 1995). Hibernation takes place from approximately October to late April. The animals appear when temperatures rise to 3–5°C, usually during first week of May. In the Ussuriyskiy Nature Reserve and several other localities in the southern part of the Primorye Territory *O. fischeri* is sympatric and found in the same habitats with *Salamandrella tridactyla*, *Bufo gargarizans*, *Rana dybowskii*, *Hyla japonica*. Reproduction of *Salamandrella tridactyla* and *O. fischeri* may take place in the same stream (Kuzmin & Maslova, 2004; 2005). In suitable habitats the population density of *O. fischeri* may be quite high; salamander abundance decreases from the waterway downstream, probably due to the presence of predatory fish species and an increase in the water temperature (Solkın, 1993).

Conservation status. Current IUCN status for this species considered all the populations from the Korean Peninsula, China and Russia, as being catalogued as Least Concern (Kuzmin *et al.*, 2004). The actual distribution range for this taxon is considerably reduced in the light of actual data, with populations only in the Russian Far East. The species seems to be not uncommon in certain areas with an estimated range of ca. 26250 km² and it is protected in two federal nature reserves in Russia: Ussuriyskiy and Lazovskiy (Kuzmin, 1999; Kuzmin & Maslova, 2004; 2005). However, the pronounced specialization of all *Onychodactylus* species which rely on clean forest streams make these salamanders quite sensitive to minor habitat changes. In the near future *O. fischeri* may be considered threatened with possible range reduction and population extinction mostly due to habitat loss (forest cuts and fallings; see Borkin & Korotkov, 1989; Griffin & Solkin, 1995; Maslova, 1998) and limited species range. *O. fischeri* is a habitat specialist, dependent on undisturbed old growth forest habitat with permanent streams and undisturbed stream substrate. The main threat consists of logging in stream headwaters. It seems that population recovery in this species is quite slow and requires at least 30–40 years (Maslova, 1998), probably due to small clutch size, long larval development, and maturity at 8–10 years. Less important factors threatening this species are cases of road-kills, collection for fishing purposes by local people (Solkın, 1993) and by amphibian hobbyists (Kuzmin & Maslova, 2004; 2005). *O. fischeri* is listed in the Red Data Books of both the USSR and Russian Federation. Kuzmin & Maslova (2005) recommended changing the IUCN red list category to Vulnerable (Vu2a). Our data on genetic diversity and taxonomy of the group indicate the significant reduction of the range of *O. fischeri* which is found to be endemic to the Russian Far East (Fig. 1) and thus are in favor of this assessment.

Onychodactylus japonicus species complex

Our data suggest that the Japanese clade of *Onychodactylus* constitutes a species complex, within which we recognize at least one confirmed candidate species, based on our and previously published data, which we describe below as *O. nipponoborealis*. Further data from Japanese populations are required to clarify this complex, so, until morphological data are available to clarify the status of the two populations showing very divergent mtDNA lineages from the rest, we treat them here as unconfirmed candidate species, and labelled tentatively as *O. cf. japonicus*.

Onychodactylus japonicus (Houttuyn, 1782)

Salamandra japonica Houttuyn, 1782: 329, pl. facing p. 336, f. 3. **Types:** not stated, but should include specimens shown on the Fig. 3 of the original description (pl. facing p. 336, f. 3). Types were supposed to be found in ZIUU (Uppsala), however our inquiry failed to identify any *Onychodactylus* specimens there; they also could have been deposited in RMNH (Leiden) or ZMA (Amsterdam). **Type locality:** initially stated as "Japan". Brame (1972: 19) restricted type locality to "Fakoneberget" (Hakone mountain, Izu Province (now border of Kanagawa and Shizuoka prefectures), Honshu, Japan. See Kuzmin, 1995: p. 13 for comment.

[*Lacerta Salamandra Japonica*—Houttuyn, 1787: p. 23. Houttuyn treats “Japansche Salamander” as a separate species, however the taxonomical status of this name remains unclear, see comm. 64 in Litvinchuk & Borkin, 2009: p. 33.]

Lacerta japonica Thunberg, 1787: 124, pl. IV, f. 1. **Types:** not stated or known to exist, though they can be possibly found in ZIUU, but should include specimens shown on the Fig. 1 of the original description (pl. IV, f. 1); Thunberg, 1787b: 30. Not *Salamandra japonica* Houttuyn, 1782. **Type locality:** "Fakoneberget" (Hakone mountain, Izu Province (now border of Kanagawa and Shizuoka prefectures), Honshu, Japan. See Kuzmin, 1995: p. 13 for comment.

Lacerta japonicus—Thunberg, 1787: 73 (*ex errore*); *fide* Stejneger, 1907: p. 42.

Lacerta Iaponica—Meyer, 1795: 29-30. See Litvinchuk & Borkin, 2009: p. 37.

Lacerta thunbergii Donndorff, 1798: 132. Description is based on Thunberg, 1787. Substitute name for *Lacerta japonica* Thunberg, 1787. See Dunn, 1923: 506 for comment.

Salamandra japonicus—Schneider, 1799: 73 (*ex errore?*).

Molge striata Merrem, 1820: 185; Gray, 1850: 31. Description is based on Houttuyn, 1782 and Thunberg, 1787. Substitute name for *Salamandra japonica* Houttuyn, 1782 and *Lacerta japonica* Thunberg, 1787. See Dunn, 1923: 507 for comment.

Salamandra unguiculata Temminck & Schlegel, 1838: 123, 129. **Types:** not stated, but should include animals figured on pl. V, figs. 1-6a of the original publication (pl. V, ff. 1-6a). RMNH 2292A was designated as the lectotype by Hoogmoed (1978: 97). Also MCZ 21320 (Barbour & Loveridge, 1946: 188), and MNHN 4692 (6 animals: lectotype and 5 paralectotypes designated by Thireau, 1986: 78–79). **Type locality:** "Elle se trouve en abundance dans les contrées montueuses des îles Nippon et Sikok, particulièrement dans les provinces Sagami, Sinano, Tanba, Tazima et Tosa, situées entre les 33 et 36 degrés de latitude boreale". We here restrict the type territory to "monts Fakone, Sagami, Japon" (see taxonomic comment). See also Geerts, 1881: 275; Göppert, 1896: 16 (ff. 15–16). Synonymy given by: Gray, 1850: 33; Duméril, Bibron, & Duméril, 1854: 114. See Boulenger, 1882: 35 and Gassó Miracle *et al.* (2007) for details.

Onychodactylus schlegeli Tschudi, 1838: 92. Substitute name for *Salamandra unguiculata* Temminck & Schlegel, 1838. See Gassó Miracle *et al.* (2007) for details. See also Duméril, Bibron, & Duméril, 1854: 113–114 (Atlas, pl. 93; f. 1). See Dunn, 1923: 507 for comment.

Onychodactylus japonicus—Bonaparte, 1839: fasc. 26; pages unnumbered; Gray, 1850: 33 (pl. III, f. 15) (gives together with *Molge striata* Merrem, 1820 at p. 31); Strauch, 1870: 60. [Also cited by: Troschel, 1877: 199 (pl. XV); Hilgendorf, 1880: 121; Boulenger, 1882: 35; Rein, 1884: 188; Cope, 1889: (pl. 46; f. 6); Fritze, 1891: 239; Okada, 1891: 65; Sclater, 1892: 37; Boettger, 1892: 58; Ichimura, 1897: 361; Tago, 1903: 464; Tago, 1904: 43; Nomura, 1905: 226–228; Stejneger, 1907: 42 (pl. V, f. 1–4, pl. VI); Tago, 1907: 239–244; Namiye, 1908: 399; Okajima, 1908: 351–381; Okajima, 1909a: 171; Okajima, 1909b: 182; Yoshizawa, 1914: 454; Dunn, 1918: 454; Okajima & Tsusaki, 1921; Okajima, 1922: 196; Dunn, 1923: 506–512; Kobayashi, 1931: 709–710; Tago, 1931: 200–210, pl. XXV; Okada, 1933: 165–166; Kudo, 1934a: 1–16, pls. I–III; Okada, 1934: 19; Sato, 1934: 465–466; Kudo, 1934b: 1–18, pl. 1; Okada, 1935: 583–584; Takashima, 1936: 23; Sato, 1937: 44–45; Okada, 1937a: 185–188, ff. 10–13; Okada, 1937b: 263–268; Sato, 1937: 45–47, ff. 4, 41, 41; Sato, 1939: 763–764; Nakamura, 1941: 422–426, f. 2; 515–521, f. 8; and many other authors.]

Onycopus sieboldii—Duméril & Bibron, 1841: 4. (Substitute name for *Onychodactylus schlegeli* Tschudi, 1838). Treated as *lapsus calami* by Dunn (1923: 507).

Onychodactylus schlegeli—Duméril & Bibron, 1841: 114.

Onychopus sieboldii—Duméril, Bibron, & Duméril, 1854: 113 (Atlas, pl. 93; f. 1).

Salamandra (Onychodactylus) unguiculata—Schlegel, 1858: 60.

Onychodactylus Schlegelii—Strauch, 1870: 60 (*lapsus calami*).

[*Onychodactylus sp.*—Parker, 1879: 188 (pl. 19, ff. 1–3).]

Onychodactylus Japonicus—Tago, 1903: 464.

Onychodactylus japonicus—Tago, 1904: pp. 41, 43, pl. I, ffs. A_I–A_{IV}. Unjustified emendation of the original spelling.

Ouychodactylus japonicus—Tago, 1904: p. 43 (*ex errore*).

Ornychodactylus japonicus—Hashimoto, 1910: p. 499 (*ex errore*).

Onychodactylus japanicus—Ye, Fei, & Hu, 1993: 28 (*ex errore*).

Vernacular and trivial names:

Chinese name: Riben Zhaoni (日本爪鰐).

English name: Japanese Clawed (Lungless) Salamander.

Japanese name: Hakone-Sansyouo (modern name, see Okada, 1934: 19); Hibihari (historical name, see Kuzmin, 1995).

Korean name: Ilbon Ggorichire Dorongnyong.

Russian name: Yaponskiy kogtistyi (bezlegochnyi) triton.

Taxonomic comment. As it is evident from the synonymy given above, there are two available valid synonyms for *Onychodactylus japonicus*: *Salamandra japonica* Houttuyn, 1782 and *Salamandra unguiculata* Temminck &

Schlegel, 1838. The first description by Houttuyn (1782) was based on a specimen collected by C. P. Thunberg from Japan, as it is stated in the original description without any specification. Five years later Thunberg himself describes *Lacerta japonica* Thunberg, 1787 from "Fakoneberget" (Hakone mt.). We assume that Thunberg had no idea about Houttuyn's description (see Thunberg, 1791), thus this publication seems to be an independent description of the species, rather than a change of its generic affiliation or a substitute name, as assumed by Frost (2009). For this reason, Brame (1972) restricted the type territory of *Salamandra japonica* Houttuyn, 1782 to "Fakoneberget" and there were several attempts to find the possible type in zoological collections in Sweden. In fact, it is more reasonable if the type specimen of *Salamandra japonica* Houttuyn, 1782 exists in Dutch collections. However, there are no specimens in Leiden or Amsterdam zoological collections, thus the type specimen seems to be lost. *Salamandra unguiculata* Temminck & Schlegel, 1838 was described from the collections made by Ph. F. von Siebold, brought from Japan to Holland and stored in RMNH, Leiden, later the name *Onychodactylus schlegeli* Tschudi, 1838 was applied to the same specimens. Siebold's collections of *Onychodactylus* in Leiden museum consist of RMNH 2289 (20 adults, mostly females dried and smoke-dried for medical purposes by local people, evidently were bought from them by Siebold during his journey from Nagasaki to Edo (Tokyo), most probably at Hakone check-point, Hakone mountain pass, Kanagawa – Shizuoka border, Fig. 8, B); RMNH 2290 (8 adults, Fig. 8, A); RMNH 2291 (7 larvae), RMNH 2292 (4 adults, Fig. 9) and RMNH 18560 (complete skeleton). These series were examined by Hoogmoed (1978: 97). Also through exchange with RMNH types are stored in Harvard (MCZ 21320; Barbour & Loveridge, 1946: 188), and Paris (MNHN 4692; 6 animals: lectotype, and 5 paralectotypes designated erroneously by Thireau, 1986: 78–79). RMNH 2292A was designated as the lectotype by Hoogmoed (1978: 97).

Considerations about the type locality of *Salamandra unguiculata* Temminck & Schlegel, 1838. In the original description of *Salamandra unguiculata* by Temminck & Schlegel, (1838) no exact designation of the type locality is given, though the distribution of the new form is described as: "*Elle se trouve en abundance dans les contrées montueuses des îles Nippon [island of Honshu or Hondo] et Sikok [island of Shikoku], particulièrement dans les provinces Sagami, Shinano, Tanba, Tajima et Tosa, situées entre les 33 et 36 degrés de latitude boreale*" (It is quite common in the mountains of islands of Nippon, Shikoku, in particular, in provinces Sagami [present Kanagawa Prefecture], Shinano [present Nagano Prefecture], Tanba [present Kyoto Prefecture], Tajima [present Hyogo Prefecture] and Tosa [present Kochi Prefecture, Shikoku island], situated in-between 33rd and 36th degrees of northern latitude), Japan (Temminck & Schlegel, 1838: 125, see Fig. 10). It is evident that this note actually describes the species range as known to Siebold, but is not the designation of the actual locality of origin of the specimens which were used in the description. The type locality for *Salamandra unguiculata* is therefore the locality of the lectotype designated by Hoogmoed (1978). Considering the high interspecific divergence within *Onychodactylus japonicus* sensu lato, a clarification of the type locality for *Salamandra unguiculata* as one of the few valid junior synonyms available, would be required. The only precise locality which is described in the original publication is the "monts Facone" or "monts Fakone" (Hakone mountain), and it is noted that Siebold personally visited this locality (Temminck & Schlegel, 1838: 125). All known type specimens, including the designated lectotype and the series seems likely to come from this locality or at least from the central part of Honshu, which is confirmed by morphological analysis of the type specimens (see Fig. 6). Thus, based on the examination of the type series and the lectotype designated by Hoogmoed (1978: 97), we consider that the type locality of *Salamandra unguiculata* Temminck & Schlegel, 1838 should be restricted to "monts Fakone" (environs of Hakone check-point at the Hakone mountain pass, prov. Sagami, now border of Kanagawa and Shizuoka prefectures, Honshu, Kanto district, Japan). A note made by E. R. Dunn (1923: p. 511): "There is considerable similarity between Schlegel's and Tago's account of the habits [of *O. japonicus*] and one wonders whether Schlegel also did not have reference to Kuroyuwa near Hakone", is also in favor of our conclusion. Iizuka *et al.* (2011) analyzed the original description of *Salamandra unguiculata* Temminck & Schlegel, 1838 and compared information on species "habitat" with memoirs on Siebold's travel from Nagasaki to Edo (Siebold, 1897) and concluded that the Hakone checkpoint seems to be the only possible locality where the type materials could have been collected by Siebold himself or his students. They also compared coloration patterns of the lectotype and paralectotypes of *Salamandra unguiculata* Temminck & Schlegel, 1838 with specimens from the Hakone environs; their data also confirm that the type series of *Salamandra unguiculata* was most probably collected near Hakone checkpoint, nowadays the bank of the Sukumo-gawa (river) at Hata-juku (station), Hakone-machi, Ashigarashimo-gun, Kanagawa Prefecture (Fig. 10, see Iizuka *et al.*, 2011: 123 for details).

A**B****2 cm**

FIGURE 8. Ph. F. von Siebold's collection of *Onychodactylus japonicus* collected in Japan between 1824 and 1829 and stored in the RNHM. (A)—RMNH-2290 (four well-preserved adult specimens showing dorsal pattern); (B)—RMNH-2289 (smoke-dried specimens of *O. japonicus*, collected by local people). Note holes in salamander heads from bamboo sticks for smoke-drying. This traditional way of salamander smoke-drying for medical purposes used to be typical for Hakone environs, central Honshu (Iwasawa, 1976). Scale bar is 2 cm. Photos by N.A. Poyarkov.

Diagnosis. A slender, relatively medium-sized hynobiid salamander, a member of the genus *Onychodactylus* on the basis of the following combination of features: absence of lungs, presence of black, claw-like horny structures on both fore- and hindlimbs in larvae and breeding adults, tail longer than the sum of head and body lengths, tail almost cylindrical, slightly compressed at the tip, vomerine teeth in transverse short, arch-shaped series almost in contact with each other, presence of large premaxillary fontanelle completely separating the nasals, presence of more than 9 caudal ribs, presence of skinfolds in larvae on the posterior edges of both fore- and hindlimbs and dermal flaps in males being developed during the breeding season, with diploid chromosome number $2n = 78$ and other typical features of the genus. *O. japonicus* is different from the other members of the genus in a combination of the following attributes. In meristic characters, the species is distinct in having 17 (16–18) presacral trunk vertebrae, 11 (11–12) costal grooves (Tab. 6), 11–12 (9–14) vomerine teeth in each vomerine tooth series (Tab. 7), relatively deep, gently curved vomerine tooth series with no gap between them (Fig. 4, E). In morphometric characters, the species is distinct in having a relatively small SVL, a comparatively longer tail in males, relatively narrower head in both sexes and a relatively smaller distance between the eyes (Tab. 4, Tab. 5) than in other species. Black, sharp claws are well developed and appear on fore- and hindlimbs in both sexes during the breeding season and may also be found outside of the reproductive season. In coloration the species is distinct in having a light, usually brightly colored dorsum (from yellow-brown to bright red), and normally showing a distinct light dorsal band which is obvious both in premetamorphic larvae, juveniles and adults (Fig. 5, F, G); the band can be discontinuous (Fig. 5, F) and can have no clear borders (Fig. 11, A). Juveniles of this species usually have a dark ground color and a distinct light dorsal band.

Description and variation.

Type specimens. No type specimens are known for *Salamandra japonica* Houttuyn, 1782 or *Lacerta japonica* Thunberg, 1787, though more intensive searches in European herpetological collections would be important (in particular, in the collections of ZIUU, ZMA and RMNH). However, both descriptions are illustrated and the specimens figured in the original publications (Houttuyn, 1782: pl. facing p. 336, f. 3; Thunberg, 1787a: pl. IV, f. 1) should be treated as types. Houttuyn (1782) indicates “Japan” as the area of origin, however since Houttuyn acquired his specimens directly from Thunberg and in his publication he clearly states that the type territory of the materials is the “Fakoneberget” (Hakone mt.), there is no reason to believe that *Salamandra japonica* Houttuyn, 1782 come from somewhere else. Specimens figured in both works are also quite similar, both showing the obvious light dorsal band on back and tail with clear edges, which corresponds well to the typical *O. japonicus* morphotype from central Honshu. Since the majority of other names proposed for this species are substitute names or misspellings, the only other name available for Japanese *Onychodactylus* remains the *Salamandra unguiculata* Temminck & Schlegel, 1838, which is fortunately represented by a large type series in European and U.S. museums. Thus, the description of the type material of this species is of certain taxonomic importance. The holotype was not designated in the original publication, however a large series of materials brought from Japan by Siebold and stored in the RMNH comprise the series which is believed to contain the type specimens. From this museum, specimens were sent to the MNHNP and the MCZ. Hoogmoed (1978: 97) designated RMNH 2292A as the lectotype, and the rest of the series as paralectotypes; later Thireau (1986: 78–79) erroneously designated MNHNP 4692 as a lectotype and 5 paralectotypes; however Hoogmoed’s designation has the priority as the first reviewer. We included measurements of the four specimens from the type series (RMNH 2292A-D, see Fig. 9) in the PCA analysis of available *Onychodactylus* samples; they clustered well within the nominative form of *O. japonicus* from central Honshu showing no significant differences from the Hinoemata population as in univariate and multivariate analysis (see Fig. 6, star-marks). Thus, we can assume that the type series of *Salamandra unguiculata* is identical with the central Honshu population of *O. japonicus* (see above). Below we give a brief description of the *Salamandra unguiculata* Temminck & Schlegel, 1838 lectotype.

Description of the lectotype. RMNH 2292A (Fig. 9), an adult male in a good state of preservation; fixed in wine spirit, stored in alcohol; with the following measurements (mm, alcohol preserved specimen): snout-vent length (SVL): 62.5; tail length (TL): 71.4; gleno-acetabular distance (GA): 39.3; forelimb length (FL): 16.8; hindlimb length (HL): 19.6; head length (HL): 13.5; head width (HW): 9.7; eye length (EL): 3.5; internarial distance (IN): 4.8; orbitonarial distance (ON): 2.4; interorbital distance (IO): 2.8; chest width (CW): 6.6; snout length (OR): 4.4; intercanthal distance (IC): 6.2. The type has 4 fingers and 5 toes without webbing; relative length of fingers $1 < 4 < 2 < 3$; relative length of toes $1 < 2 < 5 < 4 < 3$. The paralectotype has well-developed claws on all limbs. 17 trunk vertebrae (TVN); 12 costal grooves on both body sides (CGN); vomerine teeth in two slightly but

noticeably curved series and had 12 / 11 teeth (left / right series respectively). The vomerine tooth series are contact and have no signs of gap between them. Outer branches of the vomerine series are slightly longer than the inner one and end posteriorly to the end of the inner branches. The lectotype RMNH 2292A has definitely faded coloration: after almost 200 years in alcohol the dorsal surfaces are light-orange or yellowish-brown, sides of tail and body are chocolate-brown to grayish-brown and the ventral surface is creamish-gray. However, the specimen and the whole series is amazingly well-preserved (excluding dissected belly, damaged elbow of the left forelimb, 2nd and 3rd toes of the right hindlimb and a small part of tissue is absent on the ventral surface of the tail in the last third of its length), only slightly damaged and all details of the coloration pattern are clearly visible. The distinct feature is the presence of comparatively thin (ca. one half of head width) light dorsal band which is wide at the base of the head, and becomes thinner in the neck region and continues along the dorsum fading in the last third of the tail length. The edges of the light dorsal band are clearly visible and have a slightly undulating profile though they are almost parallel. There is a slight black mottling on the dorsal surface of the head between the eyes and an unclear dark middorsal line in sacrum area, no spots or mottling on the extremities or ventral sides of the body were noticed. The specimen clearly has visible male secondary sexual characters such as rounded and flattened tail tip, black claw-like structures that are well-developed on every digit, and there are well-developed skinfolds on the lateral sides of the hindlimbs. This indicates that it is likely that the specimens were collected in spring during the breeding season.



FIGURE 9. The type series of *Salamandra unguiculata* Temminck & Schlegel, 1838 (RMNH 2292). RMNH 2292A—The lectotype, adult male; RMNH 2292B-D—Paratypes, presumably from Hakone environs, central Honshu. Scale bar is 2 cm. Photos by N.A. Poyarkov.

Variation.

Morphometrics. Morphological measurements of the species representatives and their variation are shown in Tables 4 and 5. The species is in general characterized by the following morphometric parameters (ranges for males/females, 70 specimens): snout-vent length (SVL): 52.0–75.3 / 58.2–77.3; tail length (TL): 68.5–99.1 / 59.7–79.2; gleno-acetabular distance (GA): 29.1–42.2 / 30.5–40.5; forelimb length (FLL): 15.9–23.0 / 16.4–20.7; hindlimb length (HLL): 17.6–25.4 / 19.0–23.2; head length (HL): 12.2–15.7 / 13.1–17.3; head width (HW):

7.4–9.7 / 7.5–9.9; eye length (EL): 2.8–4.1 / 2.9–3.6; internarial distance (IN): 3.6–4.6 / 4.0–4.9; orbitonarial distance (ON): 2.2–3.0 / 2.0–2.6; interorbital distance (IO): 2.5–3.6 / 2.8–3.4; chest width (CW): 5.9–7.5 / 5.6–6.8; snout length (OR): 3.9–4.9 / 4.1–4.9; intercanthal distance (IC): 4.8–6.0 / 5.7–6.1 (measured on the preserved specimens). From a morphometric point of view *O. japonicus* sensu stricto (populations from central Honshu) is quite different from its congeners; in PCA analysis for males they were found to be closer related to *O. koreanus* (Korean populations) males (Fig. 6, A) rather than to other *Onychodactylus* species from the north of Honshu or the mainland NE Asia. In females scores for *O. japonicus* largely overlap with those for *O. zhaoermii* (Liaoning populations) (Fig. 6, C), to which they also show similarity in TVN and CGN (see Tab. 6). However, these species are clearly distinct in a number of morphometric and meristic characters and are unlikely to be confused with any congeners (see Results and Comparisons).

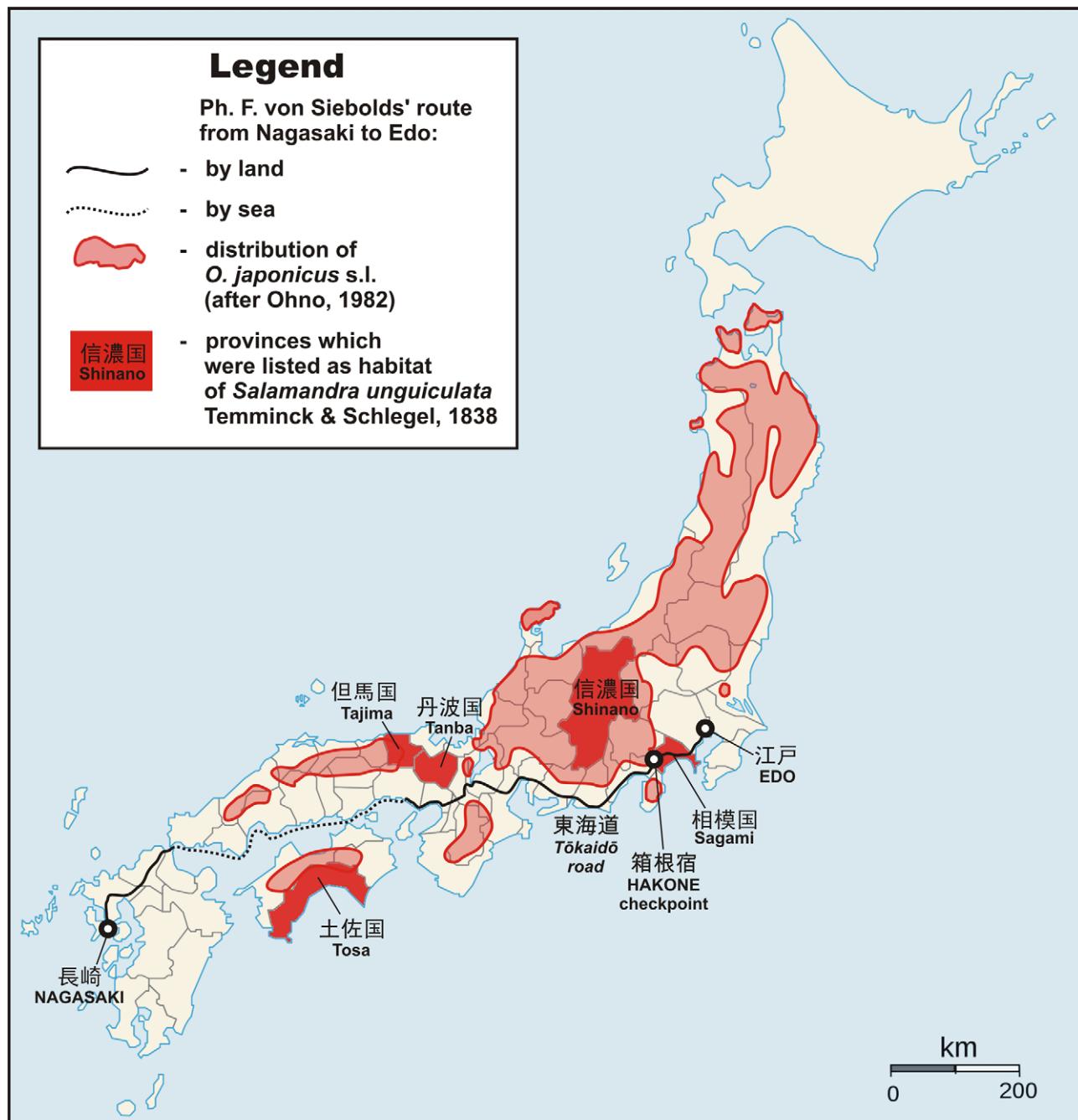


FIGURE 10. Provincial map of Japan of Edo era (*Edo jidai*) and Ph. F. von Siebold's route from Nagasaki to Edo (modern Tokyo). Province borders are shown with thin lines, those provinces which were mentioned in “Habitat” of *Salamandra unguiculata* Temminck & Schlegel, 1838 in “Fauna Japonica” are marked with red. Ph. F. Siebold's route by land and by sea is shown; the most probable area for collection of *Onychodactylus* is environs of Hakone standpoint, the last major standpoint on the Tokaido road leading to Edo.

Sexual variation. The sexual dimorphism in morphometric features in *O. japonicus* was reported by many authors (including Thireau, 1975a; Thireau, 1975b; Akita, 1982; Akita, 1983; Akita, 1985; summary by Kuzmin, 1995). Sexual variation in morphometric features is found in several measurements (see Results, Tab. 5); our results are concordant with previously published data. The sexes are significantly different in total length, mostly due to relatively longer tails in males (Tabs. 4; 5). However, we did not find significant differences in body size (though females tend to have larger SVL-values); this result is concordant with data on non-significant differences in body mass between the sexes at least out of the breeding season (see Akita, 1983b; Kuzmin, 1995). Males have significantly longer tails; and research by Akita (1983a; 1985b) shows that males also have significantly higher tails than females. In females, the head is significantly longer than those of males, while the differences in head width were found to be insignificant. No significant differences in limb length were reported. Thus, *O. japonicus* shows a different pattern of sexual variation in morphometric characters when compared with *O. fischeri*.

Secondary sexual characters. Secondary sexual characters are well developed in *O. japonicus* and allow us to distinguish sexes even out of the breeding season. Numerous data on sexual dimorphism in this species are given in several works (including Stejneger, 1907; Dunn, 1923; Sato, 1943; Thorn, 1968; Kuzmin, 1995). Similar observations were noted as with other species of the genus *Onychodactylus*, during the breeding season male *O. japonicus* develop a large skin fold on the outer surface of hindlimbs from the 5th toe to the tibia which is used by the males for clasping egg-capsules during the fertilization process. Normally this skin fold has a lighter coloration than the rest of the limb, and the remains of this fold can be seen outside of the reproductive season as well. I. Sato (1943) reported that males develop dark horny asperities on the inner surface of the hindlimbs, which can also be found on forelimbs but are always absent in females. This feature seems to be unique for *O. japonicus* among other *Onychodactylus* species. During the breeding season male *O. japonicus* have more swollen vent than females and lateral vent folds converge obliquely, whereas in females they are more or less parallel to the cloacal slit (Sato, 1943). Breeding males have a notably enlarged, flattened and somewhat gently rounded tail tip; tail tip is narrower and tapered in females (Sato, 1943). Black horny claws are well-developed in both sexes in *O. japonicus* during the breeding season on fore- and hindlimbs and can usually be present even out of the breeding season, although they are absent in juveniles, and normally absent in overwintering animals.

Color in life. *O. japonicus* shows great variation in coloration and pattern across its range. This variation was described for the first time by Sato (1937b; 1943), who defined two main coloration types: the eastern (central Honshu) and the western (western Honshu and Shikoku) types. In central Honshu, from where the type of *O. japonicus* most probably comes from, the typical coloration resembles presented in Fig. 5, G. Adults in these populations have dark background color: usually it is dark-brown or gray-brown, with dark dots on flanks. The presence of light unbroken dorsal stripe is typical for this group of populations; normally the dorsal stripe has straight or slightly waving but clearly defined borders (see Fig. 8, A and Fig. 9); often these borders are darker than the flanks, so they look almost like two dorsolateral black stripes on body and tail (Dunn, 1923). The light dorsal stripe starts broadly on the head basis behind the eyes, then narrows at neck regions and goes almost straightly along the middle of the dorsum, extending on tail dorsal surface, here its borders may become more irregular (Fig. 8, A). Usually this stripe is yellowish brown to orange or copper, though interpopulational variability is high. Specimens from one population may vary in degree of black spotting on dorsal surface. In some populations in north-central Honshu, salamanders have indistinct light dorsal stripes without clear borders (see Fig. 11, A), covered with numerous dark mottling. Body flanks below the dorsal stripe are brownish, getting cream color clouded with darker towards ventral surfaces, getting nearly uniform cream to light pinkish-brown color below. In the western part of the range, i.e. in western Honshu and Shikoku, animals have much more contrasting coloration pattern (see Fig. 11, A–C). Sides are usually much darker than in the east: coal-black to dark brown, sometimes with purple or violet tint. The dorsal stripe is normally divided into large irregular spots with broken borders, and is usually much brighter—vermillion red to orange, much contrasting with the sides (Sato, 1943; Nakamura & Ueno, 1963; Goris & Maeda, 2004). Such coloration type is never observed in central Honshu (Sato, 1943), however in Kinki area (Kansai region, southern central Honshu) populations with two types of coloration are known (Yoshikawa *et al.*, 2010a; 2010b). Recent progress in molecular taxonomy of the *O. japonicus* complex (Yoshikawa *et al.*, 2008, 2010a; this paper) revealed a number of geographically restricted lineages of unclear taxonomic status. It is quite possible that careful examination of geographic variation of coloration and pattern across *O. japonicus* complex range will evaluate characters which would be valuable for diagnostics of these lineages. No data on differences in coloration between males and females have been reported so far.



FIGURE 11. *Onychodactylus japonicus* s.str.: (A)—Adult male from Hinoemata village, Fukushima Prefecture, Japan; photo by E. Yakhontov, courtesy of N.A. Poyarkov; (B)—Premetamorphic larva of *Onychodactylus japonicus* from Kinugawa environs, Tochigi Prefecture, Japan; photo by N.A. Poyarkov.

Color in preservative. Color patterns in fixative correspond with coloration in life, but the warm tints fade from the coloration rather quickly (first to disappear are the reddish and yellowish colors), and the dark color intensity decreases to grayish-brown. However, characteristic coloration patterns do not change and can be observed even in specimens collected nearly two centuries ago (Figs. 8, 9).

Osteology and anatomy. *O. japonicus* is one of the best studied hynobiids species in terms of anatomy, since many classical works by Japanese morphologists have studied it for more than a century. A detailed description of

axial column and vertebral morphology of *O. japonicus* was given by Okajima (1908) (based on specimens from Kyoto). Skull morphology is described in detail in classical works by Okajima (1908), Okutomi (1936), and Okajima & Tsusaki (1921). Systematic description of skull morphology of *O. japonicus* is given in a monograph by Sato (1943). Hyobranchial apparatus morphology is described by Okajima (1909b; 1922), who also wrote a paper on the sense organs in *O. japonicus* (Okajima, 1909a). All these works refer to *O. japonicus* sensu stricto. Variation in the number of trunk vertebrae (TVN) and number of costal grooves (CGN) among the studied specimens of *O. japonicus* are presented in Table 6. Modal TVN-number in *O. japonicus* is 17 for both sexes, though the ranges vary (16–18 for males, mean value is 17.4 ± 0.51 ; 17–18 for females, mean is 17.2 ± 0.41). This is the smallest TVN-number known so far for the genus *Onychodactylus*. The trunk-vertebrae numbers result in the respective costal groove counts: 11 (11–12) for both males and females (based on 46 specimens, see Tab. 6).

Vomerine teeth morphology. In adults of *O. japonicus* vomerine teeth are arranged into two rather shallow, noticeably curved arch-shaped transverse series with almost equal lengths of inner and outer branches and no gap between them (Fig. 4, E). Each series begins behind inner edge of nares, curves forward and in to level of anterior edge of nares, then back and in to meet the series of the other side, however not so far back in the middle as on the sides (Dunn, 1923). Both outer and inner branches are noticeably folded in this species, the outer branch is slightly more curved than the inner one (see Fig. 4, E). The teeth at the very end of inner branch are located approximately on the same level as the posterior angle of the branch. Posterior angles of the series inner branches are located almost on the same level as the ends of the outer branches behind the nares or slightly anteriorly. Variation in the number of vomerine teeth (VTN) among the studied specimens of *O. japonicus* are presented in Table 7. In our sample the number of vomerine teeth in the species is the quite small: 9–14 (mean 12.1 ± 1.24) teeth per each branch in males and 9–13 (mean 11.0 ± 0.99) for females (based on 48 specimens, see Tab. 7).

Eggs and clutch. Reproductive biology, egg-laying, egg sacs, eggs and larvae of *O. japonicus* are described in detail in works by Akita (1982, 1983, 1985, 1996) and Akita & Miyazaki (1991). Breeding occurs in the underground portion of a stream: usually in spawning sites located in gravel and between large stones under the ground in areas of stream sources. As in other *Onychodactylus*, the eggs are deposited in two gelatinous, elliptical egg sacs, which are joined together at the distal end, from where a gelatinous stalk arises. This stalk is usually 1.5–3.5 times shorter than the total length of the sac and is employed to attach the clutch to a stone. Pairs of egg sacs are often attached to stones in a small underground cavity where cold springs emerge to form the headwater of a mountain brook (Akita, 1982, 1983). As a result of group spawning, many sacs laid by different females may be found attached to a single stone. For reproductive purposes *O. japonicus* is dependent on cool, well aerated water and availability of hiding places, where a high density of clutches may be observed (Sparreboom, 2012). Females lay two paired egg sacs with semitransparent white, strong walls. Egg sacs are elliptical in shape and joined together at the distal end where they are attached to a stone by a gelatinous stalk. Average clutch size is 11–24 eggs, egg diameter varies from 4.5 to 5.4 mm (Akita, 1985). In the laboratory, after hormonal stimulation to induce breeding, the number of eggs laid by one female was reported as an average of 11 (for two egg sacs); eggs are pale yellow in color and ca. 5mm in diameter (Iwasawa & Kera, 1980). Size of the egg sac may differ by site and is dependent on female size and perhaps also the time of deposition (Kuzmin, 1995 and references therein). Large portions of the clutches are asymmetrical with respect to the number of eggs in the egg sacs (Akita, 1982). The maximum number of ovarian eggs (36) was observed in the largest female (with total length 17 cm) (Akita, 1985).

Larval morphology and metamorphosis. The first descriptions of *O. japonicus* larvae are given in the papers by Tago (1904, 1907a, 1907b, 1931), and detailed descriptions are also provided by Sato (1937b, 1943). Kudo (1934a, 1934b, 1935) provided the first observations on the species reproduction in the wild and studied larval development in *O. japonicus*. The most detailed description of embryonic and larval development, including external larval morphology from hatchling until metamorphosis with a table of normal stages of development for *O. japonicus* was presented by Iwasawa & Kera (1980). Limb development in *O. japonicus* was studied by Iizuka *et al.* (2010). Iwasawa & Kera (1978) developed a method of inducing artificial breeding by hormonal stimulation in *O. japonicus*. The progress of embryonic development is remarkably slow. In the laboratory (water temperature approximately 10 °C), the embryos hatched after an average of 142 days (Iwasawa & Kera, 1980). In nature, larvae begin feeding long after hatching when they appear in the streams around 30–45 mm in length. At this stage the larvae are characterized by a number of features typical for the genus *Onychodactylus*: digits with black, cone-shaped sharp horny claws, a square-shaped head which is wider than the body, a well-developed labial fold, comparatively short gills, eyes slightly prominent, and posterior edges of fore- and hindlimbs with a characteristic

dermal flap disappearing towards the onset of metamorphosis (see Fig. 11, B). Claws appear when the larvae reach a total length of 25 mm approximately after 142 days of development. A low, upper caudal fold begins to develop on the back surface of the tail in the first third of its length; the lower caudal fold does not reach the cloaca on the ventral side of the tail. After hatching larvae apparently stay at the oviposition sites at underground stream sources and springs for several months, then migrate downstream and begin to feed. Total time period of larval development is fully two years or longer, and the body size of metamorphosing larvae is 70–100 mm in total length (Iwasawa & Kera, 1980). In the wild, larvae usually begin metamorphosis and migrate onto land in the fourth summer following their hatching at a total length of about 80 mm (Hayase & Yamane, 1982). Larval coloration is quite variable and varies across the species range and within individual populations. Typically, the base color in larvae is dark-brownish to blackish, and larvae develop dark pigment at a length of ca. 40 mm. Larvae get darker as metamorphosis progresses along with growth and development of melanophores. Ventral surfaces lack black spots and are always lighter than the flanks and the dorsum. Closer to metamorphosis larvae develop bright dorsal coloration, usually in a form of a light dorsal band (see Fig. 11, B) or as a series of irregular, light (yellowish, orange, reddish) blotches and spots over the dark background color. There is great variation in color, some larvae having a marked dorsal light stripe, while others do not (Dunn, 1923). This coloration is usually retained after metamorphosis. During metamorphosis the black horny claws are shed. After metamorphosis it may take several years to develop the full adult coloration, at which point the black, cornified claws develop again during the reproductive season.

Etymology. The specific name “*japonicus*” is a toponymic adjective in the nominative singular; Houttuyn gave this name indicating that the type specimens were brought from Japan.

Distribution. Endemic to Japan. Distribution of *O. japonicus* (sensu lato) is described in many works and is summarized in works by Tago, 1931; Sato, 1937b; 1943; Ohno, 1982; Kuzmin, 1995; Akita, 1996. The species inhabits mountainous areas of the Japanese islands of Honshu and Shikoku, not reaching Hokkaido. In Japan, *Onychodactylus* are found in the Chugoku region (Hiroshima, Shimane, Okayama, Tottori prefectures), Shikoku (prefectures Ehime, Kochi, Tokushima, Kagawa prefectures), Kinki or Kansai region (Hyogo, Kyoto, Nara, Shiga, Wakayama, Mie prefectures), Chubu region (Fukui, Gifu, Aichi, Shizuoka, Nagano, Ishikawa, Toyama, Niigata, Yamanashi prefectures); Kanto region (Kanagawa, Tokyo, Saitama, Gunma, Tochigi, Ibaraki prefectures) and also inhabits the southern part of Tohoku region (Fukushima, Yamagata and Miyagi prefectures). The northern border of the range of *O. japonicus* (sensu stricto) is discussed in Yoshikawa *et al.*, 2008. A number of populations in the Chugoku region, Kanto region and Ishikawa Prefecture appear to be isolated from the main part of the range. Okada (1934: 19) gives the species’ range in Japan as „Honshu, Shikoku and Kyushu“, however records from Kyushu were never confirmed by further surveys.

Comparisons. *Onychodactylus japonicus* (Houttuyn, 1782) can be distinguished from the other salamanders in the region by its slender body, smooth skin with distinct costal grooves on the flanks, very long tail, almost cylindrical at the base, slightly compressed in the middle and flattened towards its end, small and somewhat elongated head with rounded snout, and a combination of morphological features characteristic of *Onychodactylus*, such as absence of lungs, dermal flaps being developed on the outer surface of the hindlimbs in breeding males, both sexes during the reproductive season posses black horny claws on both fingers and toes, vomerine teeth in two short transverse arch-shaped series, premaxillary fontanelle large fully separating nasals, caudal ribs numerous and present on more than 5–6 postsacral tail vertebrae. *O. japonicus* (Houttuyn, 1782) can be diagnosed from its congeners by showing a lower number of trunk vertebrae (16–18) and costal grooves (11–12), and by usual presence of a distinct light dorsal band.

O. japonicus (Houttuyn, 1782) can be further distinguished from other *Onychodactylus* species by a following combination of morphological attributes:

From *O. fischeri* (Boulenger, 1886) the species differs in vomerine tooth series being notably curved (versus almost straight or slightly bended in *O. fischeri*); left and right vomerine tooth series in contact, Fig. 4, E (versus a distinct gap that is present between the vomerine tooth series in *O. fischeri*; Fig. 4, A); in having a lower trunk vertebrae number (TVN): 17–18 (versus 20–21 in *O. fischeri*) and a lower costal groove count (CGN): 11–13 (versus 14–15 in *O. fischeri*) (Tab. 6); and dorsal coloration: light dorsal stripe is normally distinct and bright with usually quite robust edges, Fig. 5, G (versus light dorsal stripe not bright, indistinct with unclear edges in *O. fischeri*. Fig. 5, A). *O. japonicus* further differs from *O. fischeri* in following morphometric features (see Tab. 4, and Tab. 5 for details): comparatively longer tail in males, narrower heads in both sexes, eyes situated closer to each other than in *O.*

fischeri for both males and females, comparatively longer fore- and hindlimbs in both sexes. *O. japonicus* (Houttuyn, 1782) can be distinguished from the members of *O. koreanus* species complex (*O. koreanus* and *O. zhaoermii*) and *O. zhangyapingi* by dorsal pattern: prominent light-colored dorsal stripe present in *O. japonicus*, background color of dorsal surface is lighter than color of body sides (versus no prominent dorsal stripe, background color of dorsal surface is dark; usually back side of body is covered with numerous small contrast light spots, blotches or vermiculations in members of *O. koreanus* species complex and *O. zhangyapingi*). *O. japonicus* (Houttuyn, 1782) can be further distinguished from *O. koreanus*, *O. zhaoermii* and *O. zhangyapingi* by the form of vomerine tooth series: comparatively deep notably curved with outer and inner branches of the series being roughly of the same length (vomerine teeth arches are symmetrical) and the lateral end of the outer branch is located roughly on the same level as the medial end of the inner branch in *O. japonicus* (versus rows of vomerine teeth are slightly curved or bended with the outer branch usually being noticeably longer than the inner branch, vomerine teeth arch asymmetrical, and the lateral end of the outer branch is located posteriorly than the medial end of the inner branch in *O. koreanus* and *O. zhaoermii*; comparatively shallow, almost straight and not curved tooth series in *O. zhangyapingi*).

From the second *Onychodactylus* species on the Japanese island of Honshu—the other member of *O. japonicus* species complex, *O. nipponoborealis*, *O. japonicus* also differs in having shallower vomerine tooth series with smaller number of vomerine teeth (usually 9–14) and almost no gap between the series, smaller SVL and GA, relatively longer tail in males, a narrower head and shorter interorbital distance. For a more detailed comparison of *O. japonicus* (Houttuyn, 1782) with the new species *O. nipponoborealis* from Northeastern Honshu and with the new *Onychodactylus* species described from the mainland Northeast Asia see “Comparisons” in taxonomic accounts for *O. nipponoborealis*, *O. koreanus*, *O. zhaoermii* and *O. zhangyapingi* given below.

Karyotype. $2n = 78$, NF = 102. Chromosomal formula: 6M+2SM/ST+16ST+6T+48a, as reported by Ikebe *et al.* (1981). Morescalci *et al.* (1979) reported 60 chromosomes in the *O. japonicus* genome, whereas a provisional estimation of the diploid set was 58 ± 2 . In a more detailed study Ikebe *et al.* (1981) counted $2n = 78$; the karyotype includes six pairs of large-sized chromosomes; 1st, 2nd and 3rd pairs are metacentrics, 5th and 6th pairs submetacentrics. In the remaining chromosome pairs, seven medium-sized and 26 micro-chromosomes can be recognized; the centromere position in micro-chromosomes is not always discernible. The interspecific karyotype variation in *O. japonicus* was studied by Ikebe *et al.* (1995). The authors reported chromosome polymorphism in chromosome 4 of *O. japonicus* in four populations examined i.e. Tsukui (Kanagawa Prefecture), Tateyama (Toyama Prefecture), Hinoemata (Fukushima Prefecture), and Jogakura (Aomori Prefecture, here treated as a distinct species). Populations of *O. japonicus* from Tsukui, Tateyama, and Hinoemata had two or three types of chromosome 4, which possibly is correlated with high interspecific variability within this species and might indicate the presence of cryptic species.

Genome size. Genome size estimated using Feulgen densitometry reported as 102.30–106.17 by Olmo (1983). Our estimate of *O. japonicus* genome size is 106.2–106.6 pg per diploid nucleus; CV = 53.1–53.3 (DNA flow cytometry; six specimens from Kinugawa-koen, Tochigi Prefecture, Japan; N.A. Poyarkov, pers. obs.); peripheral red blood cells of the Ribbed Newt, *Pleurodeles waltl*, and the Southern Crested Newt, *Triturus karelinii karelinii* (Salamandridae), were used as a reference standard for genome size measurements).

Phylogenetic position. *O. japonicus* is a member of its own species complex, which also includes its sister taxon *O. nipponoborealis* (described below) from northeastern Honshu, with a degree of divergence between them up to 9.1% in COI sequences and 3.6% in 16S rRNA sequences of uncorrected pairwise genetic distances (Fig. 3; Tab. 3). Recent phylogenetic studies revealed unexpected cryptic diversity within the *O. japonicus* complex (Yoshikawa *et al.*, 2008, 2010a) and our work has also showed deep divergence between mtDNA lineages within the group. Yoshikawa *et al.* (2008) revealed four major clades within *O. japonicus* sensu lato: clade I of Yoshikawa *et al.* (2008) correspond to our clade J from the Tohoku region described below as *O. nipponoborealis*. Three other major clades (clades II, III and IV of Yoshikawa *et al.*, 2008) are closely related to each other (with uncorrected genetic distances ranging from 5.0 to 8.8% in COI and of 2.4 to 3.3% in 16S rRNA, see Tab. 3) and form a well-supported monophyletic group. The phylogenetic relationships within this group are not completely resolved both in the work by Yoshikawa *et al.* (2008) and in the present study. Clade II of Yoshikawa *et al.* (2008) corresponds to our clade I from Iwaki, according to Yoshikawa *et al.* (2008) it is found from southern part of Tohoku to the northern part of Kanto region. The population from Sakuragawa in Ibaraki Prefecture (subclade II-B of Yoshikawa *et al.*, 2008) is isolated by lowland territories of the Kanto plain and forms the sister clade to other populations

belonging to that lineage (subclade II-A of Yoshikawa *et al.*, 2008). Clade III of Yoshikawa *et al.* (2008) consists of three major subclades: III-A from north-central Honshu (Kanto and the northern part of Chubu region, corresponds to our clade H), III-B from south-central Honshu (mostly Chubu and Kinki (Kansai) regions) and III-C from south-western Honshu (Chugoku region, corresponds to our clade G). Finally, clade IV of Yoshikawa *et al.* (2008) is found in western Japan (corresponding to our clade F) and is also divergent: the relatively small area in Kansai (Kinki) at Kii peninsula and around Biwa Lake is inhabited by subclade IV-A, whereas Shikoku island is occupied by subclade IV-B, which is also found in two isolated populations in Chugoku region of the westernmost Honshu. This clade is quite divergent from other *O. japonicus* lineages with uncorrected genetic distances from all other lineages of 5.0 to 6.2% in COI and of 2.7 to 3.3% in 16S rRNA (Tab. 3). Considering deep divergence of mtDNA haplotypes (Yoshikawa *et al.*, 2008; present study), congruent with differentiation patterns revealed by means of allozyme electrophoresis (Yoshikawa *et al.*, 2010a, 2010b), marked geographic variation in coloration and other morphological traits (Sato, 1943), we can assume that these three major clades within *O. japonicus* complex represent distinct species. The range of clade H (III-A of Yoshikawa *et al.*, 2008) includes the area around Hakone on the border of Kanagawa and Shizuoka prefectures, which is the type locality for *Salamandra japonica* Houttuyn, 1782 and *Salamandra unguiculata* Temminck & Schlegel, 1838, which are so far the only available names for the species complex (see Synonymy). Thus the nominative form of *O. japonicus* corresponds to clade H, whereas two other putative taxa remain unnamed. The western Japanese clade F (clade IV of Yoshikawa *et al.*, 2008) is almost certainly a distinct *Onychodactylus* species, since reproductive isolation in the zone of sympatry with *O. cf. japonicus* (clade G) has been shown (Yoshikawa *et al.*, 2010a, 2010b) and the two clades are morphologically clearly distinct (see Fig. 12). The status of the north Japanese clade I (clade II of Yoshikawa *et al.*, 2008) is not that certain due to less pronounced divergence in allozymes and requires careful examination. Based on the degree of divergence and the lack of other morphological or biological characters so far that allow us to describe them as species, here we tentatively consider both putative taxa as unconfirmed candidate species (shown as *O. cf. japonicus* in Fig. 3).

Habitats and natural history. A review of works on ecological preferences, habitats and natural history of *O. japonicus* is given in the monographs by Kuzmin (1995) and Akita (1996). The reproduction biology, breeding ecology, annual activity and other aspects of natural history of this species were studied in detail on Hodatsu Mt., Ishikawa Prefecture, by Akita (1982, 1983, 1985, 1996) and Akita & Miyazaki (1991). Additional information on breeding sites in central Honshu was presented by Iwasawa *et al.* (1992) and Nambu (1996). Larval ecology at Mt. Tsukuba is studied in detail by Hayase & Yamane (1982). *O. japonicus* is a typical high altitude species (Sparreboom, 2012). Nearly all of the *O. japonicus* range lies in the zone of typhoon activity with a monsoon climate; mean temperature range of the coldest month (January) is from +5°C to -5°C; mean temperature of the warmest month (August) varies from +20°C to +23°C (Kuzmin, 1995). *O. japonicus* inhabits zones of coniferous, broad-leaved, deciduous and evergreen forests, and inhabits only mountainous regions. In Honshu it occurs at average altitudes from 300 to 2,000 m, but can also be found at lower elevations, down to 20 m (Nakamura, 1941; Goris & Maeda, 2004), it may also occur at higher elevations (Kuzmin, 1995). The local altitude preferences depend on geographic position. In the northern part of its distribution in central Honshu *O. japonicus* (*sensu stricto*) inhabits a wide range of altitudes, from 20 to 2,600 m a.s.l., but is most abundant at about 2,000 m (Ohno, 1982). The climate in this part of *O. japonicus* distribution is likely to be closest to the species ecological optimum (Kuzmin, 1995). In the south and south-west of the Honshu Island (Kinki (Kansai) and Chugoku regions) the species distribution becomes discontinuous. Here the lower limit of *O. japonicus* altitudinal distribution is comparatively high and the species is found at altitudes from 300 to 2,100 m a.s.l. (Ohno, 1982). In Shikoku, the altitude preferences of *O. cf. japonicus* lie within 700–1,750 m. On Shikoku and in the westernmost Honshu (Chugoku), *O. cf. japonicus* inhabits only the mountain ridges in the central part of the islands. The species is found in moist, cool and shady places in mountain valleys covered by mixed forests, with streams having an abundance of shelters like moss-covered rocks and stony ground cover. *O. japonicus* are locally quite abundant, preferring dense woodlands near small mountain streams, rivers and lakes with clear and cold water where temperatures ranging from 9 to 12°C. During the breeding season animals migrate to aquatic habitats. During the non reproductive season animals can be found on the ground under rocks, stones, fallen trees and logs, but remain close to springs and waterfalls (Kuzmin, 1995). *O. japonicus* feeds on a variable diet of aquatic, but mainly terrestrial invertebrates (Kuzmin, 1995). During spring or September-December migrations, high concentrations of salamanders may be found (Akita & Miyazaki, 1991). The breeding period, depending on altitude and latitude,

may start in April and continue until June in the southern parts of *O. japonicus* distribution, or start mid-May and extend to the end of June in central Honshu (Thorn, 1969). In Hodatsu Mt., Ishikawa Prefecture, two breeding periods per year were reported: at a single site reproduction was registered in spring and in autumn. Males seem to be biennial breeders while females are most likely triennial breeders (Akita & Miyazaki, 1991). Egg-laying and fertilization have not been observed in the wild and have not been documented thus far.

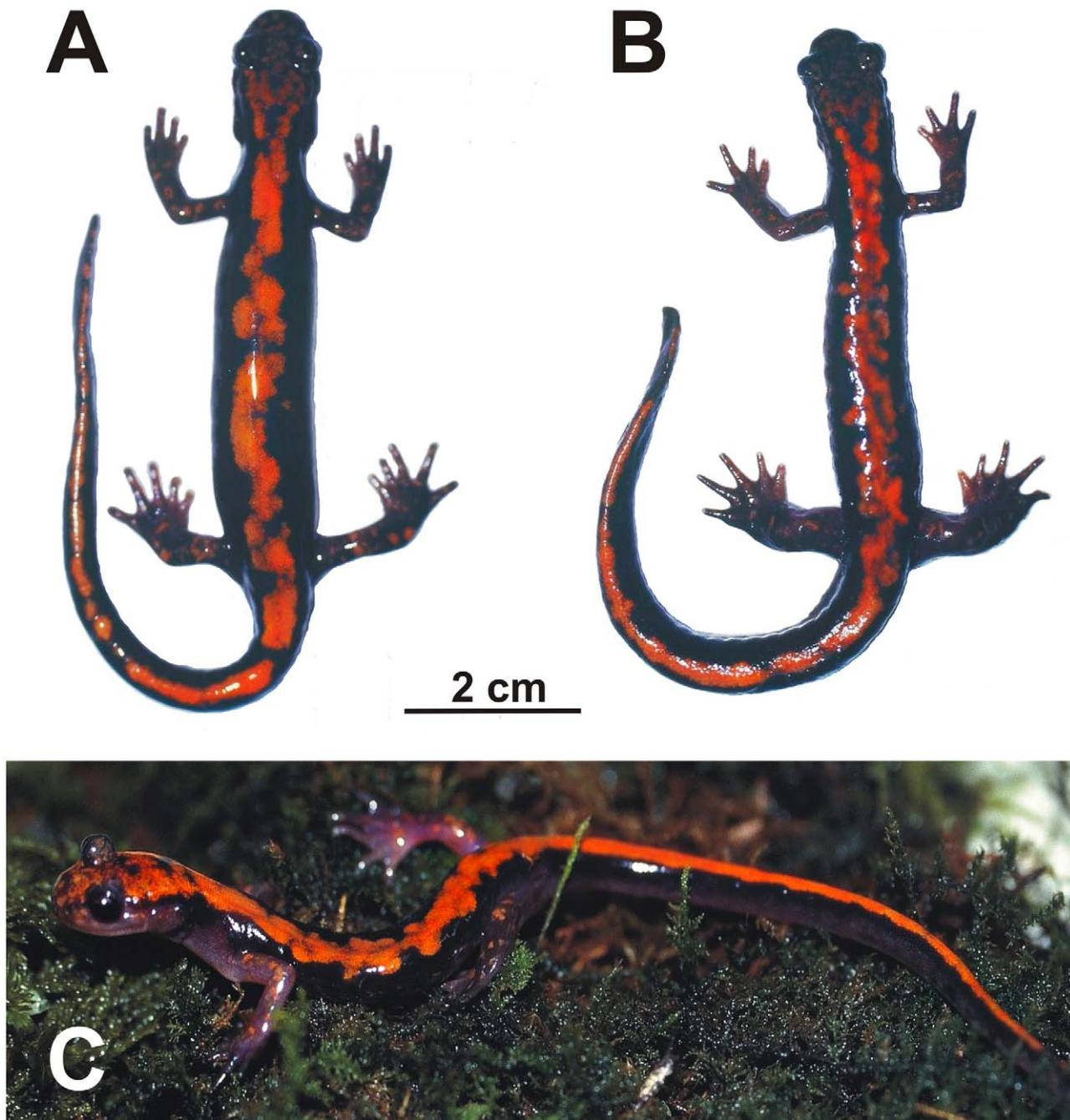


FIGURE 12. *Onychodactylus* cf. *japonicus* from Ishizuchi-san, Ehime Prefecture, Shikoku Island, Japan: (A) – Adult female, dorsal view; (B)—Adult male, dorsal view; (C)—Adult male in life, dorsolateral view. Scale bar is 2 cm. Photos by K. Iizuka.

Conservation status. *O. japonicus* is a locally abundant species and widely distributed across its range, including several protected areas, thus being one of the most common salamander species in Japan. It is therefore not included in the Red Data Book of Japan. Locally, like in Hinoemata village in Fukushima Prefecture for example, salamanders are collected during their migrations, for medicinal purposes (see Fig. 8, B) or served as a delicacy in restaurants. Habitat destruction and changes in freshwater quality may adversely affect this species (Kuzmin, 1995; Akita, 1996). Current IUCN red list status is of Least Concern (Kaneko & Matsui, 2004) and it

should be retained as such. However, future taxonomic revisions of this complex, especially from the western part of its geographic range, might result in new taxa of specific level; if so their conservation status should be reassessed.

***Onychodactylus nipponoborealis* sp. nov. Kuro-o, Poyarkov & Vieites**

[*Onychodactylus japonicus* (part)—Geerts, 1883 (?); Stejneger, 1907 (?); Tago, 1931; Inukai, 1932; Okada, 1934: 19; and many other authors.]

Recommended trivial names:

Chinese name: Riben Bei Zhaoni (日本北爪鲵).

English name: Tohoku Clawed Salamander.

Japanese name: Kita-Ohshu-Sansyouo.

Korean name: Buk-Ilbon Ggorichire Dorongnyong.

Russian name: Severoyaponskiy kogtistyi (bezlegochnyi) triton.

Holotype. NSMT-H5710, adult male, collected by Masaki Kuro-o and Masahiko Sotokawa on 15 August, 2009 (see Fig. 13, A–C).

Type locality. Near the summit of Yasute Mt., environs of Hirakawa City, Aomori Prefecture, Japan. In the mountain brooks at an altitude of 450 m a. s. l., geographic coordinates: 40° 33' N; 140° 38' E.

Paratypes. Males from the type locality (summit of the Yasute Mt., environs of Hirakawa City, Aomori Prefecture, Japan) (see Fig. 14, A): NSMT-H5711–5712 (2 adult males); ZMMU-A4295-1–4295-4 (4 adult males); females from the same locality (Fig. 14, B): NSMT-H5713–5714 (2 adult females); ZMMU-A4295-5–4295-7 (3 adult females); and ZMMU-A4297-1 (adult female from environs of Hirosaki City, Aomori Prefecture, Japan; Fig. 14, B). Animals were collected at the end of the breeding season.

Diagnosis. A slender, relatively medium-sized hynobiid salamander, and member of the genus *Onychodactylus* on the basis following combination of features: absence of lungs, presence of black claw-like horny structures on both fore- and hindlimbs in larvae and breeding adults, tail longer than the sum of head and body lengths, tail almost cylindrical, slightly compressed at the end, vomerine teeth in transverse short arch-shaped series almost in contact with each other, presence of large premaxillary fontanelle completely separating the nasals, presence of more than 9 caudal ribs, presence of skinfolds in larvae on the posterior edges of both fore- and hindlimbs and dermal flaps in males being developed during the breeding season, with diploid chromosome number $2n = 78$ and other typical features of the genus. This species is different from the other members of the genus in following combination of morphological features: in having 18 (17–20) presacral trunk vertebrae, 12 (11–14) costal grooves (Tab. 6), 17–18 (14–20) vomerine teeth in each vomerine tooth series (Tab. 7), very deep, distinctly curved vomerine tooth series with usually a little gap between them (Fig. 4, F), relatively large SVL, short tail in males and relatively longer tail in females, relatively longer gleno-acetabular distance, wider heads in both sexes and relatively greater distance between the eyes (Tabs. 4; 5), well-developed black acute claws which appear on fore- and hindlimbs in both sexes during the breeding season and may be found during the non-reproductive season, light usually brightly colored dorsum (from yellow-brown to bright red), light dorsal band usually with indistinct borders, but usually present (Fig. 5, E), juveniles and larvae usually with dark ground color and indistinct light dorsal band. The species is also distinguished from other congeners by pronounced genetic differences.

Description and variation.

Type specimens. The type series consists of 13 specimens: 7 males and 6 females.

Description of the holotype. An adult male, in a good state of preservation, fixed and preserved in ethanol 75%; SVL 70.0 mm (Fig. 13, A–C). **Head.** Head slightly depressed, head is comparatively wide, slightly longer than wide: ratio head length (HL) / head width (HW) is 1.25, head slightly wider than neck. The neck is rather short, approximately 5.5 times shorter than the head. Tongue is large, round-elliptical, adheres to the floor of the mouth but with free lateral margins, distinctly widens towards its end. Snout rather narrow and short, ratio snout length (OR) / head length (HL) is 0.29; snout tip rounded from the dorsal view, sides of snout tapering, almost

straight from eyes to nostrils. Nostrils small, with dorsolateral orientation (more lateral than dorsal), not protuberant, rather widely separated and distant from snout tip, ratio internarial distance (IN) / head length (HL) is 0.36. Eyes large and distinctly protuberant, eye diameter is shorter than snout length and noticeably shorter than the distance between external nares: ratio eye length (EL) to snout length (OR) is 0.93; ratio eye length (EL) to internarial distance (IN) is 0.76. Eyes widely spaced, interorbital distance is relatively long: ratio interorbital distance (IO) to head length (HL) is 0.38; ratio eye length (EL) to the intercanthal distance (IC) is 0.68. Eyelid present, well developed; labial folds absent; the gular fold distinct. Distinct parotid glands absent with no clear borders visible, but the parotid area is slightly swollen. Under the parotid area on lateral side of posterior part of head a large swollen subparotid protuberance is evident from the angle of the jaw to the gular fold. From the posterior corner of the eye towards the angle of the mouth there is a deep longitudinal postorbital groove. This groove edges from above a distinct protuberance located between the rear corner of the eye and the posterior end of the jaw near the angle of the mouth. The postorbital groove is slightly shorter than the eye length and does not reach the angle of the mouth angle, terminating ca. 1.5 mm above it. From the angle of the mouth upwards there is a distinct transverse supraquadrate groove, which is shorter than the postorbital groove, and it intersects with the postorbital groove above the mouth angle. From this point a deep longitudinal subparotid groove extends backward, separating the parotid area from the swollen elongated subparotid protuberance, which extends from the angle of the jaw to the gular fold. The subparotid groove curves slightly downwards posteriorly intersecting with the gular fold at its end. The subparotid protuberance is very distinct and oval-shaped, ca. 1.6 times longer than wide, greatly swollen, and from the dorsal view of the head a distinct narrowing is visible at the level of jaw angles. Head basis is notably wider than the neck. **Vomerine teeth.** Vomerine teeth are in two transverse, markedly curved very deep arch-shaped series forming a «»-shaped figure; 17 vomerine teeth in both the left and right vomerine tooth series. The left and right vomerine tooth series are not in contact with each other and there is a distinct, noticeable gap between the medial ends of the inner branches of the tooth series. At the very end the inner branches are markedly curved anteriorly; the outer tooth series branches are the same length or slightly shorter and a slightly less curved than the inner series. The posterior ends of the outer branches of the tooth series are located on the same level as the posterior ends of the inner branches. The posterior ends of the outer branches are also slightly curved anteriorly, but to a lesser degree than the ends of the inner branches. **Trunk.** Body elongated, slender and cylindrical; chest comparatively wide: ratio of chest width (CW) to body length (SVL) is 0.11. The skin of the dorsum and venter is smooth, slimy; with numerous microscopic whitish granular glands visible that are scattered over the dorsum and flanks. A middorsal groove is well developed on the dorsal side of the body from the back of head to the base of tail. Presacral trunk vertebrae number (TVN) 18; costal grooves well developed, 12 grooves are visible both on the right and left sides of the body. **Cloaca.** Cloaca slightly swollen, elongated and not protuberant. Vent longitudinal, long Y-shaped with slightly swollen edges, transverse wrinkles on the edges are not developed, a small protuberance is developed at the anterior edge of the vent. **Extremities.** Limbs well-developed, moderately slender and rather long, hindlimbs slightly longer and distinctly more robust than forelimbs; when forelimb and hind limb are adpressed towards each other to the side of the trunk, the digits tips do not meet but are close to each other: a gap between toes and fingers of the adpressed limbs is less than one costal segment (distance around ca. 0.5 costal segment); forelimb length to groin-axilla distance ratio ("Wolterstorff's index") is 0.51; hindlimb length to groin-axilla distance ratio is 0.58. No palmar or tarsal tubercles developed on palms or feet; no digital webbing. Four fingers and five toes; in order of decreasing length the relative length of fingers: 1 < 4 < 2 < 3; relative length of toes: 1 < 5 < 2 < 3 < 4. Tips of fingers and toes rounded, black cornified claws absent at all fingers and toes. Hindlimbs thicker and more robust than forelimbs however no signs of skinfolds on the posterior edges hindlimbs can be seen, posterior edges of hindlimbs rounded and muscular. **Tail.** Tail quite long, noticeably longer than the body, ratio of tail length (TL) to body length (SVL) is 1.36. The anterior three fifths of tail length it is cylindrical in transverse section and not compressed laterally; the last two fifths of its' length tail is slightly compressed laterally and oval in transverse section. No upper or lower caudal fin folds are present. From the dorsal view the last fifth of tail length tapers slightly, and the tail ends in a rather acute point. From the later view the most distal part of the tail (ca. 1.0 cm) is slightly tapered and the tail tip is gently rounded. The widest part of tail is close to the base of the tail. No autotomy has been observed in the species.

Measurements of the holotype (in mm). SVL 70.0; TL: 95.5; GA: 38.4; FLL: 19.7; HLL: 22.4; HL: 15.4; HW: 12.3; EL: 4.2; IN: 5.5; ON: 2.4; IO: 5.8; CW: 7.4; OR: 4.5; IC: 6.1 (measured on a freshly euthanized specimen).

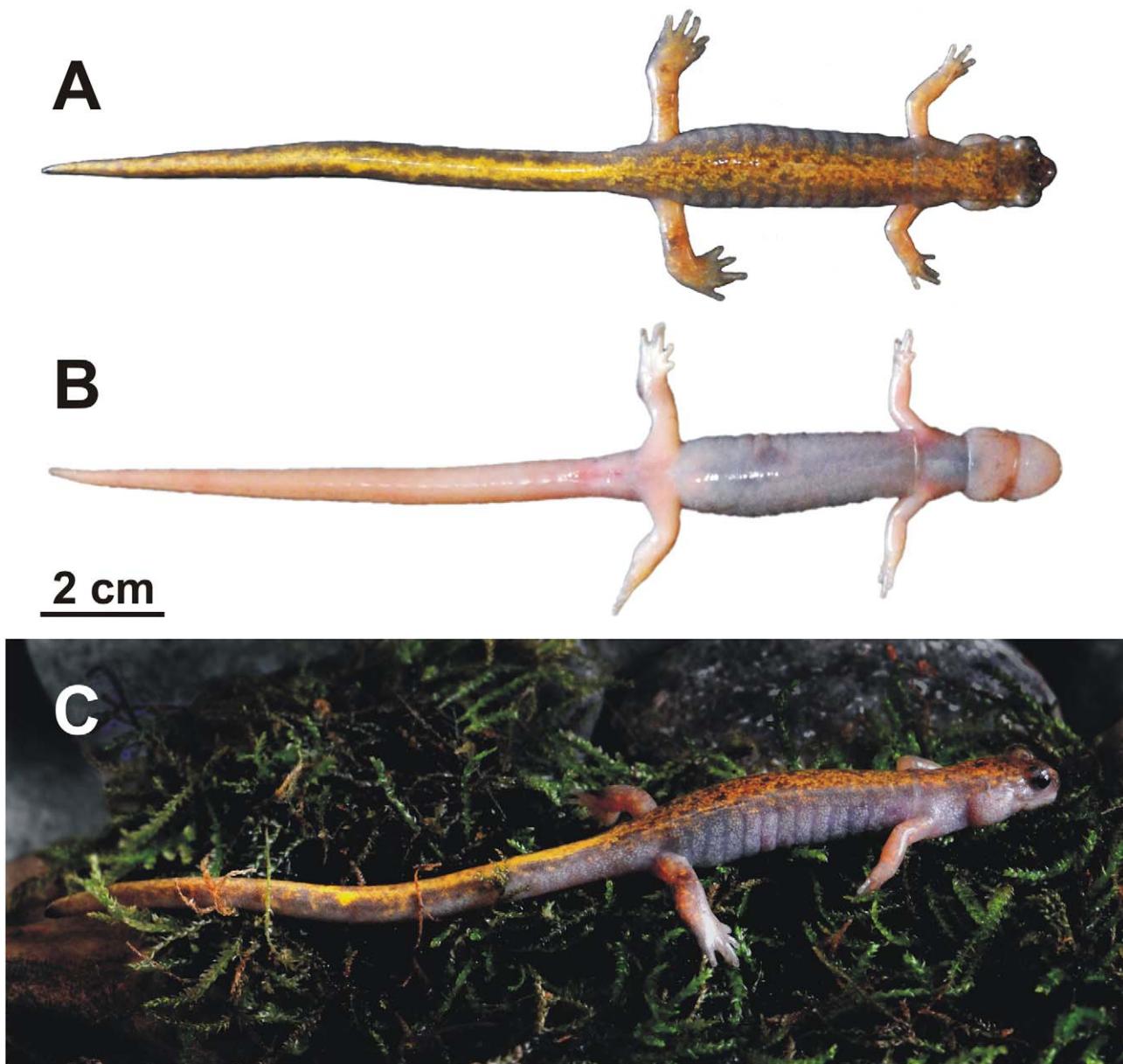


FIGURE 13. The holotype of *Onychodactylus nipponoborealis*, NSMT-H5710, adult male, from the type locality (Yasute mountain, Hirakawa environs, Aomori Prefecture, Tohoku district, Japan). (A)—Dorsal view; (B)—Ventral view; (C)—Dorsolateral view in life. Scale bar is 2 cm. Photos by M. Kuro-o.

Color of the holotype in life.

Background coloration. Dorsum light, with background coloration varying from orange to dark-orange and golden in the middorsal region, becoming more orange and copper at the scapular area and neck region (Fig. 13, A). Dorsal surface of the head and neck region is slightly darker—dark-orange, copper and dark orange-red. In life, eyes are more lightly colored than the rest of the dorsal surface of the head, the upper eyelids and the area around the eye is gray-violet to bluish. Dorsal surface of the tail is brighter and more yellow, ranging from bright yellow to golden-yellow at the base of the tail until reaching the white-yellow or ivory-beige coloration at the dorsal surface of the posterior half of the tail. Flanks of the body are dark, from the dorsolateral area the background color of the trunk is grayish-brown to dark purplish-brown becoming slightly lighter towards the ventrolateral region where it is somewhat lavender-brown to dark violet-gray. The costal grooves are darker than the costal segments—which are dark violet-gray. Flanks on the head are lighter than the sides of the body with the background color being mostly pink-brownish, plum-pinkish and off-pink, turning somewhat lighter towards the ventral surface of the head (Fig. 13, C). Sides of the tail are of the same color as the body flanks near the base of the tail, which may be

somewhat lighter in coloration (lavender-brown to dark violet-gray), and along the tail length the sides become yellowish, turning to brown-grayish and tan at the sides of the posterior third of the tail length. Background color of the ventral side of the body is generally light, its darkest region in the central area of the belly and the chest region (dark violet-gray to dark slate-blue and purple-gray); here the skin is semi-transparent and the contours of the intestinal organs can be observed. Coloration becomes lighter at the gular area and the ventral side of the head is varies from light pink to pale violet-red. The ventral sides of the fore- and hindlimbs, as well as the pelvic region is similar in coloration only somewhat lighter (light pink to peach-pink) (Fig. 13, B). Ventral sides of the hindlimbs are a bit more yellowish (off-yellow-pink). The ventral side of the tail is yellowish-pink to or beige color, sometimes becoming reddish-beige. The cloacal area is lighter in color; a whitish-pink with bright pink to purple coloration of the vent. **Pattern.** The dorsal surface of the anterior half of the tail is bright-gold and yellow, becoming less vivid towards the remainder of the tail, here the dorsal tail surface is white-yellowish, or sand-yellow becoming nearly white-beige at the tail tip (Fig. 13, A). At the anterior half of the tail length (approximately from the tail base up to the center of the tail) the bright yellow dorsal coloration forms a distinct light dorsal stripe with a nearly straight but jagged border. At the posterior region of the tail border of this dorsal stripe becomes indistinct. The light dorsal stripe narrows above the cloaca, and broadens again at the pelvic area (here it darkens to a dark-orange), from here to the scapular area there is a light, wide dorsal stripe that has an indistinct border with numerous dark spots at the edges making them appear jagged. From the base of the head to the tip of the snout the light dorsal stripes disappear where they divide into numerous light (orange, copper, reddish-orange) spots and dots with no clear visible borders. On the dorsum and dorsal surface of the head the light dorsal stripe consists of numerous light (orange to copper red) spots and irregular blotches, which are smaller on the head and reduce in size from 4–6% of SVL on the mid-dorsum to 1–2% of SVL on the dorsal head surface. The yellowish light spots are nearly indistinct on the flanks: on the dorsolateral sides of the body they are scarce (from one to two per costal segment) and small, and some irregular yellow spots are also visible on the lateral sides of the base of the tail. On the dorsal surface of fore- and hindlimbs there are irregular scattered spots and star-shaped blotches (1–3 spots in cross-section of forelimbs, and 4–5 spots in hindlimbs). They are more densely scattered on the posterior sides of the extremities, forming a faint reticulated pattern on the hindlimbs. Lateral sides of trunk are covered with numerous small (0.3–0.4 mm) light spots (off-white, whitish-blue, light gray-violet), which correspond to microscopic granular skin glands, containing a white poisonous secretion (Fig. 13, C). They are visible on the dorsal surface as well, but are more pronounced on the flanks. Here they form a dense mottling on each costal segment but are absent from the costal grooves and surrounding parts of skin, giving the impression of faint vertical stripes. On the central region of body flank there are usually 5–8 white dots across the segment. These dots disappear towards the lateral sides of the belly. Similar dots cover the lateral sides of the base of the tail (ca. one fifth of tail length), shoulder region, and lateral sides of the head. Here the size of the dots is smaller (ca. 0.2–0.3 mm) and they are especially abundant in the parotid region and at the subparotid protuberance. White dots are less numerous on the limbs and appear to be absent on the ventral sides of the body. There are no signs of any pattern or spots on the ventral surface of trunk, tail and head, which are all quite uniformly colored (Fig. 13, B). **Iris.** Iris in life is dark-copper red with numerous small golden and orange spots (which disappear in preservative). The marginal sides of the iris are brighter and have more golden spots, whereas the central region of the iris that is closer to the pupil is darker. The pupil is oval-shaped and oriented horizontally.

Color of the holotype in preservative. After three years in preservative the reddish or pinkish tint has completely disappeared: the dark dorsal coloration turns brownish or grayish, the bright orange and golden color on the dorsum and tail disappears, the light dorsal stripe loses the reddish tint and turns yellowish or light-orange; the body flanks change from violet and become grayish, and the ventral region also lose the pinkish tint and fade to an off-whitish or gray-yellowish color. The general pattern however has not changed and is clearly recognizable.

Variation. Morphology of the type series in general resembles that as described for the holotype with the following exceptions:

Morphometrics. Variation in the mensural characters among the type series of the new species are presented in Tables 4 and 5. The species is in general characterized by the following morphometric parameters (ranges for males / females, 14 specimens): snout-vent length (SVL): 66.4–75.9 / 59.5–72.2; tail length (TL): 65.5–95.5 / 65.0–82.4; gleno-acetabular distance (GA): 37.7–43.2 / 32.7–42.3; forelimb length (FLL): 18.9–20.5 / 17.5–20.8; hindlimb length (HLL): 21.9–24.4 / 20.8–23.7; head length (HL): 15.3–16.2 / 14.6–16.2; head width (HW): 10.9–13.0 / 10.8–12.9; eye length (EL): 3.9–4.8 / 3.7–4.3; internarial distance (IN): 5.1–5.9 / 4.7–5.6; orbitonarial

distance (ON): 1.7–2.7 / 1.7–3.0; interorbital distance (IO): 4.7–6.5 / 4.2–6.1; chest width (CW): 6.9–8.7 / 6.6–7.7; snout length (OR): 4.3–4.8 / 4.1–5.4; intercanthal distance (IC): 5.8–6.5 / 5.2–6.2 (measured on freshly euthanized specimens). In morphometrics, *O. nipponoborealis* is clearly distinct from its sister species *O. japonicus* in both males (Fig. 6, A) and females (Fig. 6, C). Some insignificant overlap of PCA scores is observed between *O. nipponoborealis* and *O. koreanus* (Korean populations) in males (see Results and Comparisons). However, these species are markedly different in a number of diagnostic morphological characters and can be easily distinguished in the field and in museum collections.

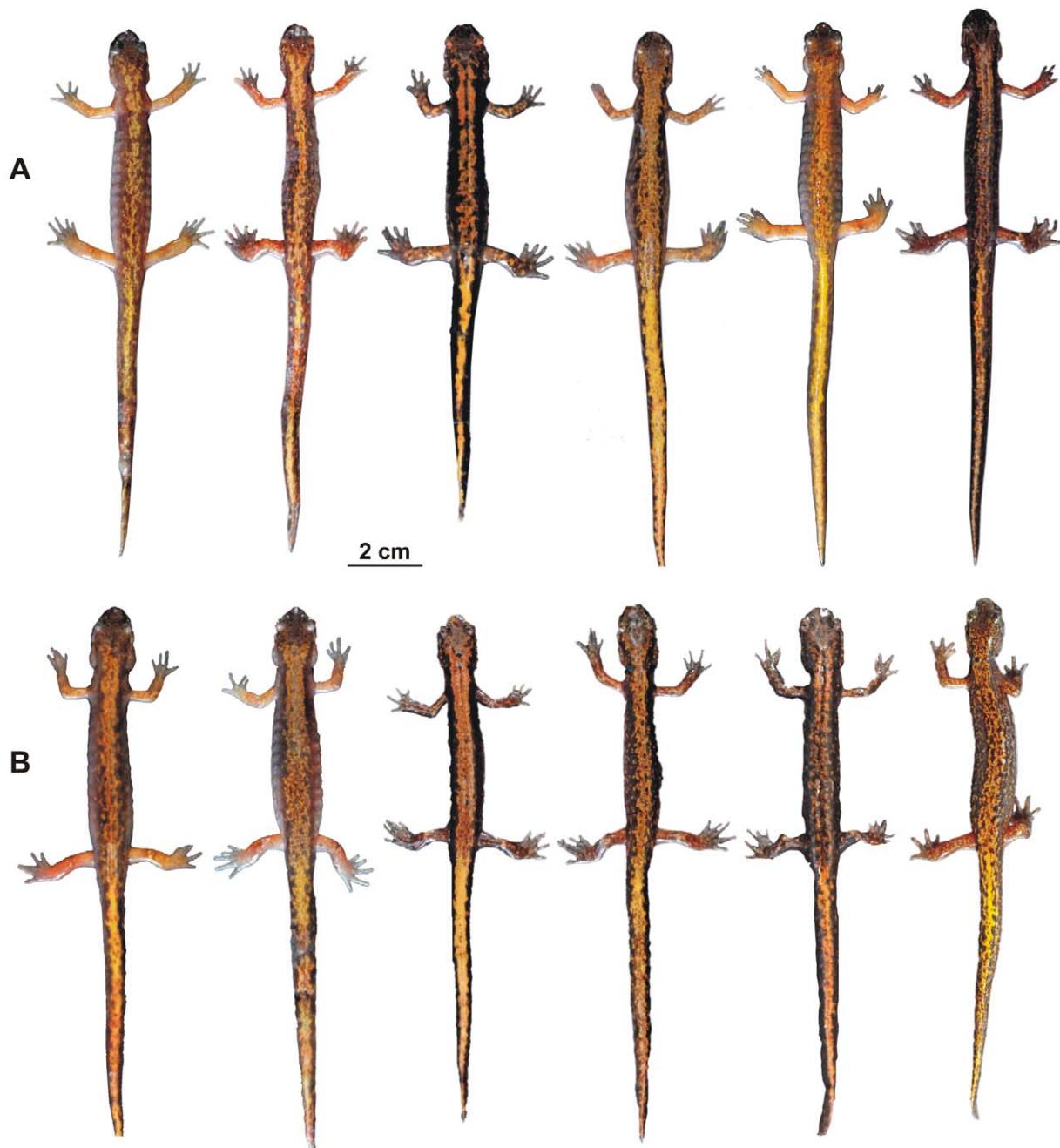


FIGURE 14. The type series of *Onychodactylus nipponoborealis* from the type locality (Yasute mountain, Hirakawa environs, Aomori Prefecture, Tohoku district, Japan), showing variation in dorsal coloration: (A)—Males (above); (B)—Females (below). Scale bar is 2 cm. Photos by M. Kuro-o.

Sexual variation. Sexual variation of morphometric features is found in several measurements (see Results, Tab. 5); our results are in general concordant with previously published data for *O. japonicus* s. stricto. Similar to other species of *Onychodactylus*, the sexes in *O. nipponoborealis* are significantly different in tail length due to

relatively longer tails in males (Tabs. 4; 5). There are no significant differences however between the sexes in body size (SVL) or axilla-groin distance (GA), this result is also concordant with data on *O. japonicus* s. stricto (Akita, 1983b). Males tend to have longer forelimbs (FLL) than females, these differences are significant for absolute values; in relative index FLL/SVL differences are non significant, but we found significant differences in Wolterstorff's index (FLL/GA) indicating that males have comparatively longer forelimbs ($p < 0.05$). Males are also found to have significantly longer internarial (IN) and intercanthal (IC) distances than females ($p < 0.005$); significant intersexual differences were found for internarial distance (IN) / head length (HL) ratio: distance between external nares is greater in males.

Secondary sexual characters. Secondary sexual characters in *O. nipponoborealis* in general resemble those in *O. japonicus*. The type series of the new species was collected after the breeding season ended so many distinctive secondary sexual traits disappeared in the paratypes. Even after the breeding season, males always have more massive and stronger hindlimbs than the females (see Fig. 14). Our field observations indicate that, similar to other *Onychodactylus* species, during reproduction, male *O. nipponoborealis* develop a large skin fold on the outer surface of hindlimbs from the 5th toe to the tibia, which likely plays an important role during the fertilization process. In our sample there are no traces of skin fold in males. The tail is always longer in males than in females, and during the reproductive season tails of male *O. nipponoborealis* are also more flattened and they have taller upper tail fins. Tail tips of males are somewhat tapered and pointed, whereas female tail tips remains rounded and their tail fins are shorter. During the breeding season males always have a more swollen cloacal area than those of females, which results in a wider tail base. In females the vent looks like a longitudinal slit with two slightly swollen parallel lateral vent folds, whereas in breeding males the lateral vent-folds are more swollen and horseshoe-shaped. During reproduction both sexes develop black horny claws on their fingers and toes, similar to that of *O. japonicus*, however they are shed after breeding is concluded; we have never observed these black claws out of the breeding season, and they are also absent in the type series of the new species (see Fig. 14). In *O. nipponoborealis* the structure of the inner surface of the legs is very similar in both sexes and we have not observed the dark horny asperities on the inner surface of hindlimbs or forelimbs, as reported by Sato (1943) for males of *O. japonicus*.

Color in life. Coloration and dorsal patterns of the paratypes in general are concordant with description of the holotype given above. Variation in coloration is minimal and is mostly pronounced in the dorsal pattern of dark flecks on the dorsum and borders of a light dorsal stripe. Variation in dorsal coloration of *O. nipponoborealis* type series is presented in Fig. 14 (A for males and B for females). In three paratypes the flanks are noticeably darker than that of the holotype: dark spots on the flanks form the appearance of dark dorsolateral stripes; in two males (Fig. 14, A) the borders of the light dorsal stripe are unclear, whereas in one female (Fig. 14, B) they are relatively straight resembling the dorsal pattern typical for *O. japonicus* s. stricto. Significant variation is observed in the pattern of small dark spots and flecks scattered on the dorsum. The degree of their development varies from a near total absence of black spots and dots on the dorsum, as in the holotype (Fig. 13, A), to numerous small dark spots and flecks of irregular shape uniformly scattered all along the dorsum (Fig. 14, B, first specimen on the left), and to larger longitudinal black flecks forming an interrupted dark dorsomedial stripe (Fig. 14, A, third specimen on the right). The intensity and tint of the bright color of the dorsal stripe may also vary from bright yellow and orange to a dull orange-brownish or copper. No sexual variation in coloration has been observed.

Color in preservative. Color patterns in preservative correspond with coloration in life, but after three years in ethanol the warm tints fade from the coloration and the color intensity decreases to grayish-brown, the same way as it is described for the holotype above.

Osteology and anatomy. There are no specific works on skeletal anatomy of *O. nipponoborealis* that we are aware of. However, Inukai (1932) discussed the taxonomy of the Hynobiidae in northern Japan and provided descriptions of skull morphology for the northern population of *O. japonicus*, which correspond to the new species *O. nipponoborealis*. Variation in the number of trunk vertebrae (TVN) and number of costal grooves (CGN) among the type series of *O. nipponoborealis* are presented in Table 6. Modal TVN-number in *O. nipponoborealis* is 18 for both sexes, though the ranges vary (17–19 for males, mean is 18.0 0.82; 18–20 for females, mean is 18.4 0.79). The trunk–vertebrae numbers result in the respective costal groove counts: 12 (11–13) for males and 13 (12–14) for females (based on 14 specimens, see Tab. 6).

Vomerine teeth morphology. In adults of *O. nipponoborealis* vomerine teeth are in two transverse, deep, strongly curved arch-shaped series with almost equal lengths of inner and outer branches (Fig. 4, F), in some specimens however the outer branches are slightly shorter than the inner branches. Normally the left and right

vomerine tooth series do not touch each other and a distinct but narrow gap is noticeable between the medial ends of the inner branches of the series. Both outer and inner branches are noticeably curved in this species, with the inner branch being slightly more curved than the outer one (see Fig. 4, F). At its terminal end the inner branch is markedly curved anteriorly: the teeth at the very end of the inner branch are located more anteriorly than the posterior angle of the branch. The posterior angles of the outer branches are also slightly more curved anteriorly, but less than in the inner branches. The medial ends of the inner branches are located on the same level or often more posteriorly compared to the lateral ends of the outer branches. Variation in the number of vomerine teeth (VTN) among the type series of the new species is presented in Table 7. In our sample the number of vomerine teeth in the species is the highest reported for the genus and is significantly higher than in *O. japonicus*: 16–18 (mean 17.1 ± 0.79) teeth per each branch in males and 15–20 (mean 17.4 ± 2.03) for females (based on 14 specimens, see Tab. 7).

Eggs and clutch. There are no specific works on the reproduction of *O. japonicus* in the northern part of its range, so documented observations of reproduction in *O. nipponoborealis* are subsequently absent. With all probability, as in other *Onychodactylus* species, breeding in *O. nipponoborealis* takes place in underground areas of mountain brooks and streams in cavities and between stones and other such refugia. In all *Onychodactylus* species the eggs are deposited in two gelatinous elliptical egg sacs, joined together at the distal ends, with the mucous-like stalk shorter than the sac length which serves to attach the clutch to a stone. Since our sample of *O. nipponoborealis* was collected after the breeding season was over, females contained no ovarian eggs so it was difficult to estimate an average clutch size in the new species.

Larval morphology and metamorphosis. Larvae of *O. nipponoborealis* appear in streams when they reach a total length of 30–45 mm and are characterized by a combination of morphological characteristics typical for all *Onychodactylus* species (see Fig. 15, B): large, square-shaped head with obtusely blunted snout, which is notably wider than the body, short gills covered with an opercular skin fold at the base, slightly prominent eyes, and all the digits on both fore- and hindlimbs bearing black, cone-shaped sharp, horny claws. On the outer surfaces of the fore- and hindlimbs a characteristic dermal flap is develops; it disappears just prior to metamorphosis. The tail fin is low, consisting of low dorsal and ventral fins which are approximately the same height. The tail fin runs along the dorsal surface of the tail from the first quarter of its length (area above the cloaca) and does not reach the cloaca on the ventral side of the tail. Metamorphosis is normally accomplished when a total length of 80–90 mm is reached; three premetamorphic larvae in our sample had total lengths of over 85 mm, but at the same time they still possessed well-developed gills and had not begun to metamorphose (stage 70 of Iwasawa & Kera, 1980) (see Fig. 15, B). It seems that larvae metamorphose during the second or third year of their life. The base color in larvae is usually light-brownish, ochre, sometimes slightly reddish-brown or orange. After larvae appear in streams, they start to develop dark pigment; small black spots first appear on body and tail flanks which become clouded with a darker (brownish, brown-grayish to plumbeous) tone. As the larvae grow (over 55 mm total length), the dark coloration spreads along the flanks to the dorsal surface of the body where it forms an unclear pattern of dark spots or variegations. Occasionally an indistinct light dorsal stripe with unclear borders becomes edged with darker color (see Fig. 15, B, specimen in the center). The ventral side is generally lighter than other body surfaces and always lack black spots. Usually a light (yellowish to orange) dorsal stripe is present on the back surface of the tail. Closer to metamorphosis the larvae become darker, the dark pigment develops unclear clouded or variegated patterns on the tail and back and light areas on the dorsum and tail become brighter. The lifespan of this species is currently unknown. In general, reproduction, embryonic and larval development of *O. nipponoborealis* have not been studied and new research in this area is essential.

Etymology. The specific name “*nipponoborealis*” is a toponymic adjective in the nominative singular, from “Nippon”—the traditional name of the Honshu or Hondo, the main island of the Japanese archipelago, and “borealis”—Latin for “northern”, referring to the northern part of Honshu—Tohoku region, inhabited by this species. We suggest Tohoku Clawed Salamander as the English common name of the species as a reference to species distribution. Recommended common names in Japanese, Russian, Korean and Chinese are given above.

Distribution. Endemic to Japan. Distribution of this form (as *O. japonicus*) is summarized by Ohno, 1982. The species is found in the mountainous areas of the northern part of the Tohoku region (Yamagata, Miyagi, Akita, Iwate and Aomori Prefectures). The southern border of distribution of this form is discussed in a detailed phylogeographic research paper by Yoshikawa *et al.*, 2008. The population of the Shimokita Peninsula in Aomori Prefecture appears to be isolated from the rest of the species range.

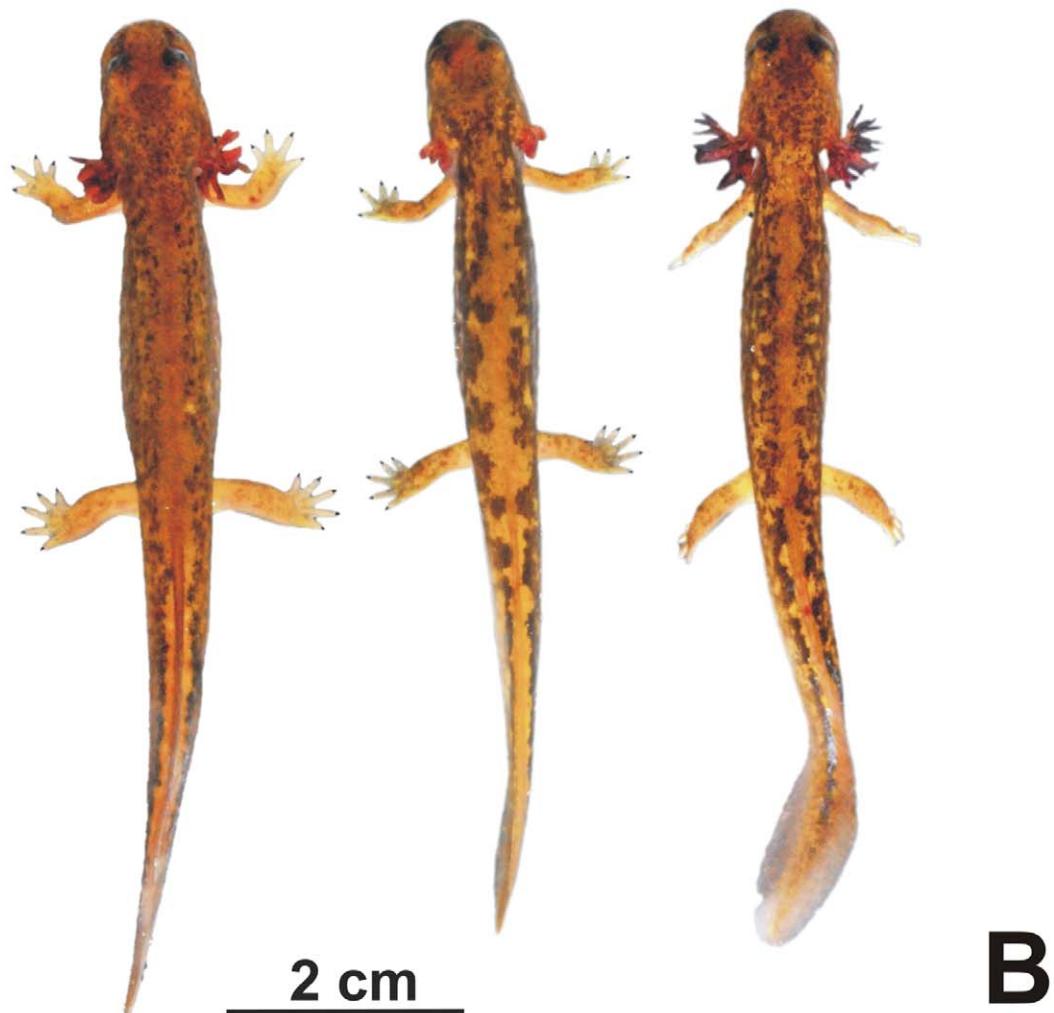


FIGURE 15. (A)—Breeding habitat of *Onychodactylus nipponoborealis* at the type locality (Yasute mountain, Hirakawa environs, Aomori Prefecture, Tohoku district, Japan); (B)—Larvae of *Onychodactylus nipponoborealis* from the type locality, dorsal view. Scale bar is 2 cm. Photos by M. Kuro-o.

Comparisons. *O. nipponoborealis* can be distinguished from the other salamanders in the region, including two sympatric *Hynobius* species, by its slender body, smooth skin with distinct costal grooves on the flanks, very long tail, almost cylindrical at the base, slightly compressed in the middle and flattened towards its end, small and somewhat elongated head with rounded snout, and a combination of morphological features characteristic of *Onychodactylus*, such as absence of lungs, breeding males develop dermal flaps on the outer surface of the hindlimbs, both sexes during the reproductive season possess black horny claws on both fingers and toes, vomerine teeth in two short transverse arch-shaped series, premaxillary fontanelle large fully separating nasals, caudal ribs numerous and present on more than 5–6 postsacral tail vertebrae. From other congeners *O. nipponoborealis* is different in average numbers of trunk vertebrae (18–19) and costal grooves (12–13) and comparatively deep vomerine tooth series, broader and longer head, longer hindlimbs, bigger gleno-acetabular distance and shorter tails in males. From *O. japonicus*, another species on the Japanese Island of Honshu, the new species is also different in having a greater SVL and GA, a greater interorbital distance, and in having a higher number of vomerine teeth (usually 16–18) with usually a distinct gap between the vomerine tooth series.

O. nipponoborealis can be further distinguished from other *Onychodactylus* species by a following combination of morphological attributes:

From *O. fischeri* (Boulenger, 1886) the new species differs in vomerine tooth series being notably curved, Fig. 4, E (versus almost straight or slightly bended in *O. fischeri*, Fig. 4, A); in having a lower trunk vertebrae number (TVN): normally 18–19 trunk vertebrae (versus 20–21 in *O. fischeri*) and a lower costal groove count (CGN): 12–13 in *O. nipponoborealis* (versus 14–15 in *O. fischeri*) (Tab. 6); and in greater vomerine tooth count: 17.3 ± 1.49 in *O. nipponoborealis* (versus 11.5 ± 1.23 in *O. fischeri*) (Tab. 7). *O. nipponoborealis* further differs from *O. fischeri* in following morphometric features (see Tab. 4, and Tab. 5 for details): comparatively longer hindlimbs in both sexes, and longer forelimbs in males, larger eyes in both sexes, wider heads in both males and females, and greater internarial and interorbital distances in both sexes.

O. nipponoborealis can be distinguished from the second *Onychodactylus* species on the Japanese island of Honshu, *O. japonicus* (Houttuyn, 1782), by the shape of the vomerine tooth series: vomerine teeth in two deep strongly curved arch-shaped series usually with a pronounced gap between them, the medial ends of the inner branches are distinctly curved forward and located on the same level as the lateral ends of the outer branches in *O. nipponoborealis*, Fig. 4, F (versus vomerine teeth in two comparatively shallow slightly curved arch-shaped figures with no gap between them on the midline, the medial ends of the inner branches are almost not recurved and located slightly anteriorly towards the lateral ends of the outer branches in *O. japonicus*, Fig. 4, E). *O. nipponoborealis* further differs in having a greater vomerine tooth count: usually more than 16 teeth per series (17.3 ± 1.49) in *O. nipponoborealis* (versus normally not more than 15 teeth per series (11.4 ± 1.16) in *O. japonicus*) (Tab. 7). It is also different in having a greater trunk vertebrae number (TVN): 18–19, normally 18 (versus 17–18, usually 17, in *O. japonicus*), and a greater costal groove count (CGN): 12–13, more often 12 (versus 11–13, usually 11, in *O. japonicus*) (Tab. 6). Dorsal pattern seems to be useful for discrimination of *Onychodactylus* species: *O. nipponoborealis* the dorsal stripe is usually not that distinct with no clear edges, and covered with dark mottling and unclear spots (Fig. 5, E), whereas in *O. japonicus* normally shows a distinct light dorsal stripe with clear contrasting edges (Fig. 5, G), however intraspecific variation of dorsal pattern in *O. japonicus* is too high to rely on this character in species diagnostics. *O. nipponoborealis* also differs by comparatively much shorter tail: in adult males TL/SVL ratio usually around 1.18 (versus tail is relatively long, in adult males TL/SVL ratio usually around 1.3 in *O. japonicus*) (Tab. 5). *O. nipponoborealis* further differs from *O. japonicus* in the following important morphometric characteristics (see Tabs. 4; 5 for details): significantly greater SVL in males; much wider and comparatively shorter head for both sexes: HL/HW ratio is around 1.32 ± 0.07 (versus narrower heads in both sexes of *O. japonicus*: HL/HW ratio is around 1.69 ± 0.07); comparatively larger eyes: EL/HL ratio is around 0.27 ± 0.01 (versus EL/HL ratio is around 0.23 ± 0.01 in *O. japonicus*); greater internarial distance; greater distance between orbits: IO/HL ratio is around 0.36 ± 0.04 in *O. nipponoborealis* (versus EL/HL ratio is around 0.21 ± 0.01 in *O. japonicus*), and comparatively shorter forelimbs in both sexes and shorter hindlimbs in females.

For a more detailed comparison of *O. nipponoborealis* with the three other new species of *Onychodactylus* described from continental Northeast Asia in this paper, refer to “Comparisons” in taxonomic accounts for *O. koreanus*, *O. zhaoermii* and *O. zhangyapingi* given below.

Karyotype. $2n = 78$, NF = 102. Chromosomal formula: 6M+2ST+16ST+6T+48a. The karyotype of *O.*

nipponoborealis (as of *O. japonicus*) reported by Ikebe *et al.* (1995) based on specimens from “Aomori Prefecture, Jogakura”. Using adults and embryos Ikebe *et al.* (1995) reported the presence of three types of chromosome 4 of *O. japonicus* in four populations examined i.e. Tsukui (Kanagawa Prefecture), Tateyama (Toyama Prefecture), Hinoemata (Fukushima Prefecture), and Jogakura (Aomori Prefecture). Two or three types of chromosome 4 were observed in Tsukui, Tateyama, and Hinoemata populations, in contrast, only one type (type 1) was observed in the Jogakura population which corresponds to the species described here. The chromosomal variations do not always directly reflect the phylogenetic relationships; however, this fact indicates that Jogakura population differs from the other three *O. japonicus* populations. Furthermore, the type 1 of chromosome 4 was observed in all of the four populations, and chromosome 4 of *O. fischeri* from Korea belongs to the type 1 as well (Iizuka & Yazawa, 1991, 1994); i.e. the karyotype of *O. japonicus* from Jogakura closely resembles the karyotype of *O. fischeri* from Korea. These facts suggest that most likely the type 1 of chromosome 4 is primitive, and the other types found in *O. japonicus* were possibly derived from the type 1 via pericentric inversion(s).

Genome size. Our estimate of *O. nipponoborealis* genome size is ca. 108.9 pg per diploid nucleus; CV = 54.45 (Feulgen densitometry; one specimen from Hirakawa, Aomori Prefecture, Japan; N.A. Poyarkov, pers. obs.; peripheral red blood cells of the Ribbed Newt, *Pleurodeles waltl*, and the Southern Crested Newt, *Triturus karelinii karelinii* (Salamandridae), were used as a reference standard for genome size measurements).

Phylogenetic position. *O. nipponoborealis* is a member of *O. japonicus* species complex, and our analyses recovered this species as the sister taxon to *O. japonicus*. *O. nipponoborealis* shows a divergence from other *O. japonicus* lineages up to 9.1% in COI sequences and 3.6% in 16S rRNA of uncorrected pairwise genetic distances (see comment on *O. japonicus* s. stricto, also Fig. 3 and Tab. 3). There is a significant genetic differentiation between the populations from the southern part of the Tohoku region (lineage J1, Yamagata Prefecture) and the northern part of Tohoku (lineage J2, Aomori Prefecture) with a divergence between them of 4.3% for COI and 2.8% for 16S rRNA. Due to the lack of morphological material from Yamagata, the taxonomic status of this population remains unclear and requires further investigations.

Habitats and natural history. Since the populations of *O. nipponoborealis* were traditionally treated as *O. japonicus* they attracted little attention and their natural history is still poorly studied. In the Tohoku region in the north of Honshu, *O. nipponoborealis* inhabit mountain coniferous, mixed and broad-leaved deciduous forests, and is found along fast-flowing mountain streams and brooks with clean, cool and well-aerated water (for the photo of habitat at the type locality see Fig. 15, A). The species is common at altitudes higher than 100 m above sea level, and is seldom found below 50 m (Ohno, 1982); normally *O. nipponoborealis* is found up to 2000 m above sea level, but occasionally may occur at higher elevations. In the Tohoku region reproduction in this species takes place from late May or June until July to early August (Ohno, 1982). As with other *Onychodactylus* species, following the hibernation period, salamanders migrate to the water for breeding and are found at dusk and night time in the running streams. After breeding they can be found in forest areas along streams, preferring moist, cool and shady places in mountain valleys under forest canopy, avoiding open areas and sunshine. Species may be locally abundant, preferring dense woodlands near small mountain streams, rivers and lakes with clear and cool water with water temperatures ranging from 9°C to 12°C. Preferable shelters include stones, tree logs and pieces of wood, moss-covered rocks, crevices and hollows in stream banks etc., but always in close proximity to streams sources and water environs. The diet of the new species is unstudied. Egg-laying and fertilization have also not been observed and documented. The new species is sympatric with the two members of the genus *Hynobius* (*H. lichenatus* and *H. nigrescens*) and also with *Bufo japonicus formosus*, *Rana ornativentris*, and *Hyla japonica*.

Conservation status. Though the species range is restricted to the mountains of northeastern Honshu, it still encompasses a comparatively large territory in Yamagata, Miyagi, Akita, Iwate and Aomori prefectures. The species is so far abundant across its range and occurs in a number of protected areas. As for *O. japonicus*, habitat destruction and changes in freshwater quality may affect the new species. We suggest that the species conservation status be designated as Least Concern according to IUCN criteria.

Onychodactylus koreanus species complex

Our data indicate that *Onychodactylus* populations from the Korean peninsula and neighboring areas of northeast China previously treated as *O. fischeri*, are not related to Russian populations of *O. fischeri* and form a

monophyletic group with *O. japonicus*. *Onychodactylus* populations from Korea and China, however, do not form a clade and are grouped into four lineages. The lineage from Jilin Province, China, is a sister clade of *O. japonicus* species complex, and three other lineages inhabiting the Liaoning Province of China and the Korean peninsula consist a monophyletic group which we treat here as a species complex. This complex comprises at least three highly divergent clades from Korea and China, which we consider here as separate species; two of them we describe below, the third one we treat as unconfirmed candidate species. Further taxonomic assessment of *Onychodactylus* populations from different areas in the Korean peninsula and northeast China is required.

***Onychodactylus koreanus* sp. nov. Min, Poyarkov & Vieites**

[*Geomolge fischeri* (part)—Mori, 1916: 119 [cit. from Sato, 1943: 314]; Doi, 1920: 123 report this species for Korea under the name *Geomolge fischeri* Boulenger, 1886. Abe, 1922 (“1921”): 328 describes a female with clawed toes and fingers from Hokkhanzan (now Hwaak-san, border of Gangwon-do and Gyeonggi-do), Korea.]

[*Onychodactylus fischeri* (part)—Dunn, 1918; Dunn, 1923 (reports on a specimen from Wonsan, Korea, CAS 32169-32172 coll. by V. Kühne (= J. C. Thompson), 07.VI.1911; 32199; 32219; 32262; 32992-32993); Tago, 1931: pl. XXVI, ff. 1-6; Inukai, 1933: 193-195, f. 1 (reports on *Onychodactylus* from Korea); Okada, 1934: 19 (gives „Khabarorka“ [sic!] as a type locality and indicates this species is found in „Corea“); Okada, 1935: 584; Takashima, 1936: 23; Sato, 1937: 45; Sato, 1937: 48-49, ff. 43, 44; Sato, 1943: 314-319; Miyadi & Koba, 1940: 21, f. 3; and many other authors.]

[*Onychodactylus japonicus* (part)—Tago, 1931: 200-210; pl. XXVI. K. Tago in his review of tailed amphibians of the Japanese empire treated all populations of *Onychodactylus* from “Chosen” (the old Japanese name of Korea) or “Corea” as *Onychodactylus japonicus*. The spotted pattern of dorsal coloration of the animal depicted on pl. XXVI clearly indicates that it is in fact *O. koreanus*.]

[*Onychodactylus sischeni* (part)—Won, 1971: p. 30 (*ex errore*). Unjustified change of the original spelling.]

[*Onychodactylus fisheri* (part)—Shim, 2001: p. 143; Uchiyama, Maeda, Numata & Seki, 2002: p. 55. Unjustified emendation of the original spelling.]

Recommended trivial names:

Chinese name: Hanguo Zhaoni (????).

English name: Korean Clawed Salamander.

Japanese name: Korai-Sansyouo (proposed name), Chosen-Sansyouo (historical name, see Okada, 1934: 19).

Korean name: (Hanguk) Ggorichire Dorongnyong.

Russian name: Korëyskiy kogtistyi (bezlegochnyi) triton.

Holotype. EWNHM 80316; an adult male collected during the breeding season in May, 2005 by Mi-Sook Min (see Fig. 16, A).

Type locality. SinGi-Myeon environs, Samcheok-shi, Gangwon-do, Korea, 400 m a. s. l.; geographic coordinates: 37° 20' N; 129° 03' E.

Paratypes. EWNHM 80317, EWNHM 80318 (two adult males), EWNHM 80315 (adult female), all from the same locality and collection data as for the holotype (see Fig. 16; Fig. 17); DRV-5050 (adult male) and DRV-5051 (adult female) from Naejang-san Mt. environs, Naejang-san NP (Sinung environs), Damyang-shi, Jeollanam-do, Korea, 208 m a. s. l.; geographic coordinates: 35° 24' N; 126° 55' E; and ZMMU-A-4064-1-4064-7 (2 juveniles, 5 premetamorphic larvae) from the environs of Jiri-san Mt., Jiri-san NP, Sancheong, Gyeongsangnam-do, Korea, geographic coordinates: 35° 19' N; 127° 43' E.

Referred material. EWNHM 80319–80320; MVZ DRV-5056 (Gyeongsangbuk-do, Sangju-shi, Songni-san, Daemok-ri environs); MVZ 233472; MVZ 233473 (Gangwon-do, Hwajon-ri, Nam-myon, Hongcheon-gun); MVZ 233474; MVZ 233475 (Gyeonggi-do, Yangpyeong-gun, Danwol-myon, Hyangso-ri); EWNHM 80321–80322 (Daejeon, Seo-gu, Jangan-dong, Jangtae-san); EWNHM 80323–80325 (Chungcheongnam-do, Nonsan-shi, Beolkok-myeon); EWNHM 80327–80328 (Chungcheongbuk-do, Cheongju-shi, Gadeok-myeon); MVZ DRV-5057 (Jeollabuk-do, Jeonju-shi, Kunhangsan environs); MVZ 233476 (Jeollanam-do, Jangseong-gun, Bukii-myon, Baekyang-sa Temple); MVZ 163735 (Jeollabuk-do, Jeongsan); EWNHM 80326 (Gyeongsangbuk-do, Kwangdeok-san), Korea (see Appendix 1).

Diagnosis. A slender, relatively medium-sized hynobiid salamander, a member of the genus *Onychodactylus* on the basis following combination of features: absence of lungs, presence of black claw-like horny structures on both fore- and hindlimbs in larvae and breeding adults, tail longer than the sum of head and body lengths, tail

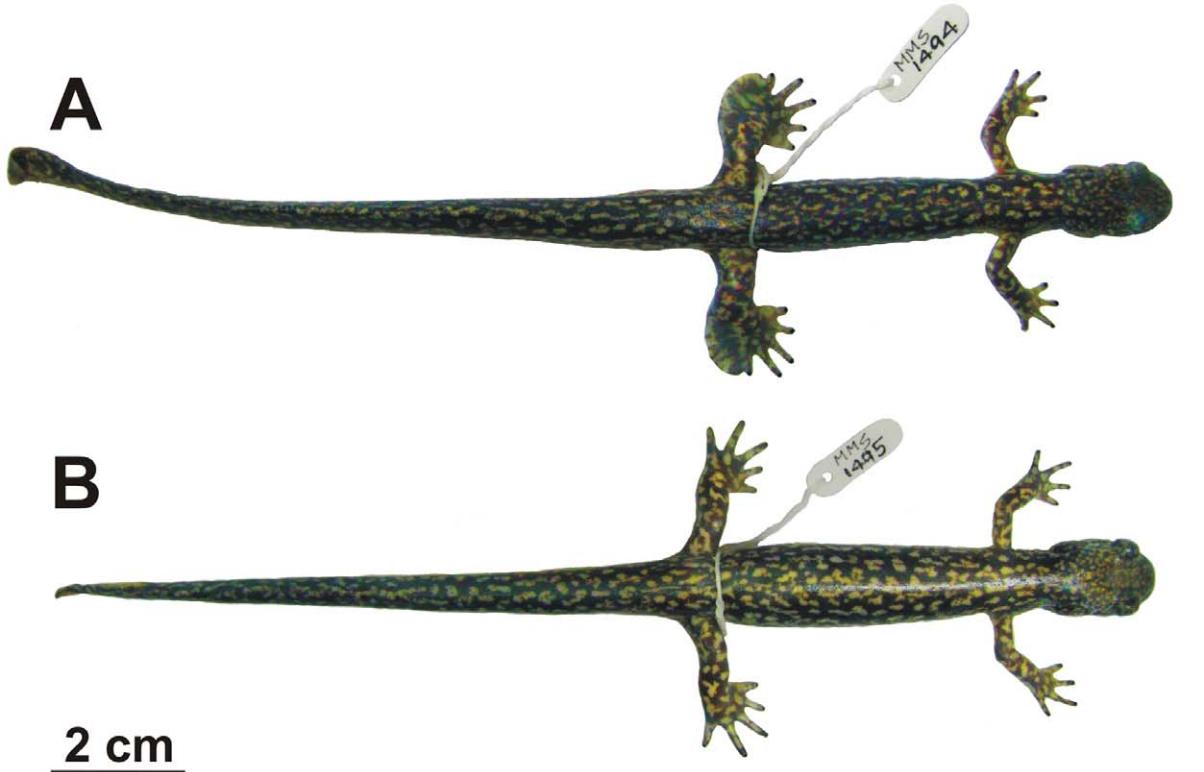


FIGURE 16. The type series of *Onychodactylus koreanus*: (A)—The holotype, EWNHM 80316, adult male from the type locality (SinGi-Myeon environs, Samcheok-shi, Gangwon-do, Korea); dorsal view in preservative; (B)—The paratype, EWNHM 80315, adult female, from the type locality; dorsal view in preservative; (C)—The paratype, EWNHM 80329, adult female from the type locality, dorsolateral view in life. Photos by M.-S. Min.

almost cylindrical, slightly compressed at the end, vomerine teeth in transverse short arch-shaped series almost in contact with each other, presence of large premaxillary fontanelle completely separating the nasals, presence of more than nine caudal ribs, presence of skinfolds in larvae on the posterior edges of both fore- and hindlimbs and dermal flaps in males being developed during the breeding season, with diploid chromosome number $2n = 78$ and other typical features of the genus. This species can be diagnosed from the other members of the genus by a following combination of adult characters: 19 (18–20) presacral trunk vertebrae, 13 (12–14) costal grooves (Tab. 6), 16–17 (10–20) vomerine teeth in each vomerine tooth series (Tab. 7), comparatively shallow, slightly curved vomerine tooth series usually with a gap between them (Fig. 4, C), with the outer branches of vomerine tooth series being longer than the inner branches and with the outer ends of the series located more posteriorly than their anterior ends, comparatively larger eyes in both sexes and relatively narrower heads in both sexes (Tabs. 4; 5), black acute claws usually appearing on hindlimbs in males and sometimes in females during the breeding season which may be absent in both sexes out of the reproductive season, dark ground color of dorsum, head and tail (black to brown) with numerous, small (size $< \text{SVL}/30$) light (yellow, golden to red-orange) non-confluent round or oval spots and ocelli (Fig. 5, D), light ocelli usually numerous, light variegations absent, light reddish or brownish ventral side; light dorsal band always absent, juveniles with dark ground color of the trunk with a contrasted spotted coloration, and distinct genetic differences.

Description and variation.

Type specimens. The type series consists of 13 specimens: 4 males, 2 females, 2 juveniles and 5 premetamorphic larvae.

Description of the holotype. An adult male, in a good state of preservation, fixed in formalin and preserved in 75% ethanol, with a SVL of 71.7 mm (measured on the preserved specimen) (see Fig. 16, A). **Head.** Head moderately depressed, comparatively long and narrow, head noticeably longer than wide: ratio of head length (HL) / head width (HW) is 1.60, head noticeably wider than neck. Neck appreciably long, approximately 3.5 times shorter than head. Tongue large, elliptical, distinctly widens towards its terminal end. Snout rather short, ratio of snout length (OR) / head length (HL) is 0.31; snout rounded from the dorsal view, gently sloping from eyes to nostrils. Nostrils small, with dorsolateral orientation, not protuberant, widely separated and distant from snout tip, ratio of internarial distance (IN) / head length (HL) is 0.33. Eyes very large and distinctly protuberant, eye diameter is longer than snout length and is slightly longer than the internarial distance: ratio of eye length (EL) to snout length (OR) is 1.10; ratio of eye length (EL) to internarial distance (IN) is 1.02. Orbita close to each other, interorbital distance short: ratio of interorbital distance (IO) to head length (HL) is 0.21; ratio of eye length (EL) to the intercanthal distance (IC) is 0.98. Eyelids present, well-developed; labial folds absent; the gular fold is distinct. Distinct parotid glands are absent with no clear borders visible. From the posterior corner of eye towards the angle of the mouth there is a distinct longitudinal postorbital groove, edging a slight protuberance located above the posterior ends of the jaw near the mouth angle. The postorbital groove is noticeably shorter than the eye length and does not reach the angle of the mouth; upwards from the mouth angle there is a distinct transverse supraquadrate groove, which is approximately two times shorter than the postorbital groove; it intersects with the postorbital groove above the angle of the mouth. From this point a distinct longitudinal subparotid groove points backward, separating the parotid area from the swollen elongated subparotid protuberance, which continues from the angle of the jaw to the gular fold. At their posterior end the subparotid grooves gently curve downwards subtly intersecting with the gular fold at the end. The subparotid protuberance is distinct, elongated, oval-shaped, noticeably swollen. From the dorsal view a distinct narrowing of the head is visible at the level of the angle of the jaw, and the base of the head appears noticeably wider than the neck. **Vomerine teeth.** Vomerine teeth in two transverse subtly bended shallow arch-shaped series, forming a <Trunk. Body elongated, cylindrical and slender; chest rather narrow: chest width (CW) / SVL ratio 0.14. The dorsum and venter skin is smooth, slimy; scattered with many microscopic granular glands especially well visible on the dorsum. Dorsally, a middorsal groove is visible, extending from the base of tail to the base of the head. Nineteen presacral trunk vertebrae (TVN) are present and 13 costal grooves are clearly visible both on the right and left sides of the body. **Cloaca.** Cloaca

elongated, slightly protuberant, with Y-shaped longitudinal vent and slightly swollen edges with transverse wrinkles, at the anterior edge of the vent a small protuberance is present. **Extremities.** Limbs slender, well-developed, with hindlimbs slightly longer and more distinctly robust than the forelimbs; when forelimb and hind limb are adpressed towards each other against the flank, the digit tips do not meet; a distinct gap more than 1.5 costal segments is present between toes and fingers of the adpressed limbs; forelimb length to groin-axilla distance ratio ("Wolterstorff's index") is 0.54; hindlimb length to groin-axilla distance ratio is 0.61. No distinct palmar or tarsal tubercles are present on palms or feet. Four fingers and five toes without digital webbing; in order of decreasing length the relative lengths of the fingers are: $1 < 4 < 2 < 3$; relative length of toes: $1 < 2 < 5 < 4 < 3$. Tips of fingers and toes are rounded, black cornified claws are evident on all fingers and toes, each claw base is wide-V-shaped from the dorsal view, and the claw's distal end is slightly curved and pointed. Each hindlimb posess a large fleshy skinfold which begins at the distal phalanx of the fifth toe and goes along the posterior edge of the hindlimb. There is a distinct cutting at the fold basis between the skinfold and the fifth toe; size of the cutting is comparable with the last phalanx of the fifth toe. The skin fold reaches its' maximal width at the level of the tarsus where it is distinctly wider than the length of the fifth toe. It narrows at the knee and completely disappears at the posterior edge of femoral base. Edges of the skinfold are slightly rounded and undulated however without major prominences. **Tail.** Tail is very long, ca. one and a half times longer than the body: tail length (TL) to body length (SVL) ratio is 1.54. At the anterior third of its length the tail is cylindrical in transverse section and not compressed laterally; in the middle third of its length the tail is slightly compressed laterally and oval-shaped in transverse section. The posterior third of its length the tail is distinctly laterally compressed. No caudal fin is evident on the major part of the tail, a feeble upper caudal fin fold, originating at a point approximately one fifth of the distance from the base to the tail tip and gradually increasing posteriorly is evident and no lower tail fin fold is present. The most distal part of the tail (ca. 1.5 cm) is slightly tapered and the widest part of the tail is ca. 2 cm from the tail tip, which is rounded. In the preserved specimen the tail tip (ca. 5 mm) is curved on the right (from a dorsal view). No tail autotomy has been reported in the species.

Measurements of the holotype (in mm). SVL 71.7; TL: 110.3; GA: 35.7; FLL: 19.5; HLL: 21.6; HL: 16.0; HW: 10.0; EL: 5.4; IN: 5.3; ON: 2.6; IO: 3.3; CW: 5.4; OR: 4.9; IC: 5.5 (measured on the preserved specimen).

Color of the holotype in life.

Background coloration. Dorsum dark, blackish. The background color is blackish-brown to dark-chocolate brown on the back, varying to dark-lavender-brown at the flanks of body and tail and to dark-reddish brown at the dorsal surface of head and tail. Flanks of tail and body are distinctly lighter, gray-beige or reddish-gray, with a noticeable lavender to pinkish tint. The costal grooves are somewhat darker than the costal segments. Background color of the lateral sides of the head is pinkish-beige to light orange-beige. Background color of ventral side is dark pinkish-gray, or lavender-gray, and is distinctly lighter than the dark dorsal background color, the chest is slightly darker. Ventral side of the belly is a semitransparent. The gular region is more or less the same color but is slightly brighter and more pinkish than the body's ventral coloration. The cloacal area is lightly colored in gray-beige with a slight pinkish hue, the same color as the ventral aspect of the tail. The ground color of the dorsal limb surface is slightly lighter than the dorsal background coloration; it is dark brown to grayish-brown. The ventral sides of the limbs are lightly colored in pinkish-gray or orange-beige; they are lighter than the ventral coloration of the body and chest. In life the eyes are evidently lighter colored than the rest of the dorsal surface of the head, the upper eyelids and the area around the eye is gray-bluish to grayish-violet in coloration. A similar bluish or violet tint appears on the flanks and sides of the tail, as well as on the distal parts of fore- and hindlimbs. The cornified claws on fore- and hindlimbs are black. **Pattern.** On the dorsal side of the body, head and tail numerous light colored spots and ocelli are present. They are golden-yellow to golden-orange, they vary in size from very small on the head (less than 1 mm) to distinctly large and slightly longitudinally elongated ocelli with black centers on the scapular area (size up to 5 mm; black spots are ca. 1 mm) and longitudinally elongated sometimes confluent spots on the dorsal side of the tail and hindlimbs (length up to 10 mm). The light spots on the dorsal and lateral sides of the tail show a tendency to merge, and eventually there are no signs of any light dorsal bands or stripes present on neither the tail nor on the dorsum. The light spots on the head are very small and numerous (up to 10–15 spots across the top of the head on the dorsal surface). In the scapular region they become larger (up to 4–7 spots across the back), and more elongated towards the pelvic area (up to 7–10 spots across the back in the middle of body; 6–8 across the pelvic area). On the sides of the body the light spots become smaller, more elongated and less intense in coloration; they merge with the light ventral coloration along the belly margins and light spots are absent on the

ventral side of the body. Almost no pattern or markings are visible on the ventral side of body, tail or head. On the limbs, there are light spots similar to that of dorsum, but they are larger and have a more irregular shape and are sometimes confluent; their size increases as they progress distally, and finally they merge with the light coloration of the ventral sides of the limbs. The fingers and toes are thus lightly colored with a few dark spots on the dorsal sides and dark-black acute claws. The posterior skin flap on the hindlimbs is lighter colored than the dorsal portion of the hindlimb with several light and dark spots forming irregular cross-bars (number 4–5). **Iris.** Iris in life is golden-brown with tiny orange and yellow spots (which disappear in preservative); upper and lower marginal sides of the iris are lighter and brighter than the medial part surrounding the pupil. The pupil is horizontal and oval-shaped.

Color of the holotype in preservative: After five years in preservative the bright colors fade first, the reddish or pinkish tint disappears completely: the dark dorsal coloration loses the reddish tint and turns dark gray or brownish; the light spots at the dorsal sides of head, body and tail turn whitish, olive-yellow, gray-yellow to dark-beige; and the ventral sides become light gray-yellowish or whitish in color. The bluish tint from the sides vanish with the upper eyelid being slightly lavender-grayish. However, the principal pattern of the original coloration does not change and is clearly recognizable (see Fig. 16, A).

Variation. Morphology of the paratypes in general resembles that of the holotype except as follows:

Morphometrics. Variation in mensural characters among the type series of the new species are presented in Tables 4 and 5. The species is in general characterized by the following morphometric parameters (ranges for males / females / juveniles, 49 specimens): snout-vent length (SVL): 36.0–77.9 / 41.8–78.6 / 43.2–46.7; tail length (TL): 51.2–110.3 / 42.1–90.6 / 43.6–47.6; gleno-acetabular distance (GA): 24.0–41.5 / 21.4–42.8 / 22.6–23.5; forelimb length (FLL): 12.2–20.1 / 11.6–20.7 / 11.3–13.1; hindlimb length (HLL): 14.7–23.3 / 13.2–24.2 / 12.8–15.0; head length (HL): 12.3–16.6 / 11.2–16.7 / 10.2–11.1; head width (HW): 9.1–11.3 / 7.5–11.8 / 7.9–8.2; eye length (EL): 4.0–5.4 / 3.3–5.2 / 3.0–3.2; internarial distance (IN): 4.6–5.6 / 4.0–6.2 / 3.7–4.2; orbitonarial distance (ON): 1.9–2.9 / 2.0–3.0 / 1.5–1.8; interorbital distance (IO): 3.2–3.9 / 3.1–3.9 / 3.1–3.5; chest width (CW): 5.4–10.8 / 4.8–10.9 / 4.7–5.2; snout length (OR): 4.1–5.4 / 3.7–5.6 / 3.4–3.8; intercanthal distance (IC): 5.4–7.0 / 4.6–6.5 / 4.9–5.4 (measured on the preserved specimens). Morphologically *O. koreanus* is most similar to the Chinese species: *O. zhangyapingi* (Jilin populations) and *O. zhaoermii* (Liaoning populations). The latter is however well discriminated from *O. koreanus* by means of the PCA analysis, whereas there is a significant overlap in PCA scores for males of *O. koreanus* and *O. zhangyapingi*, but not in females (Fig. 6). These two species are nevertheless clearly distinct in certain morphological characters and pronounced genetic differences (see Results and Comparisons).

Sexual variation. *O. koreanus* demonstrates pronounced sexual variation in morphometric traits and significant differences are found for several measurements and ratios (see Results, Tab. 5). We found significant differences in body size (SVL): males have longer SVL-distance than females ($p < 0.005$). As in other *Onychodactylus* species, males *O. koreanus* have significantly longer tails than females, and these differences are significant for absolute and relative TL-values ($p < 0.005$). There are significant differences between the sexes in absolute values of axilla-groin distance (GA), but not the relative GA/SVL-ratio. Males have significantly longer and narrower heads than females ($p < 0.05$), differences between values of HL/HW ratio are also significant ($p < 0.05$). Males have larger eyes than females ($p < 0.05$); distance between external nares is greater in males than in females and they show longer internarial (IN, IN/HL) and orbitonarial (ON) distances ($p < 0.005$). Males also show significantly longer snout lengths than females (OR, OR/HL; $p < 0.005$) and longer intercanthal distances (IC; $p < 0.05$). There are no significant differences found however between the sexes in the relative length of limbs: males tend to have longer forelimbs (FLL) and hindlimbs (HLL) than females, but these differences are significant only for absolute values.

Secondary sexual characters. Along with pronounced sexual dimorphism in morphometric traits, *O. koreanus* shows a number of secondary sexual characters, especially well pronounced during the reproductive season, but also noticeable during the non breeding season. Males always have longer and more flattened tails than females: during the reproductive season males develop comparatively higher dorsal tail fins than females, and in males the tail tip is enlarged, tapered and more pointed than in females. Males always have massive and thick hindlimbs, which develop on the outer edge a wide fleshy skinfold, running from the level of the distal phalanx of the fifth toe and along the posterior edge of the hindlimb to the tibia, where there is usually a distinct cutting at the base of the fold between the skinfold and the fifth toe (as described for the holotype). Park (2005), who observed

the courtship and fertilization process in *O. koreanus* in the wild, reported on significant male-male competition and assumed that the primary role of such dermal flaps may be in clasping the already laid egg sacs in order to protect them from insemination by rival males. In *O. koreanus* evidence of hindlimb folds are often noticeable out of the breeding season; the complete reduction of the hindlimb folds actually takes more than two months to occur (Park, 2005). Park (2005) also reports the presence of black aspertities on the inner surface of the hind feet in breeding *O. koreanus* males, although we have never observed such structures in this species. In males of *O. koreanus* the vent is more swollen than in females, and while these differences are especially more pronounced during the breeding period, it may also be observed outside of the reproductive season. In males, during the breeding season, the vent becomes a longitudinal slit with slightly swollen, bended longitudinal lateral folds on the sides and joined at the tip by two shorter oblique slits directed forward, and joined one fourth its length back from the tip by two other similar slits. This opening of the vent between tip and posterior short slits (Dunn, 1923) in females is a simple longitudinal slit. As is typical for members of the genus *Onychodactylus*, during reproduction *O. koreanus* develop black cornified claws on fingers and toes, which are found in both males and females. Usually, black claws are absent out of the breeding season, however, even during the reproductive period within one population both males and females with or without claws can be found. Within our sample, types of *O. koreanus* collected from the SinGi-Myeon environs (Samcheok-shi) all posses black claws (EWNHM 80316-80318, males; EWNHM 80315, female, see Fig. 16, A-C; Fig. 17, A); referred materials from other localities in Korea (EWNHM 80320; EWNHM 80322-EWNHM 80329) lack black claws. The extent of claw development seems to be connected with the animals' reproductive status and varies among populations (Park, 2005).

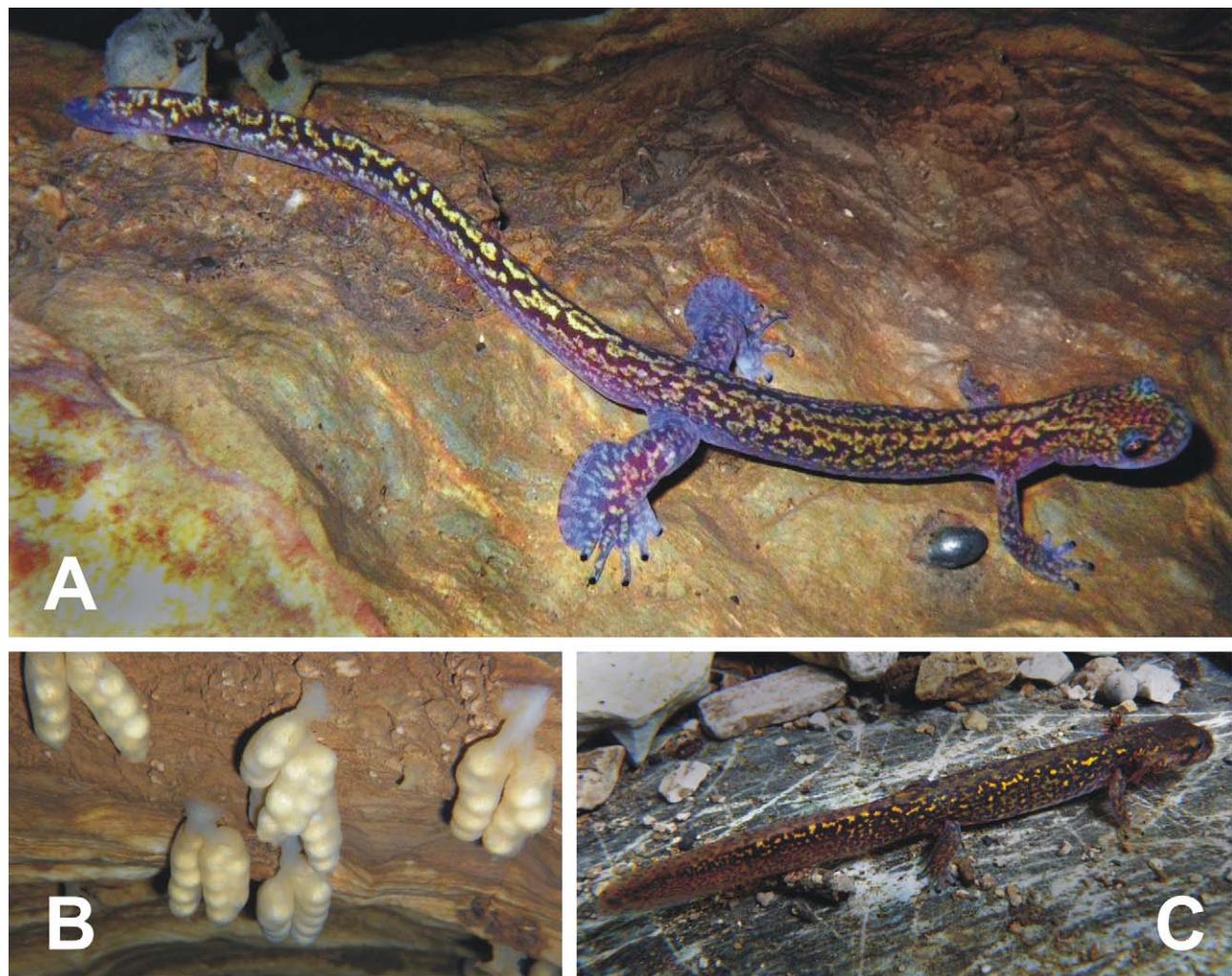


FIGURE 17. *Onychodactylus koreanus*: (A)—Adult male at life during breeding season showing enlarged skinfold on hindlimbs, photo from the type locality (SinGi-Myeon environs, Samcheok-shi, Gangwon-do, Korea); (B)—Egg-laying site of *Onychodactylus koreanus* at the type locality; paired egg sacs with large eggs can be seen; (C)—Premetamorphic larva of *Onychodactylus koreanus* from the type locality. Photos by M.-S. Min.

Color in life. Coloration of the type series in general corresponds well with the coloration of the holotype; variation is insignificant and mostly pronounced in the dorsal pattern of small light spots and ocelli, which seems to allow for individual specimen recognition. In some specimens the small light spots and ocelli are mottled all over the dorsal surfaces in a consistently uniform pattern, as in the holotype (Fig. 16, A). In other specimens, especially on the tail and occasionally on the dorsum as well, this mottling takes the form of two indistinct dorsolateral stripes (Fig. 17, A). Significant variation is also found in the form of light spots. Usually they are roundish or in the form of ocelli with a dark spot in the center (Fig. 16, B, C), however in some specimens the light spots tend to get elongated longitudinally, especially in the pelvic area and further up on the tail, and in those instances individual spots have a tendency to merge, forming irregular interrupted light stripes on the tail and dorsum (Fig. 17, A). The intensity of the dark ground base color may also vary from very dark, almost black, as in the holotype (Fig. 16, A), to lighter, brownish colors, like dark purple-brown, or gray-brown. The color of dorsal light spots and ocelli also varies from pale-yellow, bright yellow or golden, to orange and sometimes almost orange-red, in those examples (more often in juveniles) the flanks and the ventral sides have also somewhat reddish coloration (Uchiyama *et al.*, 2002). Color intensity may also be the subject of seasonal variation – coloration of salamanders of the land phase is usually duller than during the reproductive season. No variation in coloration between the sexes has been recorded.

Color in preservative. Coloration patterns correspond to those of live specimens, however, bright colors tend to fade away and disappear; the base color of the dorsal surface usually fades to dark gray or brownish; the light spots fade to a creamy white, and the dark brown is slightly less warm in tone turning grayish-brown, as described for the holotype (see Fig. 16, A, B).

Osteology and anatomy. We are not aware of any specific anatomical descriptions of *O. koreanus* except those of Dunn (1923), who based his description of *O. fischeri* entirely on specimens from the Korean peninsula (4 adults and 224 larvae from Wonsan, Gangwon-do, now North Korea) which undoubtedly belong to the new species *O. koreanus*. A figure and systematic description of skull morphology of *O. koreanus* is given in a monograph by Sato (1943) (as *O. fischeri*). Variation in the number of trunk vertebrae (TVN) and number of costal grooves (CGN) among the type series of *O. koreanus* are presented in Table 6. Modal TVN-number in *O. koreanus* is 19 for both sexes, ranges vary: 17–19 for males, mean is 18.7 ± 0.55 ; 18–20 for females, mean is 18.9 ± 0.53 . The trunk–vertebrae numbers result in the respective costal groove counts: 13 (11–13) for males and 13 (12–14) for females (based on 36 specimens, see Tab. 6).

Vomerine teeth morphology. Adults of *O. koreanus* have vomerine teeth arranged in two transverse shallow gradually curved arch-shaped series with the outer branches of the series being noticeably longer and much less curved than the inner branches (Fig. 4, C). The series begins behind at the middle of the nares, curving forward and to the level of the anterior edge of the nares, then back and in, but not so far back in the center as on the sides, and is separated from its other series by a distinct gap (Dunn, 1923). Dunn (1923) reported on a specimen from Wonsan with a gap being one-half the width of the naris. In our series the gap between the left and right vomerine tooth series is narrow, but always distinct, with a width ranging from 1/4 to 1/3 the width of the naris. Both outer and inner branches are slightly curved in this species, with the outer tooth series branches being longer and less curved than the inner branches. At the very end the inner branches are slightly curved anteriorly. The ends of the inner branches of the tooth series are located noticeably posteriorly than the ends of the outer branches (see Fig. 4, C) (almost equal to the width of the naris). Variation in the number of vomerine teeth (VTN) among the type series of the new species is given in Table 7. In our sample the number of vomerine teeth in the species is high and is significantly higher than in *O. fischeri*: 12–13 (mean 17.2 ± 2.24) teeth per each branch in males; 13–20 (mean 17.1 ± 2.26) for females and 15–19 (mean 16.7 ± 1.65) for juveniles (based on 28 specimens, see Tab. 7). Juveniles tend to have less curved and shallower vomerine tooth series with the outer branches being much longer than inner branches.

Eggs and clutch. *O. koreanus* females lay two small, paired egg sacs, elliptical in shape with white, semitransparent walls and are joined together at the distal end and attached to stones and similar objects by a mucous-like stalk. Many different sacs may be found attached to a single stone (see Fig. 17, B). For the first time, egg-laying and fertilization of this species was observed in the wild by Park (2005) at Hwansun-gul cave, Samcheok-shi, Kangwon-do, South Korea. The oviposition site of *O. koreanus* was found in a permanent brook 1.5 m in depth inside a cave. The bottom of the brook was covered by rocks, pebbles, and sand. The main oviposition site was on the wall of the brook, located 40 cm below the surface of the water in the shallowest portion, and was two meters wide and one meter high. Most egg sacs were attached by gelatinous stalks to the side of the rock walls.

A total of 173 pairs of egg sacs were found at the oviposition site. Park (2005) reported the mean length of egg sacs(n=8) was 35.7 ± 2.6 mm, and the mean width of the egg sacs was 15.6 ± 2.3 mm. Egg sacs were connected to gelatinous stalks ($L = 12.9 \pm 2.25$ mm, n=5). The number of eggs within an egg sac ranged from 2 to 13 (8.62 ± 1.95 , n=52), and the clutch size (number of eggs per egg sac pair) from 10 to 22 (16.92 ± 2.93 , n=25). Egg diameter ranged from 4.9–7.2 mm (5.95 ± 0.52 mm, n=86) (data from Park, 2005).

Larval morphology and metamorphosis. The pattern of embryonic and larval development has not been documented in detail, but is most likely typical for rheophilous salamanders and resembles those of *O. japonicus* (Iwasawa & Kera, 1980; Kuzmin, 1995). Spawning and hatching of larvae occur in underground breeding sites. Early larval development is subterranean; in Korea the larvae appear in brooks when they reach lengths from 30 to 40 mm. Larvae demonstrate morphology typical for *Onychodactylus* (see Fig. 17, C): they have square-shaped heads that are wider than their bodies with rounded a snout, eyes slightly prominent, digits with coal-black cone-shaped sharp, horny claws, with a fold of skin along the outer edge of fore- and hindlimbs which disappears before metamorphosis, and the gills are quite short with the base of the gill rachis covered with an opercular skin fold. Tail fin is low, developed on the dorsal surface of the tail in the first third of its length and not reaching the cloaca on the ventral side of the tail; dorsal tail fin is higher than the ventral fin. Background color of premetamorphic larvae is usually dark-brown or gray-brown on the dorsum and cream-colored or beige on the ventral surfaces. This dark base color is mottled with numerous golden or yellowish spots and flecks (Fig. 17, C). They tend to become larger and more elongated on the dorsum, sometimes forming indistinct broken light dorsolateral stripes, usually extending to the tail. This color pattern changes upon metamorphosis—where the ground color on the dorsum becomes darker (to brownish-black), and the yellow spots become brighter and more numerous. This coloration pattern is retained by juveniles after metamorphosis. Before metamorphosis, the black claws are shed. Larvae will leave the water after two or three years. The age of *O. koreanus* larvae (data published as of *O. fischeri*) ranged from 0 to 3 years and *O. koreanus* larvae may metamorphose when they are at least two years old in late summer or early autumn (Lee *et al.*, 2008). Larvae complete metamorphosis and migrate onto land at a total length of 70 to 100 mm.

Etymology. The specific name “*koreanus*” is a toponymic adjective in the nominative singular, referring to the Korean peninsula inhabited by this species. We suggest Korean Clawed Salamander as the English common name of the species as a reference to the species distribution. Recommended common names in Korean, Russian, Chinese and Japanese are given above.

Distribution. The new species is documented to date only from South Korea, where it inhabits mountain areas of Baekdudaegan Mts. and Taebaeksanmaek Mts. (reported from provinces Gangwon-do, Gyeonggi-do; Chungcheongbuk-do; Chungcheongnam-do; Gyeongsangbuk-do; Gyeongsangnam-do; Jeollabuk-do; Jeollanam-do). Distribution of *O. koreanus* in Korea was summarized in Kang & Yoon, 1975; Yang *et al.*, 2001 and Kim, 2009. The species inhabits mountainous areas of the Korean peninsula excluding Jeju Island and offshore islands of Korea. In Korea, *O. koreanus* ranges from mountains in the north of the country southwards along the main mountain system of the peninsula – Taebaeksan range. In the middle region of South Korea the species range is divided and runs along the Sobaeksan range, which branches southwestward from the Taebaeksan range, to as far as the highest peak of the mainland Korea – the Jirisan Mt. Mountain populations in the southern part of the Korean peninsula may be isolated from the main distribution range of the species. An isolated *Onychodactylus* population inhabits the Yangsan Mt. in the southeast of the peninsula. *O. koreanus* are found in the environs around Seoul (Bukhan Mts. NP), Gyeonggi-do (Yongmun Mt), Gangwon-do (Jeongseon, Sokcho (Seoraksan Mts. NP), Taebaek, Chuncheon, Wonju (Chiaksan Mts NP), Hongcheon, Pyeongchang (Odaesan)), Chungcheongbuk-do (Songnisan Mt. NP), Chungcheongnam-do (Gongju (Gyeryongsan Mt. NP), Daejeon, Nonsan, Geumsan, Cheongwon, Cheonan, Seocheon), Jeollabuk-do (Muju (Deogyusan Mt. NP), Jeongeup (Naejangsan Mt. NP), Jinan), Jeollanam-do (Jirisan Mts. NP), Gyeongsangbuk-do (Bongwha, Yeongju), and Gyeongsangnam-do (Hapcheon, Sancheong, Yangsan). The species most likely inhabits neighboring regions of North Korea, but since no collections or other materials were available, the extent and distribution of the new species in the northern half of Korean peninsula remains unknown. To date *Onychodactylus* (as *O. fischeri*) were reported from the following provinces of North Korea: Hamgyeongbuk-do, Hamgyeongnam-do, Yanggang-do, Changang-do, Pyongannam-do; N and S Hwanghae-do (Won, 1971). However whether they are inhabited by *O. koreanus* or another species of *Onychodactylus* will require clarification and further studies.

Comparisons. *O. koreanus* can be distinguished from the other salamanders in the region, including a sympatric *Hynobius* species, by its slender body, smooth skin with distinct costal grooves on the flanks, very long

tail, almost cylindrical at the base, slightly compressed in the middle and flattened towards its end, small and somewhat elongated head with rounded snout, and a combination of morphological features characteristic of *Onychodactylus*, such as absence of lungs, breeding males develop dermal flaps on the outer surface of the hindlimbs, both sexes during the reproductive season posses black horny claws on both fingers and toes, vomerine teeth in two short transverse arch-shaped series, premaxillary fontanelle large fully separating nasals, caudal ribs numerous and present on more than 5–6 postsacral tail vertebrae. From a sympatric plethodontid salamander *Karsenia koreana* the new species is further distinguished by absence of nasolabial groove, tail obviously compressed towards the end and larger body size.

From other congeners, *O. koreanus* differs in the average number of trunk vertebrae (19) and costal grooves (13), and typical coloration of juveniles and adults—dark ground color with numerous bright, small round spots and / or ocelli and no distinct dorsal band. *O. koreanus* can be further distinguished from other *Onychodactylus* species by a following combination of morphological attributes:

O. koreanus can be distinguished from *O. fischeri* (Boulenger, 1886) by the following combination of morphological traits: lower trunk vertebrae number (TVN = 18–19) and costal groove count (CGN = 12–13) (versus TVN = 20–21 and CGN = 14–15 in *O. fischeri*) (Tab. 6); rows of vomerine teeth are slightly curved or bended with the outer branch usually being noticeably longer than the inner branch, vomerine tooth arch asymmetrical, and the lateral end of the outer branch is located posteriorly than the medial end of the inner branch in *O. koreanus*, Fig. 4, C (versus almost straight or slightly bended vomerine tooth series with outer and inner branches of the series being roughly of the same length and the lateral end of the outer branch is located roughly on the same level as the medial end of the inner branch in *O. fischeri*, Fig. 4, A); vomerine teeth numerous, VTN = 17.1 ± 2.11 (per row) in *O. koreanus* (versus VTN = 11.5 ± 1.23 in *O. fischeri*) (Tab. 7); and dorsal coloration: no prominent dorsal stripe, background color of dorsal surface is dark; usually back side of body is covered with numerous small contrast light spots, Fig. 5, D (versus light dorsal stripe present, indistinct with unclear edges in *O. fischeri*, Fig. 5, A). *O. koreanus* further differs from *O. fischeri* in following morphometric features (see Tabs. 4; 5 for details): comparatively smaller SVL, longer tail in males, comparatively longer hindlimbs in both sexes and forelimbs in males, longer and wider heads in both sexes, larger eyes and greater internarial distance in both males and females.

O. koreanus can be distinguished from the members of *O. japonicus* species complex in the following ways: *O. japonicus* (Houttuyn, 1782) and *O. nipponoborealis* by dorsal pattern: no prominent dorsal stripe, background color of dorsal surface is dark; usually back side of body is covered with numerous small contrast light spots or blotches in *O. koreanus*, Fig. 5, D (versus prominent light-colored dorsal stripe present in members of *O. japonicus* species complex, background color of dorsal surface is lighter than color of body sides, Fig. 5, E-G). *O. koreanus* can be further distinguished from *O. japonicus* (Houttuyn, 1782) and *O. nipponoborealis* by the form of vomerine tooth series: rows of vomerine teeth are slightly curved or bended with the outer branch usually being noticeably longer than the inner branch, vomerine tooth arch asymmetrical, and the lateral end of the outer branch is located posteriorly than the medial end of the inner branch in *O. koreanus*, Fig. 4, C (versus comparatively deep notably curved vomerine teeth with outer and inner branches of the series being roughly of the same length (vomerine tooth rows are almost symmetrical) and the lateral end of the outer branch is located roughly on the same level as the medial end of the inner branch in *O. japonicus*, Fig. 4, E and *O. nipponoborealis*, Fig. 4, F). *O. koreanus* can be further diagnosed from *O. japonicus* (Houttuyn, 1782) by having a greater vomerine tooth count (VTN): VTN = 17.1 ± 2.11 in *O. koreanus* (versus VTN = 11.4 ± 1.16 in *O. japonicus*) (Tab. 7); and by having a greater trunk vertebrae number (TVN): 18–19, usually 19 (versus 17–18, usually 17, in *O. japonicus*) and a greater costal groove count (CGN): 12–13, usually 13 (versus 11–13, usually 11 in *O. japonicus*) (Tab. 6). Male *O. koreanus* also differs from *O. nipponoborealis* males in modal trunk vertebrae and costal groove counts: CGN = 13 (versus CGN = 12 in *O. nipponoborealis*), TVN = 19 (versus TVN = 18 in *O. nipponoborealis*). *O. koreanus* further differs from *O. japonicus* and *O. nipponoborealis* in following morphometric features (see Tabs. 4; 5 for details): shorter SVL in females, comparatively wider and shorter heads in both sexes, greater distance between nostrils in both sexes, larger eyes than in *O. japonicus* and *O. nipponoborealis*, and a greater distance between orbits for both males and females (in members of *O. japonicus* species complex eyes situated closer to each other than in *O. koreanus*), comparatively shorter forelimbs in both sexes and hindlimbs in females. *O. koreanus* males have significantly longer tails than in male *O. nipponoborealis*, and shorter axilla-groin distances in both sexes.

O. koreanus can be distinguished from the second member of its species complex, *O. zhaoermii*, by a following combination of morphological attributes: a greater trunk vertebrae number (TVN) and costal groove

count (CGN): modal trunk vertebrae number is 19 (18–19) for both males and females, modal costal groove number is 13 (12–13) for both sexes (versus lower TVN and CGN counts in *O. zhaoermii*: modal costal groove number is 11 for males (trunk vertebrae—17), 12 for females (trunk vertebrae—18) (Tab. 6). *O. koreanus* further differs from *O. zhaoermii* in shape of vomerine teeth series: inner branch of vomerine tooth arch is not recurved at the medial end, but may be slightly bended, Fig. 4, C (versus inner branch of vomerine tooth arch is notably curved forward at the medial end in *O. zhaoermii*, Fig. 4, D); it also differs in modal vomerine teeth number (VTN): vomerine teeth usually more than 16 per each row, mean 17.5 ± 2.21 (versus vomerine teeth usually less than 16 per each row, mean 13.8 ± 1.3 in *O. zhaoermii*) (Tab. 7). *O. koreanus* also differs from *O. zhaoermii* in dorsal pattern: dark background color of dorsum is covered with numerous small light (bright-yellow to golden) not confluent relatively regular round or oval spots and dots, not forming reticulate pattern, light ocelli with dark centre are present and numerous, Fig. 5, D (versus dark background color of dorsal surface is covered with numerous bright (orange to copper-red) irregular confluent blotches and spots, normally forming a sparse reticulate pattern, light ocelli are absent or rare in *O. zhaoermii*, Fig. 5, C). *O. koreanus* further differs from *O. zhaoermii* in the following important morphometric characteristics (see Tabs. 4; 5 for details): smaller SVL and axilla-groin distances in females; comparatively longer and wider head in both sexes: HL/SVL ratio is 0.24 ± 0.02 (versus 0.21 ± 0.02 in *O. zhaoermii*), HW/SVL ratio is 0.17 ± 0.01 (versus 0.14 ± 0.01 in *O. zhaoermii*); comparatively larger eyes and greater internarial distance in both sexes.

O. koreanus can be diagnosed from *O. zhangyapingi* by dorsal pattern: dark base color of dorsal surface is covered with numerous small bright-yellow to golden not confluent regular round or oval spots and dots, never forming reticulate pattern, light ocelli are present and numerous, Fig. 5, D (versus dark base color of dorsum is covered with numerous yellowish to pinkish lines or variegations of irregular shape, forming a marbling or dense reticulate pattern; light-colored ocelli on dorsal surface of body and limbs are always absent in *O. zhangyapingi*, Fig. 5, B). *O. koreanus* can be further distinguished from *O. zhangyapingi* by the shape of vomerine tooth series: rows of vomerine teeth are slightly bended with the outer branch usually being noticeably longer than the inner branch, its lateral end is located posterior towards medial ends of the inner branches, Fig. 4, C (versus vomerine teeth rows are almost straight with inner branch of almost the same length as outer branch, lateral end of the outer branch is on the same level as the medial end of the inner branch in *O. zhangyapingi*, Fig. 4, B). In males of *O. koreanus* modal trunk vertebrae number (19) and costal groove count (13), is bigger than in *O. zhangyapingi* males (TVN 18; CGN 12), but for females differences are not significant (Tab. 6). *O. koreanus* further differs from *O. zhangyapingi* in the following important morphometric characteristics (see Tabs. 4; 5 for details): smaller SVL and axilla-groin distances in females; both sexes of *O. koreanus* have comparatively shorter tail than in *O. zhangyapingi*; comparatively longer and wider head in females: HL/SVL ratio is 0.25 ± 0.02 (versus 0.20 ± 0.02 in *O. zhangyapingi*), HW/SVL ratio is 0.18 ± 0.01 (versus 0.14 ± 0.01 in *O. zhangyapingi*); comparatively larger eyes, shorter snout and greater internarial distance in both males and females.

Karyotype. $2n = 78$, NF = 102. Chromosomal formula: 6M+6SM+8ST+10T+48a. The karyotype of *O. koreanus* as of *O. fischeri* reported by Sessions *et al.* (1982) based on a specimen from “Korea”, and by Iizuka and Yazawa (1991; 1994), based on two specimens from Mt. Seoraksan [Soraksan], Gangwon-do, five specimens from Mt. Puk’ansan [Bukhansan], suburb of Seoul, Gyeonggi-do, 21 specimens from Mt. Jirisan, Gyeongsangnam-do, and 16 specimens from Mt. Songnisan, Chungcheongbuk-do. The karyotype was reported to be similar with Aomori population of *O. japonicus* (here treated as a distinct species *O. nipponoborealis*) by Ikebe *et al.* (1995).

Genome size. Our estimate of *O. koreanus* genome size is 102.5–103.5 pg per diploid nucleus; CV = 51.25–51.75 (DNA flow cytometry; three specimens from Jirisan NP, Jeollanam-do, Korea; N.A. Poyarkov, pers. obs.; peripheral red blood cells of the Ribbed Newt, *Pleurodeles waltl*, and the Southern Crested Newt, *Triturus karelinii karelinii* (Salamandridae), were used as a reference standard for genome size measurements).

Phylogenetic position. Phylogenetic analyses suggest that this species is sister to *Onychodactylus* populations from Liaoning Province of China, being more closely related to species inhabiting Japanese islands than to *O. fischeri* from Russia (see Fig. 3). *O. koreanus* is a member of its own species complex, which also includes its sister taxon *O. zhaoermii* (described below) from Liaoning, with a degree of divergence between them up to 7.4% in COI sequences and 2.1% in 16S rRNA sequences of uncorrected pairwise genetic distances (Fig. 3; Tab. 3). *O. koreanus* bears significant cryptic diversity, with two distant lineages being found: lineage D is found in the mountain regions throughout the country, whereas lineage E is only known from an isolated mountain area of Yangsan of Gyeongsangnam-do in the southwest region of the peninsula. The two Korean lineages are consistently recovered as monophyletic and are moderately divergent (p-distances of 5.6 to 5.8% in COI and 1.9% in 16S

rRNA). We do not have adult specimens from Yangsan in our sample and thus lack any morphological or biological characters that would allow us to describe them as species, so their taxonomic status remains unclear. However, based on the degree of divergence and possible geographic isolation of this form, we tentatively consider the Yangsan population of *Onychodactylus* as an unconfirmed candidate species (shown as *Onychodactylus* sp. in Fig. 3). Korean populations of clade D show a low divergence ranging from 0 to 1.4% in COI or from 0 to 0.7% in 16S rRNA. Two reciprocally monophyletic lineages are revealed: clade D1 is restricted to the northern part of South Korea and is reported from Gangwon-do, it is likely that this lineage extends to North Korea; clade D2 encompasses all other populations studied and is distributed from Gangwon-do along the Taebaeksan Mountains to the south, and then southwestwards along the Sobaeksan to the Jirisan Mt.

Habitats and natural history. As other *Onychodactylus* species, *O. koreanus* prefers moist, cool and shady places in mountain forests; in Korea it occurs from 10 to 1915 m being most abundant from 20 to 1350 m a.s.l. (Song & Lee, 2009). This species is usually found in clean, fast-running streams in mountain areas, in association with pine trees or deciduous forests, yet it has also been found in caves. They prefer streambeds with numerous logs, an abundance of moss-covered stones, rocks, and pebbles; high humidity and low water temperatures seem to be an important factor, and they are found in streams with water temperatures that range from 6°C to 14°C. Hibernation takes place from approximately late October to April. The animals appear when temperatures rise to 3–5°C. It can be observed in sympatry with *Hynobius* species (*H. leechii* complex), brown frogs of the genus *Rana* (*Rana coreana*, *Rana dybowskii*), and it has been found under stones together with the plethodontid salamander, *Karsenia koreana* (Vieites, pers. obs.). Lee *et al.* (2009) described the ecology of this species in the Odaesan National Park; Chang *et al.* (2005) provided a record for Unmun Mt. Breeding takes place in streams, most likely, usually underground. Reproduction was observed for the first time in the wild and described by Park (2005). This observation occurred from the 20th of May until the 29th of June, when water temperatures rise from 6°C to 10°C. Water temperature at the spawning site was measured at a depth of 30 cm and was 10.4°C. During reproduction, mating males and females aggregate in areas where the females attach clutches to submerged stones and males release sperm, probably fertilizing multiple clutches in the process; during reproduction males outnumbered females by 20 to 1. While a female attaches an egg sacs to the substrate, many males congregate and attempt to grasp the egg sac before oviposition is completed; during this process males form a mating ball, scrambling for access to the egg sacs (Park, 2005). Adults feed on various insects including dragonflies (Odonata), millipedes (Diplopoda), caddisflies (Trichoptera), bees (Hymenoptera; Apoidea), spiders (Arachnida), and earthworms (Annelida, Lumbricidae) (Yoon *et al.*, 1996).

Conservation status. The species inhabits a large part of the Korean peninsula, being common in some areas but scarce in other parts of the range. The extent of its distributional range, with presumably large populations and its occurrence in some protected areas suggest that its conservation status be of Least Concern according to IUCN criteria.

***Onychodactylus zhaoermii* sp. nov. Che, Poyarkov & Yan**

[*Onychodactylus fischeri* (part)—Gee & Boring, 1929: 18; Boring, 1930: 41; Chang, 1936: 71–72; Ji, Lui, Lui, Chou, Huang, Wun, & Cho, 1987: 21–22 and many other authors.]

[? *Onychodactylus sischeni* (part)—Won, 1971: p. 30 (*ex errore*). Unjustified change of the original spelling. The taxonomic status of North Korean *Onychodactylus* populations is unsure; we assume the presence of two Chinese and the South Korean lineages in North Korea.]

[*Geomolgo fischeri* (part)—Ji, Lui, Lui, Chou, Huang, Wun, & Cho, 1987: 21 (erroneous citation from Boulenger, 1886: 416). Unjustified emendation of spelling.]

[*Onychodactylus fisheri* (part)—Ji, Lui, Lui, Chou, Huang, Wun, & Cho, 1987: 21 (erroneous citation from Nikolskii, 1914 "1913: 260). Unjustified emendation of spelling.]

[*Onychodactylus fischeris* (part)—Wang, Li, Wang, & Liang, 2008: 223 (*ex errore*).]

Recommended trivial names:

Chinese name: Liaoning Zhaoni (辽宁爪鲵).

English name: Liaoning Clawed Salamander.

Japanese name: Ryounei-Sansyouo.

Korean name: Lyaoning Ggorichire Dorongnyong.

Russian name: Lyaoninskiy kogtistyi (bezlegochnyi) triton.

Holotype. KIZ06130; an adult male collected during the breeding season on May 9, 2010, by Jing Che and Fang Yan (see Fig. 18, A, B; Fig. 19, A, C).



FIGURE 18. The holotype of *Onychodactylus zhaoermii*, KIZ06130, adult male, from the type locality (Huashan environs, Sanjiazi district, Xiuyan County, Liaoning Province, China): (A)—In life, lateral view, left side; (B)—In life, close-up of head and body, right side. Photos by J. Che.

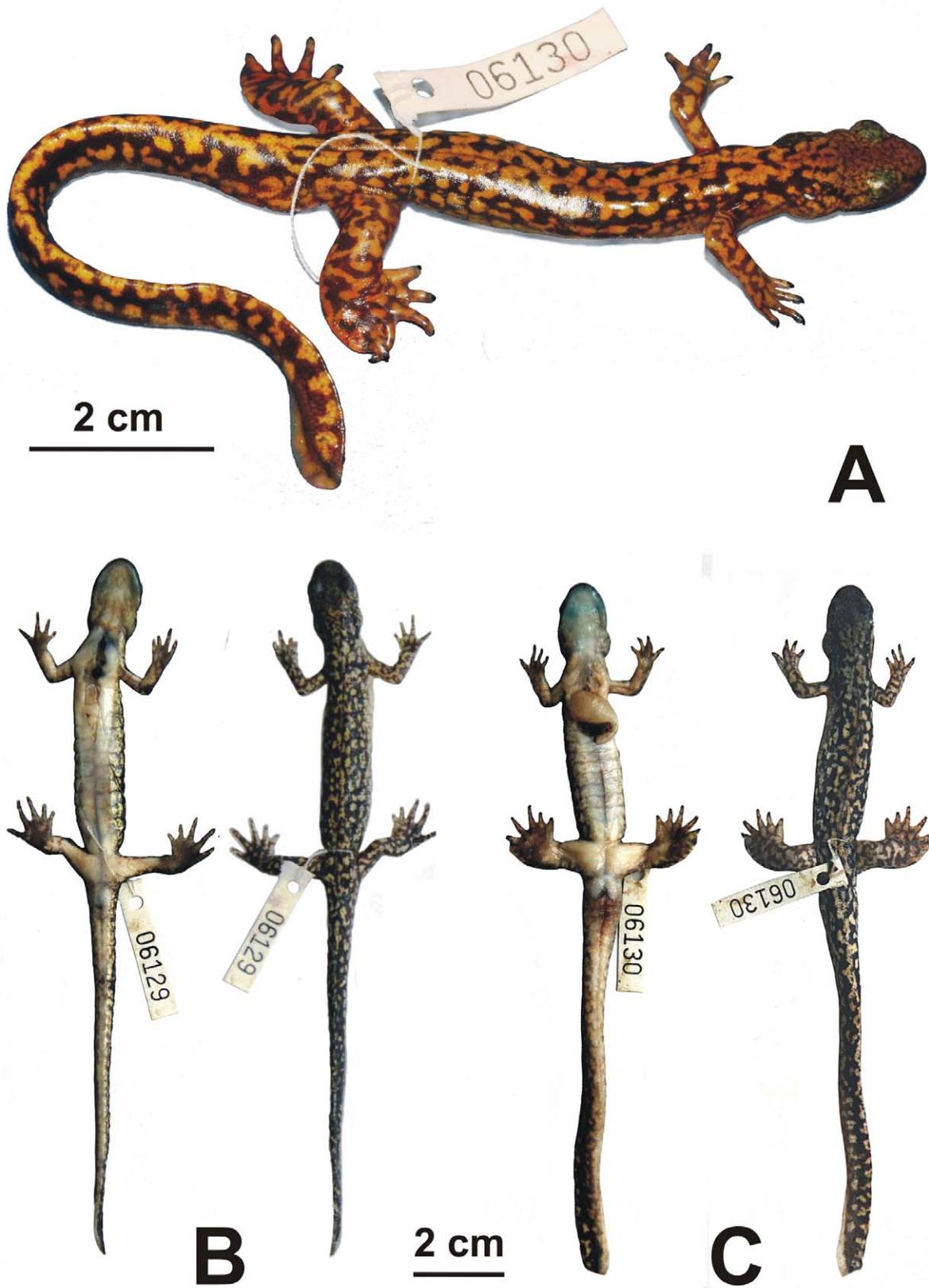


FIGURE 19. (A)—The holotype of *Onychodactylus zhaoermii*, KIZ06130, adult male, from the type locality (Huashan environs, Sanjiazi district, Xiuyan County, Liaoning Province, China); in life, dorsal view; (B)—the paratype female KIZ06129 from the type locality showing absence of black claws on digits; in preservative, ventral and dorsal views; (C)—the holotype KIZ06130 in preservative, ventral and dorsal views. Photos by J. Che.



FIGURE 20. (A)—Breeding habitat of *Onychodactylus zhaoermii* at the type locality (Huashan environs, Sanjiazi district, Xiuyan County, Liaoning Province, China); (B)—The paratype female, KIZ06129, from the same locality at reproduction site.

Type locality. Huashan village environs, Sanjiazi subcounty, Xiuyan County, Liaoning Province, China, altitude 542 m a. s. l.; geographic coordinates: 40° 28' N; 123° 16' E (see Fig. 20, A).

Paratypes. KIZ06132 (adult male), KIZ06056–06058, KIZ06129, KIZ06131, KIZ06133 (six adult females), collected from the same locality as the holotype on May 9, 2010, by Jing Che and Fang Yan (see Fig. 19, B; Fig. 21).

Diagnosis. A slender, relatively medium-sized hynobiid salamander, a member of the genus *Onychodactylus* on the basis following combination of features: absence of lungs, presence of black claw-like horny structures on both fore- and hindlimbs in larvae and breeding adults, tail longer than the sum of head and body lengths, tail almost cylindrical, slightly compressed at the end, vomerine teeth in transverse, short arch-shaped series almost in contact with each other, presence of large premaxillary fontanelle completely separating the nasals, presence of more than nine caudal ribs, presence of skinfolds in larvae on the posterior edges of both fore- and hindlimbs and dermal flaps in males developing during the breeding season and other typical features of the genus. This species can be distinguished from the other members of the genus by a following combination of adult morphological characters: 17–18 presacral trunk vertebrae, 11–12 costal grooves (Tab. 6), usual presence of 13–14 (12–16) vomerine teeth in each vomerine tooth series (Tab. 7), comparatively shallow but noticeably curved vomerine tooth series with a distinct gap between them (Fig. 4, D), with the outer branches of vomerine tooth series being slightly longer and less curved than the inner branches and with the outer ends of the series located more posteriorly than their anterior ends, comparatively longer tail in both sexes, smaller eyes in males and relatively narrower heads in both sexes (see comparisons and Tabs. 4; 5 for the details), black acute claws appearing on hindlimbs in males and sometimes in females during the breeding season, they may be absent in both sexes out of the reproductive season and in females even during the breeding season, ground color of dorsum, head and tail almost equally covered with a dark background color (black to violet-brown) and numerous light (orange to copper-red) small (size < SVL/30) irregular confluent elongated spots, dots and variegations, forming a thick reticulate pattern (Fig. 5, C), light ocelli may be present but sparse, light reddish or orange on the ventral side; light dorsal band always absent, juveniles with a dark ground color of the trunk with a contrasted spotted coloration, and distinct genetic differences.



FIGURE 21. The type series of *Onychodactylus zhaoermii* from the type locality (Huashan environs, Sanjiazi district, Xiuyan County, Liaoning Province, China), showing variation in dorsal coloration: males (KIZ06130; KIZ06132); females (KIZ06056–06058; KIZ06129; KIZ06131; KIZ06133). Scale bar is 2 cm. Photos by J. Che.

Description and variation.

Type specimens. The type series consists of eight adult specimens: 2 males and 6 females, all collected during the breeding season.

Description of the holotype. An adult male, in a good state of preservation, fixed and preserved in 75% ethanol, with a SVL of 68.1 mm (measured on the preserved specimen). **Head.** Head moderately depressed, comparatively long and narrow, head noticeably longer than wide: head length (HL) / head width (HW) ratio is 1.57, head slightly wider than neck, head distinctly widens towards the base of the head. Neck long, approximately 3.0 times shorter than head. Tongue large, elliptical, distinctly widens towards its end. Snout short, snout length (OR) / head length (HL) ratio is 0.29; snout obtusely rounded from the dorsal view, gradually sloping from the eyes to the nostrils in lateral view. Nostrils small, with dorsolateral orientation, not protuberant, widely separated and distant from snout tip, internarial distance (IN) / head length (HL) ratio is 0.29. Eyes distinctly protuberant, moderate size: eye diameter is smaller than snout length and a smaller than the internarial distance: ratio eye length (EL) to snout length (OR) is 0.83; ratio eye length (EL) to internarial distance (IN) is 0.84. Orbita rather close to each other, interorbital distance short: interorbital distance (IO) to head length (HL) ratio is 0.22; eye length (EL) to the intercanthal distance (IC) ratio is 0.64. Eyelids present and well-developed; labial folds absent; the gular fold is distinct. Distinct parotid glands are absent with no clear borders visible. From the posterior corner of eye towards the angle of the mouth there is a distinct longitudinal postorbital groove, edging a slight protuberance located above the posterior ends of the jaw near the angle of the mouth. The postorbital groove is noticeably shorter than the eye length and does not reach the angle of the mouth; upwards from the angle of the mouth there is a distinct transverse supraquadrate groove, which is approximately 1.5 times shorter than the postorbital groove, and it intersects with the postorbital groove above the angle of the mouth. From this point a very noticeable longitudinal subparotid groove extends posteriorly, separating the parotid area from the distinctly swollen elongated subparotid protuberance, which extends from the angle of the jaw to the gular fold; at the posterior end the subparotid groove extends downwards intersecting with the gular fold at its end. The subparotid protuberance is well-developed and noticeably swollen, elongated, bean-shaped, from the dorsal view of the head a distinct narrowing is visible at the level of the angles of the jaw, and the base of the head looks noticeably wider than the neck and is approximately 1.2 times wider than the widest measurement of the head at the angle of the mouth.

Vomerine teeth. Vomerine teeth in two transverse slightly curved, shallow, arch-shaped series, forming a «~»-shaped figure; 14 vomerine teeth in the left vomerine tooth series and 15 vomerine teeth in the right series; the left and right vomerine tooth series are clearly separated from each-other with a narrow but a distinct gap which is noticeable between the medial ends of the inner branches of the tooth series; at the very end each inner branch noticeably curves anteriorly; the outer tooth series branches are slightly longer and are not curved but bend slightly compared with the inner branches; the lateral ends of the outer branches of the tooth series are located slightly more posteriorly than the medial ends of the inner branches. **Trunk.** Body elongated, cylindrical and slender; slightly wider than the base of the head from a dorsal view; chest narrow: chest width (CW) / SVL ratio 0.15. The dorsum and venter skin is smooth, slimy; scattered with numerous microscopic granular glands. On the dorsal side of the body a deep dorsomedial groove is visible, extending from the sacral area to the base of the head, where it bifurcates into two short anterior grooves. Seventeen presacral trunk vertebrae (TVN); and 11 costal grooves are clearly visible both on the right and left sides of the body. **Cloaca.** Cloaca is oval-shaped, elongated, strongly swollen and noticeably protuberant, a Y-shaped longitudinal vent with clearly swollen edges and 5-6 transverse wrinkles on each side: at the anterior edge of the vent two oval protuberances are present. Because of the swollen cloacal region, the base of the tail is noticeably wider than the rest of its length.

Extremities. Limbs are well-developed, with hindlimbs noticeably longer and much more robust than the forelimbs; forelimb length (FLL) to hindlimb length (HLL) ratio is 0.80; when forelimb and hind limb are adpressed towards each other against the flank, the tips of the digit touch each other but do not overlap; forelimb length to groin-axilla distance ratio ("Wolterstorff's index") is 0.54; hindlimb length to groin-axilla distance ratio is 0.68. Two indistinct palmar tubercles are present at the base of the palm, and no clear tarsal tubercles are present on the feet. Four fingers and five toes without digital webbing; in order of decreasing length the relative length of fingers: 1 < 4 < 2 < 3; relative length of toes: 1 < 2 < 5 < 4 < 3. Tips of fingers and toes rounded, black cornified claws are well-developed in all fingers and toes, each base of the claw is wide-V-shaped from the dorsal view, and the claw's distal end is distinctly curved and pointed. On the hindlimbs a wide, fleshy skinfold develops from the level of the distal phalanx of the fifth toe and extends along the posterior edge of the hindlimb to the base of the limb. No cutting is visible near the fifth toe at the base of the fold. The skin fold edge is slightly rounded and reaches its maximal width at the level of the tarsus where it is the same wide as the length of the fifth toe. It becomes narrower at the knee and disappears completely at the posterior edge of the femur near the

base of the limb. Edges of the skinfold are slightly rounded and do not undulate. **Tail.** Tail is very long, slightly less than one and a half times longer than the body: tail length (TL) to body length (SVL) ratio is 1.41. In the anterior fifth of its length tail is almost cylindrical in transverse section, rapidly becoming compressed laterally and posteriorly from the cloacal region; the anterior third of the length tail is slightly compressed laterally, oval in transverse section; and in the posterior two thirds of the tail length it is distinctly laterally compressed and flattened. A distinct caudal fin develops in the posterior third of tail's length, a pronounced upper caudal fin fold originating at a point one third of the distance from tail-tip to its base and gradually increases as it extends posteriorly; lower tail fin fold is present and originates approximately a quarter way down posteriorly of the tail length. The highest point of the tail fin is approximately 1.5 cm from the tail tip. Tail tip is enlarged, tapered and obtusely pointed at the end. No autotomy has been reported in the species.

Measurements of the holotype (in mm). SVL 68.1; TL: 96.3; GA: 35.6; FLL: 19.3; HLL: 24.2; HL: 15.9; HW: 10.1; EL: 4.0; IN: 4.7; ON: 2.2; IO: 3.5; CW: 10.4; OR: 4.8; IC: 6.2 (measured on the preserved specimen). Color of the holotype in life.

Background coloration. Dorsal surfaces of body, tail, head and hindlimbs have a very dark background coloration which is often dark-violet-brown to blackish-red-brown and almost black on the medial parts of dorsum, head and tail. Towards the dorsolateral areas, especially on the flanks and on the dorsal surface of the fore- and hindlimbs the background coloration becomes somewhat lighter, more violet-brownish, chocolate-brown to a dark-lavender brown or pinkish-gray on the extremities and body flanks. Body and tail flanks are noticeably lighter and have a lavender-brown to gray-violet (lateral parts) or gray-pinkish (ventrally) background coloration. The costal grooves are somewhat darker than the costal segments which are very visible on the lateral sides of the belly. The lateral surfaces of the head are colored light violet to pinkish-gray on the upper and lower jaws, the subparotid protuberance is much darker being brownish-violet, the axilla and groin have a lavender-brown to pinkish background coloration. Ventral surfaces of the body are much lighter than the dark dorsal areas with pinkish-beige to lavender or pinkish-gray background color. The border between the light ventral and dark dorsal and lateral surfaces is not well delineated and extends up along the sides of the belly. Ventral side of the belly is semitransparent; and the chest is not darker than the rest of the ventral surface. Gular area is more brightly colored and darker than the belly and chest and is a dark-pinkish or lavender, the area beneath the lower part of the jaws is somewhat darker. The cloacal area is distinctly darker than the ventral coloration of the body and tail, it is pinkish- or lavender brown, and somewhat reddish on the medial aspect. The ventral surface of tail is lighter, pinkish-beige or gray-brownish. The background coloration of the limbs is lighter and brighter than that of the dorsum, violet to purple-brown, digits, palms and feet have lavender-violet base coloration with a distinct bluish tint, especially on the hindlimb skinfolds. Limb ventral surfaces are much lighter than the dorsal sides and are distinctly lighter than the ventral coloration of the body and chest, the background color is warm, pinkish-gray or pinkish-beige. In life the upper eyelids and the area around the eye are bluish to gray-beige in coloration. Cornified claws on the fore- and hindlimbs are completely black. **Pattern.** Dorsal surfaces in this species are covered with numerous light-colored irregular blotches, spots and variegations, that are so numerous that they cover the body surface almost equally with respect to a dark background coloration. This gives the impression of a light ground coloration; however these light spots develop mostly after metamorphosis and gradually appear on the dark dorsal surface. The light colored blotches and variegations are bright copper-orange on the dorsum, becoming orange-brownish on the dorsal surface of the head and are bright orange or reddish-orange on the dorsal surfaces of the tail and extremities. Light blotches are irregularly shaped and sized: round spots are rare, usually the spots are elongated longitudinally. A number of such elongated blotches appear along the middorsal groove. Despite the light blotches on the dorsal and lateral sides of the tail they show a tendency to merge, and there are no signs of a light dorsal band or stripe present on the dorsum. The dorsal surface of the anterior half of the tail blotches tend to merge forming an irregular and often interrupted light band. Blotches and spots here are numerous and tend to merge forming variegations with a sparse reticulate pattern. Very few roundish light spots and almost no light-colored ocelli are found. On the dorsum the blotches are quite large (length up to 10–15 mm, usually less; 1–2 mm wide): on the cross-section of the dorsum in the scapular area above the chest there are 3–4 light colored blotches, up to 6–7 blotches across the back in the middle of body and 5–6 blotches across the back in the pelvic area above the cloaca. Light spots become much smaller on the head (less than one mm) and are quite numerous (more than 15 spots across the head and on the dorsal surface); here they occur quite densely covering more than half of the dorsal surface of the head. Light spots on the upper eyelids are very small (around than 0.5 mm) and have a greenish-yellow color, which combined with a bluish background coloration creates a green-bluish effect. On the head, there are fewer light spots or they

may be absent from the area around the naris, between the naris and the anterior corner of the eye, and from the posterior corner of the eye along the postorbital groove to the subparotid groove; this creates the effect of an ill-defined dark stripe running from the naris across the eye and along the postorbital and subparotid grooves to the gular fold. Light spots and blotches are also fewer on the lateral sides of the base of the head which looks almost like two dark lateral stripes; the bright-orange blotch of irregular shape occupies only the middle portion of the occipital area. Light blotches are largest on the scapular area and tend to become more elongated towards pelvic area and the base of the tail. Light blotches on the body flanks become smaller, less elongated, often oval or roundish and the orange color is paler and turns to grayish-orange or yellowish; they are still lighter and brighter than the light ventral coloration along the belly margins; and light blotches are absent on the ventral side of the body. There is almost no pattern or blotches on the ventral side of body and head; and on the ventral surface of tail irregular dark spots and marbling can be found. Light blotches on dorsal surface of the limbs are brightly colored in reddish-orange or copper-orange, they are smaller than those on the dorsum and confluent; they become smaller in the distal direction, and the most distal blotches merge with the light coloration of the ventral limb surface. Fingers and toes are faintly colored (copper-orange) with few dark grayish spots on the dorsal surface and terminate in dark-black acute claws. The skin flap on the posterior edge of the hindlimb has a bright copper-orange band with irregular borders. **Iris.** Iris in life is dark-brown, almost black with tiny golden and yellow-greenish spots (which disappear in preservative); iris margins are darker than the central area surrounding the pupil. The pupil is horizontal and oval-shaped.

Color of the holotype in preservative. After two years in preservative (75% ethanol) the bright tints faded from the specimens' coloration: red, orange or pink tint completely disappeared, the dark dorsal coloration lost the violet reddish tint and turned blackish, dark grey or brownish; the light spots at the dorsal sides of head, body and tail turned whitish, gray-yellow to dark-beige; and the ventral sides became light beige, gray-yellowish or whitish in color (Fig. 19, C). Bluish tint from the sides vanished at the upper eyelid region and turned a lavender-grayish. However, the principal pattern of the original coloration has not changed and is clearly recognizable: location, size and intensity of dorsal the spots correspond well to the coloration in life (see Fig. 19, A, C).

Variation. Morphology of the paratypes generally resembles that of the holotype with the following exceptions:

Morphometrics. Variation in morphometric characters among the type series of the new species are presented in Tables 4 and 5. The species is in general characterized by the following morphometric parameters (ranges for males / females, 8 specimens): snout-vent length (SVL): 62.5–68.1 / 71.9–81.2; tail length (TL): 82.5–96.3 / 71.4–94.9; gleno-acetabular distance (GA): 33.5–35.6 / 39.2–45.4; forelimb length (FLL): 17.6–19.3 / 20.5–22.4; hindlimb length (HLL): 21.0–24.2 / 24.3–26.4; head length (HL): 14.7–15.9 / 14.9–16.8; head width (HW): 9.8–10.1 / 10.5–11.6; eye length (EL): 3.6–4.0 / 4.1–5.0; internarial distance (IN): 4.4–4.7 / 4.6–5.7; orbitonarial distance (ON): 2.2–2.3 / 2.3–2.8; interorbital distance (IO): 3.5–4.0 / 3.4–4.4; chest width (CW): 9.3–10.0 / 8.7–14.0; snout length (OR): 4.5–4.8 / 4.8–5.4; intercanthal distance (IC): 6.2–6.2 / 6.2–7.0 (measured on the preserved specimens). In our PCA analysis *O. zhaoermii* females were found to morphologically resemble *O. japonicus* s. stricto females (see Fig. 6, C). Nevertheless these species are clearly different in a number of mensural and meristic characters and can be hardly mistaken (see Results and Comparisons). Results of the PCA analysis for *O. zhaoermii* males are not significant due to the small sample size.

Sexual variation. In our sample of *O. zhaoermii* comparisons of morphometric traits between the sexes are not reliable due to the limited number of males available. However, we found differences for some measurements and ratios (see Results, Tab. 5). All available males had a much smaller body size (SVL) than the females in our sample (SVL was nearly one cm less in the studied males). Males of *O. zhaoermii* were found to have relatively significantly longer tails, differences are significant only for relative TL-values (TL/SVL); this pattern is observed in all species of *Onychodactylus* and may be is correlated with higher agility of males during the reproductive period (see Park, 2005, for discussion). *O. zhaoermii* females have longer relative groin-axilla distance (GA/SVL), which is concordant with higher TVN in females of this species: larger body size may be connected with higher fecundity in females (Kuzmin, 1995). Despite a limited sample size, males show relatively longer snout (OR/SVL) and longer intercanthal distance than that in females. In a majority of the ratios the differences are not significant due to the small sample size.

Secondary sexual characters. In general, secondary sexual characters in *O. zhaoermii* are similar to those of *O. koreanus* and other *Onychodactylus* species. Males have thicker and more massive hindlimbs than females and

during the breeding season a fleshy skin fold develops on the outer edge of hindlimbs. However, this seems to be little less prominent than in *O. koreanus*: in the latter species there is usually a distinct cutting at the base of the fold between the skinfold and the fifth toe, whereas in available males of *O. zhaoermii* we have never observed such cuttings (Figs. 18–21). Males of *O. zhaoermii* also have longer, higher and more flattened tails than females, the tail tip in breeding males is enlarged, tapered and pointed at the end (Fig. 18, A); tail tips in females are rounded or obtusely pointed. The cloacal area in males are much more swollen and the base of the tail is thicker than those in females (Fig. 19). During reproduction, males develop Y-shaped longitudinal vents with clearly swollen edges and 5–6 transverse convolutions on each side, with two oval protuberances present at the anterior edge of the vent. During the same time period, females develop vents that are longitudinal slits with no noticeable anterior protuberances (Fig. 19, B, C). Black claws develop on the digits during the reproduction season both by males and females, and as a rule they are absent out of the breeding season. There is an intrapopulation variation on the degree of development of the black claws: even within the type series of *O. zhaoermii*, representing one population sampled during the reproductive period, and one breeding female (KIZ06129) lacked these black claws both on the fingers and toes (Fig. 19, B). Most likely, after the breeding cycle has concluded the salamanders shed and black claws disappear with the skin; it is likely however that the presence or absence of these cornified claws is connected with an animal's reproductive status. We have never observed any dark, horny asperities on the inner surface of the hindlimbs or forelimbs in *O. zhaoermii*.

Color in life. Coloration of the paratypes in general corresponds with the coloration described for the holotype; variation is minimal and mostly pronounced in the dorsal pattern of small light spots and blotches, which seems to allow for individual specimen recognition. Variation in dorsal coloration of *O. zhaoermii* type series is presented in Fig. 21. There is almost no variation in the dark ground color, which is almost black to dark-brown in all specimens. The color of light dorsal spots varies from bright yellowish-orange and copper-orange to a darker, somewhat reddish copper-brown tint (as in KIZ06056 and KIZ06057 in Fig. 21). Some variation is noticed in the dorsal pattern: in some specimens, as in the holotype, dorsal light blotches merge forming an irregular pattern (Fig. 19, A, C), whereas in other specimens the blotches are concentrated more densely on the middle of the dorsum, forming an indistinct and interrupted dorsal stripe (as seen in the first specimen from the left in Fig. 21); or, to the contrary, smaller but confluent spots are spread out forming a uniform and dense light mottling (as in the female KIZ06131 in Fig. 21). In one male (KIZ06132 in Fig. 21) light spots on the tail formed an unclear dorsal tail stripe. In all animals two dark unspotted areas are visible on the base of the head and neck region forming two short lateral stripes, which disappear as they extend onto the body flanks. No sexual variation in coloration has been recorded.

Color in preservative. Color patterns of the paratypes in preservative correspond to those in life, however, the orange or pink tint completely disappears; the base color of the dorsal surface fades to blackish, dark gray or brownish; and the dark brown coloration is slightly less warm in tone turning grayish-brown, as described for the holotype (Fig. 19, B, C).

Osteology and anatomy. The Xiuyan population of *Onychodactylus* from Liaoning Province of China, described here as *O. zhaoermii*, was for many years the focus of various morphological research studies by scholars from northeastern China, these included a detailed description of the skeletal system (Wang *et al.*, 2004), where authors provided a general description of the skull, postcranial skeleton, hyoid apparatus, thoracic and pelvic girdles and limb skeleton with figures and photos. Other anatomical investigations on this species include an analysis of skin ultrastructure in adult and juvenile salamanders (Lu *et al.*, 2004; Guo *et al.*, 2009), description of the digestive tract (Zhao *et al.*, 2004), and a number of papers on morphology of the neural system (Wang *et al.*, 2007; 2008a). According to our understanding, these papers all refer to *O. zhaoermii*. Variation in the number of trunk vertebrae (TVN) and number of costal grooves (CGN) among the type series of *O. zhaoermii* are presented in Table 6. Modal TVN-number in *O. zhaoermii* is 17 for males (no variation) and 18 for females, with range 17–18, mean is 17.7 ± 0.52 . The trunk-vertebrae numbers result in the respective costal groove counts: 11 for males and 12 (11–12) for females (based on 8 specimens, see Tab. 6).

Vomerine teeth morphology. In adults of *O. zhaoermii* vomerine teeth are arranged in two transverse comparatively shallow slightly curved arch-shaped series with outer branches of the series being longer and much less curved than the inner branches (Fig. 4, D), in general this pattern closely resembles that of *O. koreanus* (Fig. 4, C). The tooth series are separated from each other by a distinct gap, in our series the gap between the left and right vomerine tooth series was slightly wider than in *O. koreanus*, but narrower than in *O. fischeri* sensu stricto, with a range from 1/3 to 1/2 the width of naris. In *O. zhaoermii* both outer and inner branches are slightly curved, with the

outer tooth series branches being slightly longer and much less curved than the inner branches. At the very end the inner branches of the tooth series are distinctly curved anteriorly, much more so than in observed specimens of *O. koreanus*. The ends of outer branches of the tooth series are located slightly more posteriorly than the ends of the inner branches (see Fig. 4, D). Variation in the number of vomerine teeth (VTN) in the type series of the new species are given in Table 7. In our sample the number of vomerine teeth in the species is high and is significantly higher than in *O. fischeri*: 14–15 (mean 14.3 ± 0.35) teeth per each branch in males and 11–16 (mean 13.6 ± 1.46) for females (based on 8 specimens, see Tab. 7).

Eggs and clutch. In his review of the biology of the Xiuyan population of *Onychodactylus*, Li (2004) reports that females lay a pair of egg sacs, in which the total clutch size (the amount of eggs in two egg sacs laid by one female) varies from 12 to 17 eggs, but is usually around 13 eggs; number of eggs in the two egg sacs within one clutch may differ. Egg diameter varies from 3.5 to 5.0 mm. The total length of the egg sac, including the stalk, is usually from 60–100 mm or slightly more. Egg sacs are connected to each other by a gelatinous stalk which serves to attach the egg clutch to stones or dead branches (Li, 2004; similar information is reported by Fei *et al.*, 2006). This is unusual for a species of *Onychodactylus*, since all known clutches of other species were laid in underground areas of a stream or under large stones, but never attached to branches (a pattern more typical for *Hynobius* and *Salamandrella* species). However, it seems that these data are based on some unpublished reports, not on direct observations; thus, documented observations on egg-laying, clutches and embryonic development in *O. zhaoermii* are lacking to date. Examination of the ovaries in six *O. zhaoermii* females from the type series had shown that each female had from 3 to 24 eggs, (1 to 12 eggs per ovary), which allows us to assume that the average clutch size is approximately 18.83 ± 7.86 eggs per egg sac pair, or about 9.42 ± 4.17 eggs per egg sac.

Larval morphology and metamorphosis. There are no specific works describing larval morphology of Liaoning *Onychodactylus*. A general description of larval biology is provided by Li (2004); Guo *et al.* (2009) discuss gill development in larvae on a histological level. They are characterized with the main morphological features typical for all *Onychodactylus* larvae, including a large and wide head with a blunted snout, labial folds present, three pairs of short gills, slightly prominent eyes, fingers and toes bearing black conical horny claws, outer edges of the fore- and hindlimbs bear a dermal flap, and the tail fin is shallow in height. The larval period lasts at least two to three years (Li, 2004). We have observed *O. zhaoermii* larvae at the type locality in shallow parts of mountain streams and they are relatively easy to find at night, but also can be found during the daytime: larvae hide under stones and small rocks on the bottom of the substrate during the daytime and emerge at dark. Larval coloration most resembles that which was described for *O. koreanus*. Larvae feed on small crustaceans, tubifex worms, small tadpoles, and insect larvae (Lin, 2004). No information on metamorphosis in *O. zhaoermii* is known to date.

Etymology. The specific epithet “*zhaoermii*” is a patronymic noun in the genitive singular; derived from the name of Professor Zhao Er-Mi, an academician of the Chinese Academy of Sciences, who contributed greatly to the development of zoological and especially herpetological research in China and is one of the leading experts on hynobiid salamanders of the World. We suggest Liaoning Clawed Salamander as the English common name of the species as a reference to distribution of the new species. Recommended common names in Chinese, Russian, Korean and Japanese are given above.

Distribution. To date this species is known only from Liaoning Province of China though discoveries in neighboring parts of Jilin Province and North Korea are anticipated. Currently, they are found in Qianshan Mountains and the mountain areas of Liaodong peninsula in Liaoning Province of China. Distribution in Liaoning Province (as *O. fischeri*) is discussed by Ji *et al.* (1987), Kuzmin (1995), Li (2004) and Fei *et al.* (2006). They may also be discovered in the mountainous areas of North Korea in the neighboring provinces of Pyonganbuk-to, Changang-do and Pyongannam-do, where *Onychodactylus* have been previously reported (as *O. fischeri*, see Won, 1971). Since no geographic barrier is known to separate the ranges of *O. zhaoermii* and *O. zhangyapingi* and since both species have been documented from just a few localities, the extent of *O. zhaoermii* distribution in China and North Korea requires further clarification using morphological and molecular methods.

Comparisons. *O. zhaoermii* can be distinguished from the other salamanders in the region, including sympatric *Hynobius leechii*, by its slender body, smooth skin with distinct costal grooves on the flanks, very long tail, almost cylindrical at the base, slightly compressed in the middle and flattened towards its end, small and somewhat elongated head with rounded snout, and a combination of morphological features characteristic of *Onychodactylus*, such as absence of lungs, breeding males develop dermal flaps on the outer surface of the

hindlimbs, both sexes during the reproductive season posses black horny claws on both fingers and toes, vomerine teeth in two short transverse arch-shaped series, premaxillary fontanelle large fully separating nasals, caudal ribs numerous and present on more than 5–6 postsacral tail vertebrae.

O. zhaoermii can be further distinguished from other *Onychodactylus* species by a following combination of morphological attributes:

O. zhaoermii can be distinguished from *O. fischeri* (Boulenger, 1886) by the following combination of morphological attributes: significantly lower trunk vertebrae number (TVN = 17–18) and costal groove count (CGN = 11–12) (versus TVN = 20–21 and CGN = 14–15 in *O. fischeri*) (Tab. 6); rows of vomerine teeth are slightly curved or bended with the outer branch usually being noticeably longer than the inner branch, vomerine tooth arch asymmetrical, and the lateral end of the outer branch is located posteriorly than the medial end of the inner branch in *O. zhaoermii*, Fig. 4, D (versus almost straight or slightly bended vomerine tooth series with outer and inner branches of the series being roughly of the same length and the lateral end of the outer branch is located roughly on the same level as the medial end of the inner branch in *O. fischeri*, Fig. 4, A); vomerine teeth numerous, VTN = 13.8 ± 1.3 (per row) in *O. zhaoermii* (versus VTN = 11.5 ± 1.23 in *O. fischeri*) (Tab. 7); and dorsal coloration: no prominent dorsal stripe, background color of dorsal surface is dark; back side of body is covered with numerous contrast light blotches and variegations forming sparse reticulate pattern, Fig. 5, C (versus light dorsal stripe present, indistinct with unclear edges in *O. fischeri*, Fig. 5, A). *O. zhaoermii* further differs from *O. fischeri* in following morphometric features (see Tabs. 4; 5 for details): comparatively longer tail in males, comparatively longer hindlimbs in both sexes and forelimbs in males, and larger eyes in both males and females. *O. zhaoermii* can be distinguished from the members of *O. japonicus* species complex: *O. japonicus* (Houttuyn, 1782) and *O. nipponoborealis* by dorsal pattern: no prominent dorsal stripe, background color of dorsal surface is dark; usually back side of body is covered with numerous small contrast light spots or blotches in *O. zhaoermii*, Fig. 5, C (versus prominent light-colored dorsal stripe present in members of *O. japonicus* species complex, background color of dorsal surface is lighter than color of body sides, Fig. 5, E–G). *O. zhaoermii* can be further distinguished from *O. japonicus* (Houttuyn, 1782) and *O. nipponoborealis* by the form of vomerine tooth series: rows of vomerine teeth are slightly curved or bended with the outer branch usually being noticeably longer than the inner branch, vomerine tooth arch asymmetrical, and the lateral end of the outer branch is located posteriorly than the medial end of the inner branch in *O. zhaoermii*, Fig. 4, D (versus comparatively deep notably curved with outer and inner branches of the series being roughly of the same length (vomerine tooth rows are symmetrical) and the lateral end of the outer branch is located roughly on the same level as the medial end of the inner branch in *O. japonicus*, Fig. 4, E and *O. nipponoborealis*, Fig. 4, F). *O. zhaoermii* further differs from *O. japonicus* (Houttuyn, 1782) by the presence of a distinct gap that is usually present between the vomerine tooth series, Fig. 4, D (versus left and right vomerine tooth series being in contact, Fig. 4, E in *O. japonicus*), and in a greater vomerine tooth count (VTN): VTN = 13.8 ± 1.3 in *O. zhaoermii* (versus VTN = 11.4 ± 1.16 in *O. japonicus*) (Tab. 7). *O. zhaoermii* differs from *O. nipponoborealis* in a lower vomerine tooth count (VTN): VTN = 13.8 ± 1.3 in *O. zhaoermii* (versus VTN = 17.3 ± 1.49 in *O. nipponoborealis*) (Tab. 7). *O. zhaoermii* further differs from *O. japonicus* and *O. nipponoborealis* in the following morphometric features (see Tabs. 4; 5 for details): larger SVL in females, comparatively shorter and wider heads in both sexes, greater distance between orbits in both sexes, larger eyes than in *O. japonicus* (but no significant differences in EL with *O. nipponoborealis*), and comparatively shorter hindlimbs in both sexes.

O. zhaoermii can be distinguished from the second Chinese *Onychodactylus* species, *O. zhangyapingi*, described below, by the shape of vomerine tooth series: rows of vomerine teeth are slightly curved with the outer branch usually being noticeably longer than the inner branch, its lateral end is located posterior towards medial ends of the inner branches, inner branch of vomerine tooth arch is notably curved forward at the medial end, Fig. 4, D (versus vomerine teeth rows are almost straight with inner branch of almost the same length as outer branch, lateral end of the outer branch is on the same level as the medial end of the inner branch, and the inner branch is not curved forward in *O. zhangyapingi*, Fig. 4, B). The species is further diagnosed from *O. zhangyapingi* by significantly lower vomerine teeth count: VTN in *O. zhaoermii* is 13.8 ± 1.3 (versus mean VTN = 16.4 ± 1.03 in *O. zhangyapingi*, see Tab. 7). *O. zhaoermii* also differs from *O. zhangyapingi* in dorsal pattern: in *O. zhaoermii* dorsal surface has dark background color and is covered with numerous bright (orange to copper-red) irregular confluent blotches and spots, normally the light blotches are numerous and cover dorsum almost equally with the dark background color, which creates an overall effect of light coloration, see Fig. 5, C; Fig. 18 (versus dark base color

of dorsum is covered with numerous yellowish to pinkish thin lines or variegations of irregular shape, forming a marbling or reticulate pattern; but the dark background color prevails and animal looks dark in *O. zhangyapingi*, see Figs. 5, B; 22; 23). *O. zhaoermii* also differs from *O. zhangyapingi* in the following morphometric features (see Tabs. 4; 5 for details): by significantly longer fore- and hindlimbs—FLL/SVL ratio is 0.28 0.01, HLL/SVL ratio is 0.33 ± 0.01 (versus FLL/SVL ratio is 0.25 ± 0.01 , HLL/SVL ratio is 0.30 0.01 in *O. zhangyapingi*) and by comparatively shorter snout.

For a more detailed comparison of *O. zhaoermii* with *O. koreanus*, the third new species of *Onychodactylus* described from continental Northeast Asia in this paper, refer to “Comparisons” section in taxonomic accounts for *O. koreanus* given above.

Karyotype. Information on the chromosomes of *O. zhaoermii* is absent, to date all works on the karyology of Chinese populations referred as *O. fischeri* were based on materials from Tonghua County and surrounding areas of Jilin Province (Zhao *et al.*, 1991), which are, according to our data, inhabited by a different species: *O. zhangyapingi* (see below).

Genome size. Our estimate of *O. zhaoermii* genome size is 88.0 pg per diploid nucleus; CV = 44.0 (DNA flow cytometry; one specimen from the type locality (Huashan village environs, Sanjiazi subcounty, Xiuyan County, Liaoning Province, China); J. Che, pers. obs.; peripheral red blood cells of the Goldfish, *Carassius auratus* (Cyprinidae), were used as a reference standard for genome size measurements. Due to different reference species used this genome size estimate is cannot be compared with the data reported for *O. fischeri*, *O. japonicus*, *O. nipponoborealis* and *O. koreanus*).

Phylogenetic position. *O. zhaoermii* is a member of *O. koreanus* species complex. Phylogenetic analyses suggest that this species is sister to *O. koreanus* and *Onychodactylus* sp. from Yangsan, with a degree of divergence between them ranging from 6.0 to 7.4% in COI sequences and from 1.9 to 2.1% in 16S rRNA sequences of uncorrected pairwise genetic distances (Fig. 3; Tab. 3), being more closely related to Japanese *Onychodactylus* species than to *O. fischeri* from Russia (see Fig. 3).

Habitats and natural history. Natural history data for *O. zhaoermii* are quite scarce. The preliminary description of the biology and ecological preferences of *Onychodactylus* from Xiuyan County of the Liaoning Province (type locality of *O. zhaoermii*) is given in the paper by Li (2004). He reports that *O. zhaoermii* are found at altitudes around ca. 600 m a.s.l. We collected the type series from an altitude of ca. 550 m a.s.l., it is likely that in Huashan environs the new species inhabits mountainous forests at elevations ranging from 500 to 800 m a.s.l. Wang *et al.* (2008b) discuss physiology and temperature preferences of *O. zhaoermii*. The new species inhabits cold running torrents and permanent brooks in mountain valleys under dense forest canopy. Li (2004) reports that salamanders have a very limited distribution in the environs of Huashan village and are found only in four to five local mountain streams in a relatively small area. Preferable habitats are located in broad-leaved deciduous forests with dense undergrowth that have numerous lianas and mosses on the ground. Streams are surrounded by lush vegetation; the ground is covered by large amounts of leaf litter; stream banks posses numerous moist shelters such as tree logs, pebbles, moss-covered stones and rocks. Streams where salamanders are found have water temperatures ranging from 6°C to 14°C, they are shallow and with a rapid current, contain clean water with numerous pebbles and gravel on the bottom; and the water's pH is slightly acidic (Li, 2004). Hibernation begins in late September to early October and lasts until early April; at that time the animals become active before the snow melts completely and they migrate along the stream in search of breeding sites (Li, 2004). During our field surveys in Liaoning Province in early May, adult specimens were usually found in the evening and night time on the streamside covered with moist litter, mosses and rocks (see Fig. 20, A), and may be found in the water as well (Fig. 20, B). Larvae were found in the running streams with cool water temperatures (varying from 12°C to 14°C) under rocks and pebbles. To date, the reproduction of *O. zhaoermii* has not been observed in the wild or under captive conditions. Li (2004) reports adult salamanders to be active from April to May. We have observed males and females in reproductive state in early May, and it is likely that the breeding season lasts from the middle of April when water temperature rises above 6°C until at least late May. *Onychodactylus zhaoermii* is sympatric with *Hynobius leechii*, *Rana dybowskii*, *Bufo gargarizans* and *Bombina orientalis* (Li, 2004; our data). However microhabitat preferences in these species are different and we did not observed breeding of other amphibian species in the same parts of the streams where *O. zhaoermii* were found.

Conservation status. Due to the limited area of distribution in China, *O. fischeri* was listed as an endangered species in the Red Data Book of China (Zhao, 1998). Our data on genetic diversity and taxonomy of the group

indicate that this area is even more limited for *O. zhaoermii* which is found to be restricted to several mountain systems in Liaoning and, possibly, in Jilin provinces of China. Distribution limits and population status of the new species are not clear; we also do not know whether or not this species is found in North Korea or not. However, threats to *O. zhaoermii* are significant and primarily include habitat destruction of the habitat due to intensive logging, farming activity with the application of herbicides, water pollution and building construction (Li, 2004); these activities have intensified each year in the study area. According to a report by Li (2004) the Huashan population of *O. zhaoermii* is decreasing. As a specialized reophilous form adopted to life in clean cool mountain streams, *O. zhaoermii* is sensitive even to minor changes in its environment. Moreover, salamanders are being collected for the pet trade: according to the information from local people, during last two years several hundreds of *O. zhaoermii* adults were collected in Huashan environs and, presumably, sold. Thus, we recommend including *O. zhaoermii* in the China Red Data Book of Endangered Animals and suggest that its IUCN red list conservation status is Vulnerable (Vu2a) according to IUCN criteria.

Onychodactylus zhangyapingi sp. nov. Che, Poyarkov, Li & Yan

[*Onychodactylus fischeri* (part)—Mori, 1928 “1927”; Gee & Boring, 1929; Chang, 1936 and many other authors.]

[? *Onychodactylus sischeni* (part)—Won, 1971: p. 30 (*ex errore*). Unjustified change of the original spelling. The taxonomic status of North Korean *Onychodactylus* populations is uncertain; we assume presence of both Chinese and South Korean lineages in North Korea.]

Recommended trivial names:

Chinese name: Jilin Zhaoni (吉林爪鲵).

English name: Jilin Clawed Salamander.

Japanese name: Kitsurin-Sansyouo.

Korean name: Jilin Ggorichire Dorongnyong.

Russian name: Girinskiy kogtistyi (bezlegochnyi) triton.

Holotype. KIZ06075, an adult male collected during the breeding season on 11th of May, 2010, by Jing Che, Cheng Li, Fang Yan, and Xiao-Dong Zhang (see Fig. 22, A–C).

Type locality. Heisonggou environs, Linjiang County, Jilin Province, China; 330 m a. s. l.; geographic coordinates: 41° 28' N; 126° 35' E (see Fig. 24, A).

Paratypes. KIZ06074; KIZ06121-06123; KIZ06136 (five adult males from the same locality as the holotype, Heisonggou environs, Linjiang County, Jilin Province, China; 330 m a. s. l.); KIZ06076-06077; KIZ06082 (three adult females from the same locality as the holotype, Heisonggou environs, Linjiang County, Jilin Province, China; 330 m a. s. l.); KIZ06037-06039; KIZ06113; KIZ06120; KIZ06124 (six adult females from Xiaonangou environs, Linjiang County, Jilin Province, China; 558 m a. s. l.); KIZ06135 (one adult female from Laolitougou environs, Linjiang County, Jilin Province, China; 436 m a. s. l.), collected on 3–12 of May, 2010, by Jing Che, Cheng Li, Fang Yan, and Xiao-Dong Zhang (see Fig. 23, A, B; Fig. 25). All three localities are quite close to each other. Exact locality information and geographic coordinates data to the scale of seconds is kept by the museum (KIZ) holding the type specimens and is available upon request.

Referred material. KIZ-LC0704027-LC0704030, four premetamorphic larvae, collected in June, 2007, by Cheng Li and Xiao-Dong Zhang. KIZ01787-01788, KIZ01853-01854 from Xiaonangou environs, Linjiang County, Jilin Province, China; 558 m a. s. l.; collected on 17th, June, 2010, and KIZ01798, KIZ01826-1838, KIZ01840-01845 from the Wunufeng National Forest Park, Ji'an County, Jilin Province, China; 435 m a. s. l.; collected on 18th, June, 2010, by Jun-Xiao Yang, Cheng Li, and Xiao-Dong Zhang.

Diagnosis. A slender, relatively medium-sized hynobiid salamander, a member of the genus *Onychodactylus* on the basis following combination of features: absence of lungs, presence of black claw-like horny structures on both fore- and hindlimbs in larvae and breeding adults, tail longer than the sum of head and body lengths, tail almost cylindrical, slightly compressed at the end, vomerine teeth in transverse short arch-shaped series almost in contact with each other, presence of large premaxillary fontanelle completely separating the nasals, presence of more than nine caudal ribs, presence of skinfolds in larvae on the posterior edges of both fore- and hindlimbs and dermal flaps in males developing during the breeding season, with diploid chromosome number $2n = 78$ and other

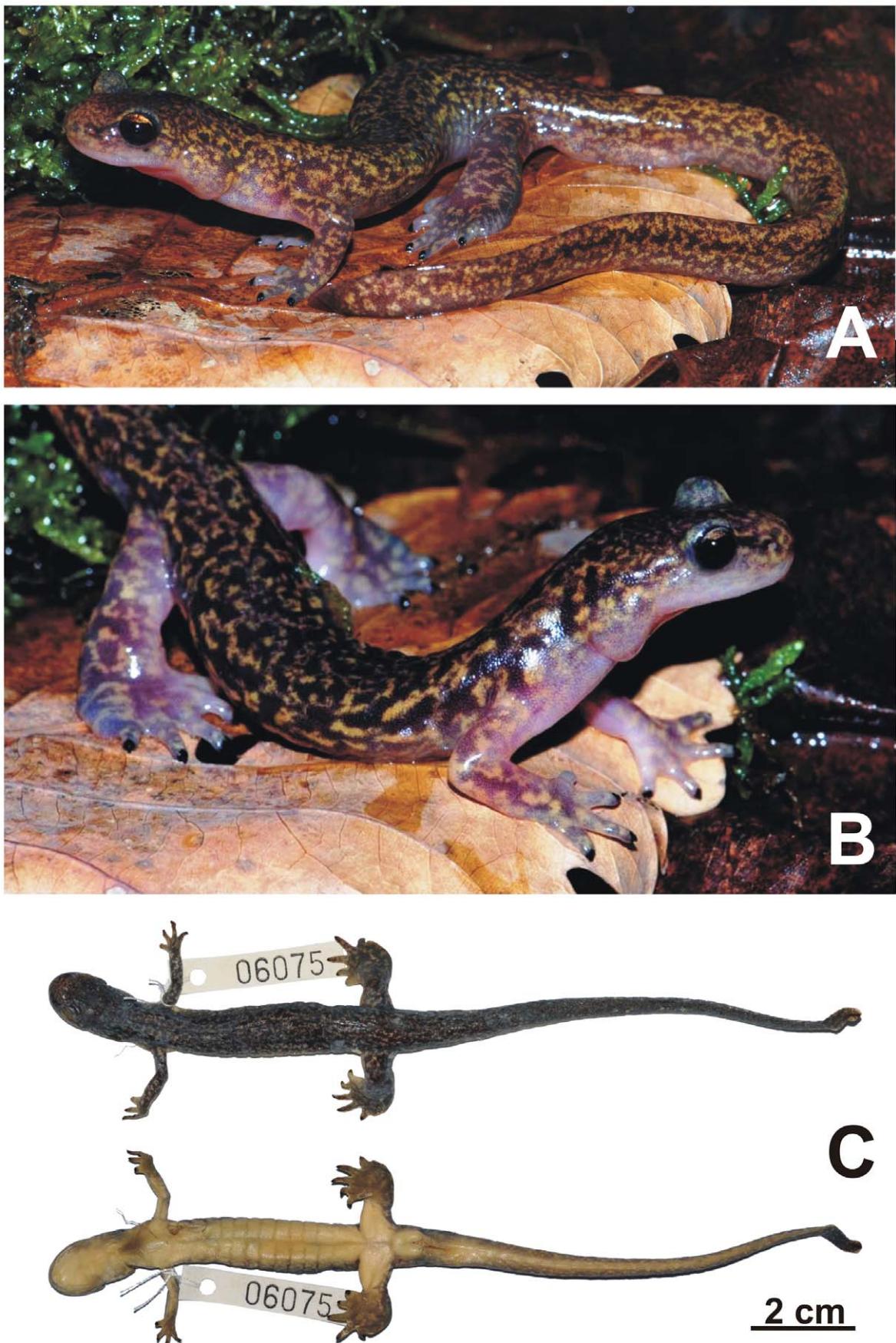


FIGURE 22. The holotype of *Onychodactylus zhangyapingi*, KIZ06075, adult male, from the type locality (Heisonggou envirions, Linjiang County, Jilin Province, China): (A)—In life, lateral view, left side; (B)—in life, close-up of head and body, right side; (C)—in preservative, ventral and dorsal views. Photos by J. Che.

typical features of the genus. The species is different from the other members of the genus by combination of following morphological attributes: in having 18 (17–19) presacral trunk vertebrae and 12 (11–13) costal grooves in both males and females (Tab. 6), 16–17 (14–18) vomerine teeth in each vomerine tooth series (Tab. 7), shallow, very straight vomerine tooth series usually without a gap between them (Fig. 4, B), with the outer branches of vomerine tooth series being the same length or slightly longer than the inner branches, and the outer and inner ends of the series located on the same level, inner branches of vomerine teeth are not curved, outer branches bent slightly towards the end, comparatively larger SVL and narrower heads in both sexes (Tabs. 4; 5), black acute claws well developed in both sexes, appearing both on fore- and hindlimbs in males during breeding and may be present in both sexes out of the reproductive season, dark ground color of dorsum, head and tail (black to brown) with numerous small (size < SVL/20) light (pinkish, yellowish, or whitish) lines, confluent spots and vermiculations forming a sparse reticulated or thin marble pattern (Fig. 5, B), light pinkish or yellowish ventral side; light dorsal band always absent, juveniles and larvae with characteristic contrast coloration: very dark ground color of the trunk with few large, bright (yellow to orange) blotches, and distinct genetic differences in mtDNA sequences.

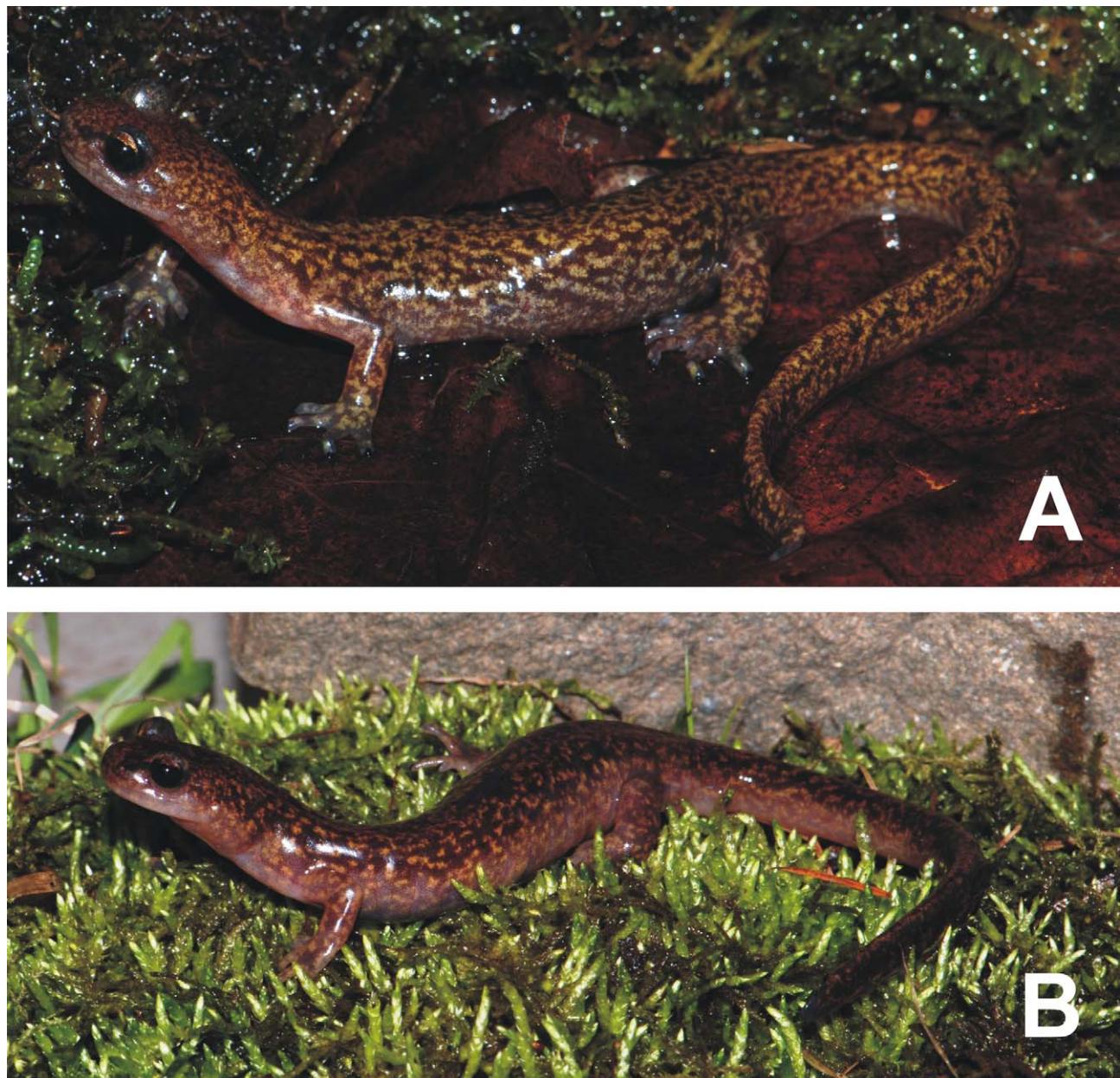


FIGURE 23. (A)—The paratype of *Onychodactylus zhangyapingi*, KIZ06076, adult female, from the type locality (Heisonggou environs, Linjiang County, Jilin Province, China); in life, lateral view, left side; (B)—The paratype female KIZ06077 from the type locality in life, lateral view, left side. Photos by J. Che.

Description and variation.

Type specimens. The type series consists of 16 adult specimens: 6 males and 10 females, all collected during the breeding season.

Description of the holotype. An adult male, in a good state of preservation, fixed and preserved in 75% ethanol, with a SVL of 66.2 mm (measured on the preserved specimen). **Head.** Head depressed, oval-shaped, comparatively long and narrow, head noticeably longer than wide: ratio head length (HL) / head width (HW) is 1.58; head is slightly wider than the neck. Neck long, approximately 4.0 times shorter than head. Tongue large, elliptical, distinctly widens towards its end. Snout quite short, ratio snout length (OR) / head length (HL) is 0.31; snout subtly rounded from the dorsal view, flattened, slightly sloping from the eyes to the nostrils, obtusely rounded from the lateral view. Nostrils dorsolateral, small not protuberant, widely separated and distant from snout tip, internarial distance (IN) / head length (HL) ratio is 0.24. Eyes quite large and protuberant, eye diameter slightly shorter than snout length and distinctly longer than the internarial distance: ratio eye length (EL) to snout length (OR) is 0.91; ratio eye length (EL) to internarial distance (IN) is 1.15. Orbita rather close to each other, interorbital distance quite small: interorbital distance (IO) to head length (HL) ratio is 0.19; ratio eye length (EL) to the intercanthal distance (IC) is 0.75. Eyelids present and well-developed; labial folds absent and the gular fold is distinct. Distinct parotid glands absent with, although the parotid area is slightly swollen with no clearly visible borders. Longitudinal postorbital groove distinct starting at the posterior corner of the eye and heads backwards towards the angle of the mouth, this groove separates two slight protuberances: one located behind the posterior corner of eye and another above the posterior ends of the jaw near the angle of the mouth. The postorbital groove is more than twice shorter than the eye length and does not reach the angle of the mouth; upwards from the angle of the mouth there is a distinct transverse supraquadrate groove, which is almost the same length as the postorbital groove, it intersects with the postorbital groove above the angle of the mouth. From here a deep longitudinal subparotid groove extends backward, separating the parotid area from the swollen subparotid protuberance, which extends from the angle of the jaw to the gular fold. At the posterior end the subparotid grooves curves slightly downwards intersecting with the gular fold at its end. The subparotid protuberance is distinct, elongated, bean-shaped and noticeably swollen, the anterior corner of the subparotid protuberance is narrow, and the posterior edge is lightly rounded. Form the dorsal view of the head there is a distinct narrowing that is visible at the level of the jaw angles, and the base of the head looks somewhat wider than the neck. **Vomerine teeth.** Vomerine teeth in two transverse almost straight rather shallow arch-shaped series, forming a «»-shaped figure; 17 vomerine teeth in the left vomerine tooth series and 16 vomerine teeth in the right vomerine tooth series; the left and right vomerine tooth series are almost in contact with each other with a no noticeable gap between the medial ends of the inner branches of the tooth series; both outer and inner branches of the tooth series are almost straight and are not bent or curved, they are nearly the same length (the outer tooth series branches are slightly longer); the ends of the outer branches of the tooth series are located somewhat more posteriorly than the ends of the inner branches. **Trunk.** Body elongated, slender and cylindrical with a rather narrow chest: chest width (CW) / SVL ratio 0.13. The dorsum and venter skin is smooth, slimy; scattered with many microscopic white granular glands especially well visible on the body and head flanks. A distinct middorsal groove extends on the dorsal side of body from the base of the tail to the base of the head. Eighteen presacral trunk vertebrae (TVN); 12 costal grooves are clearly visible on both sides of the body. **Cloaca.** Cloaca is oval-shaped, elongated, noticeably swollen and protuberant (tail base is distinctly wider in the cloacal region from a dorsal view); Y-shaped longitudinal vent has distinctly swollen edges with 3-4 transverse wrinkles on each side, at the anterior edge of the vent a distinct transverse bean-shaped protuberance is present with the posterolateral edges being more swollen than the central part; the anterior edge of the vent is bordered with an inverse V-shaped thin but distinct skinfold. **Extremities.** Limbs well-developed, with forelimbs being slender and hindlimbs noticeably longer and distinctly more robust than the forelimbs; the forelimb length (FLL) to hindlimb length (HLL) ratio is 0.79; when forelimb and hind limb are adpressed towards each other against the flank, the digit tips do not touch; a distinct gap of about 0.5 costal segment is evident between the toes and fingers of the adpressed limbs; the “Wolterstorff’s index” (forelimb length to groin-axilla distance ratio) is 0.47; hindlimb length to groin-axilla distance ratio is 0.60. No distinct palmar or tarsal t are found on the palms or feet. Four fingers and five toes without digital webbing are present; the relative length of fingers (in order of decreasing length) is as follows: 1 < 4 = 2 < 3; relative length of toes: 1 < 2 = 5 < 4 < 3. Tips of fingers and toes are rounded and covered with black cornified claws, which are present on all fingers and toes; each claw base is diamond-shaped from the dorsal view, the distal end of the claw is distinctly curved and pointed. Large fleshy skinfolds are developed on posterior edges of the hindlimbs; each skinfold begins at the distal phalanx of the fifth toe and runs along the posterior edge of the hindlimb until reaching the groin area at the base of the hindlimb. There is a small cutting at the fold’s edge near the

fifth toe; the size of the cutting is comparable with the size of the claw on the fifth toe. The maximal width of this skin fold occurs at the level of the tarsus where it is somewhat wider than the length of the fifth toe. The fold becomes narrower at the knee and completely disappears at the posterior edge of the femur at limb's base. Skinfold edges are lightly rounded. **Tail.** The tail is quite long, nearly one and a half times longer than the body: the ratio of tail length (TL) to body length (SVL) is 1.46. Tail is not compressed laterally and almost cylindrical in transverse section in the anterior third of its length; posteriorly the tail is slightly compressed laterally and becomes oval in transverse section in the middle third of its length; the tail is distinctly laterally compressed and flattened in the posterior third of its length. No caudal fin is present throughout the tail length, a feeble upper caudal fin fold is present in the posterior fifth of tail length where it gradually increases posteriorly; no distinct lower tail fin fold is present. The distal part of the tail (ca. 1.5 cm) is slightly tapered; the tallest part of tail occurs in the cloacal area. Tail tip is obtusely rounded. No autotomy has been reported in the species.

Measurements of the holotype (in mm). SVL 66.2; TL: 96.4; GA: 36.0; FLL: 16.9; HLL: 21.5; HL: 15.3; HW: 9.7; EL: 4.4; IN: 3.8; ON: 2.2; IO: 3.0; CW: 8.6; OR: 4.8; IC: 5.9 (measured on the preserved specimen).

Color of the holotype in life.

Background coloration. Dorsal surfaces of trunk, tail, head and extremities show a dark background coloration. In life it is dark violet-blackish on the middle part of the dorsum and head, turning gray-violet or dark purple on the dorsolateral surfaces of the trunk and the lateral sides of the head and tail. The background color of the body flanks become much lighter—lavender or light gray-violet, at the axilla, groin and the lateral surfaces of head in the area of the upper and lower jaws and subparotid protuberance the ground color is pinkish. Background color tends to be darker on the medial part of the limb dorsal surface and is much lighter on the anterior and posterior edges of the limb. Bluish tint is also found on the digits, lateral sides of the tail and ventral surfaces. The costal grooves seem to be darker than the costal segments and are beige-brownish; this is especially visible from the ventral side. The transition between dark dorsal and light ventral coloration on the body flanks is gradual. Ventral side of the body shows a much lighter background coloration, in life it is mostly a light lavender-beige, pinkish-gray to light-violet color. Cloacal region and the anterior part of the chest are somewhat darker than the rest of the ventral surfaces; they are colored grayish-violet or beige-grayish. Ventral side of the belly is semitransparent: at the midventral area the vena abdominalis is clearly seen through the skin as a dark bluish line (not visible in the preserved specimen). The gular region is not brighter or darker than the belly and chest; it is light lavender-beige and pinkish-grey. The cloacal region is slightly darker than the ventral surface of the tail and belly in its posterior half around the vent, where it is pinkish-brown to beige with a reddish tint along the vent. The ventral surface of the tail is pinkish-beige to grayish-beige, becoming somewhat darker towards the end. The extremities have a somewhat lighter and brighter background color than the dorsum: dorsal surfaces of the fore- and hindlimbs in life have a violet, light purple or bluish-grey background coloration; the ground color tends to get lighter in the distal direction: fingers, toes, palms and feet have a lavender-bluish background coloration with a bluish tint. The dermal skinfolds on the posterior edges of the hindlimbs are bright bluish-violet. Ventral surfaces of the limbs are lighter than the dorsal sides and are the same color as the belly and chest or slightly darker, the background color is pinkish-beige. In life the upper eyelids and the area around the eye are bluish-violet. Cornified claws on the digits are completely black. **Pattern.** Dorsal surfaces of the trunk, tail, head and extremities are covered with numerous light-colored lines, elongated confluent spots and vermiculations forming a dense irregular reticulated pattern, resembling that of marble. However, numerous, light lines and marbling cover much less of the surface than the dark background color, which gives the impression of a dark-colored salamander. The light lines and vermiculations are bright golden-yellowish to light-orange. They cover the dorsal surfaces of the body almost uniformly, and are the same size and irregular pattern as those on the head, dorsum, tail and limbs. On the head however, they are smaller and form slight golden mottling over the purple background of the dorsal surface and are especially small in the anterior region of the head. Round spots, ocelli or large blotches are always absent. No signs of a light dorsal band or stripe are present on the dorsum or tail. Light pattern is somewhat brighter on the dorsum and dorsal surface of tail than on the limbs, where it is gray-yellowish rather than bright-golden. On the flanks of the body the golden marbling gradually becomes less bright and completely disappears at the ventrolateral sides of the belly. On the lateral sides of the head a few golden spots are present on the subparotid protuberance and near the angle of the mouth. Light spots on upper eyelids are very small (less than 0.5 mm) and have a bluish-green color; the upper eyelid looks bluish or greenish in life. No distinct dark stripes are found on the head. No signs of pattern can be found on the ventral surfaces of the body and head; on the ventral surface of the tail irregular beige marbling and small gray-yellowish spots are found. On the dorsal surface of the fore- and hindlimbs the size of the pattern gradually decreases distally: palms, feet and digits are covered with small, light yellowish spots and small irregular blotches. The skin flap on the

posterior edge of the hindlimb shows a number (4-6) of irregular yellowish cross-stripes. **Iris.** Iris in life is almost black with tiny golden and copper spots (which disappear in preservative) at the upper and lower margins, the central area surrounding the pupil is darker and does not have bright spots. Pupil is horizontal and oval-shaped.

Color of the holotype in preservative. After two years in preservative (75% ethanol) the bright tints faded from the coloration: the dark dorsal coloration was lost and the violet reddish tint turned dark gray or brownish; the light pattern at the dorsal sides of the head, body and tail turned gray-yellow to dark-beige; and the ventral sides are light beige or yellowish-gray. However, the principal color pattern corresponds to that of a live specimen and are readily recognizable (see Fig. 22, C).

Variation. Morphology of the paratypes in general resembles that described for the holotype with the following peculiarities.

Morphometrics. Variation in morphometric characters among the type series of the new species are presented in Tables 4 and 5. The species is in general characterized by the following morphometric parameters (ranges for males / females, 16 specimens): snout-vent length (SVL): 61.4–67.6 / 61.0–84.2; tail length (TL): 76.9–96.4 / 69.1–95.2; gleno-acetabular distance (GA): 32.1–36.9 / 32.3–48.3; forelimb length (FLL): 16.5–17.4 / 16.7–20.0; hindlimb length (HLL): 18.2–21.5 / 20.3–23.7; head length (HL): 14.4–15.3 / 14.0–16.8; head width (HW): 9.0–9.8 / 9.4–11.9; eye length (EL): 3.5–4.4 / 3.7–4.8; internarial distance (IN): 3.8–5.0 / 4.0–4.9; orbitonarial distance (ON): 1.8–2.5 / 2.0–2.5; interorbital distance (IO): 3.0–3.7 / 3.5–4.2; chest width (CW): 7.9–10.0 / 7.1–11.1; snout length (OR): 4.5–5.0 / 4.4–6.0; intercanthal distance (IC): 5.2–6.1 / 5.6–7.1 (measured on the preserved specimens). In the PCA analysis *O. zhangyapingi* males were found to be similar to males of *O. koreanus*, their PCA scores largely overlap, whereas PCA scores for females of the two species are well-discriminated (Fig. 6). *O. zhangyapingi* and *O. koreanus* are however markedly distinct in certain morphological characters and pronounced genetic differences, so these species can be easily diagnosed (see Results and Comparisons).

Sexual variation. *O. zhangyapingi* shows little sexual variation in morphometric traits, however some significant differences were found in several measurements (see Results, Tab. 5). As in other species of the genus *Onychodactylus*, males of *O. zhangyapingi* have significantly longer tails than the females of this species (Tab. 4; 5). Intraspecific variation in limb length is quite high: in males when forelimb and hind limb are adpressed towards each other against the flank, digit tips are separated with a distinct gap of about 0.5–1.0 costal segments, whereas in females a gap about 1.5–2.5 costal segments is present between toes and fingers of the adpressed limbs. Male *O. zhangyapingi* have significantly longer (HL/SVL; $p < 0.005$) and narrower (HL/HW; $p < 0.05$) heads than females. Compared to females, males tend to have relatively shorter snouts (OR/HL) and relatively wider chests (CW/SVL) ($p < 0.05$). Finally, we found significant differences in relative interorbital length (IL/HL), which is longer in females ($p < 0.05$). There are no significant differences however between the sexes in body size (SVL), axilla-groin distance (GA, both for absolute and relative values) and relative length of extremities. In general, the degree of differentiation in morphometric features among sexes in *O. zhangyapingi* is comparatively weak.

Secondary sexual characters. Secondary sexual characters in *O. zhangyapingi* are typical for the genus *Onychodactylus*, they are mostly pronounced during the reproductive season, but some of the characters are traceable out of the breeding season as well. Hindlimbs are distinctly broadened, more massive and crooked in males than in females with feet orientated to a specific angle to the tibia (Fig. 25); these differences are evident out of the breeding period. During reproduction, on the outer edge of the hindlimbs a fleshy skin fold develops in males, it starts at the fifth toe (no cutting is present between the skinfold and the fifth toe) and extends to the tibia up until the knee-joint, the fold reaches its maximum width at the middle of feet (Fig. 22, Fig. 25). Tails in male *O. zhangyapingi* are longer and more flattened than in females, tail tip is distinctly flattened and acutely pointed, by contrast, in females it is rounded (Fig. 22, A). Tail base is also thicker in males than in females, since the cloacal area in males is distinctly more swollen and slightly protuberant. During reproduction the male's vent has a Y-shaped form with distinctly swollen edges and several transverse wrinkles on each side, with two oval protuberances present at the anterior edge of the vent; at the anterior corner of the vent two converging lateral folds are present forming an inverted V-shape (Fig. 22, C). Female vents are simple longitudinal slits with no noticeable anterior protuberances; the cloacal region of males is approximately twice as wide as those of females. Black cornified claws are well developed on the digits during the reproductive season in both sexes. In the type series of *O. zhangyapingi*, as well as in all available museum collections from Jilin Province, all adult specimens examined showed the presence of black claws on both fingers and toes, however all these samples were collected in late spring—early summer, i.e. potentially during the reproductive season. It is most likely that black claws are

absent in *O. zhangyapingi* out of the breeding season similar to other *Onychodactylus* species. We have not observed dark horny asperities on the inner surface of the hindlimbs or forelimbs in *O. zhangyapingi*.

Color in life. Coloration of the type series corresponds well with the coloration of the holotype; variation is moderate and mostly pronounced in the dorsal pattern of small light lines and vermiculations; dorsal pattern seems to be individualistic which will allow for individual specimen recognition. Variation in the dorsal coloration of *O. zhangyapingi* type series is given in Fig. 25. There is certain intrapopulational variation in the intensity of the dark base coloration in this species: in the majority of the paratypes the ground color is quite dark, the same as in the holotype: dark violet-blackish or dark-gray covered with dense light mottling or a reticulate pattern; in some specimens the black spots and mottling are developed to a lesser degree and the salamander looks much lighter than the holotype (like KIZ06122, see Fig. 25). There is significant variation in the dorsal pattern of slight lines and vermiculations: in the majority of the specimens, as in the holotype, the dorsal surfaces are covered with numerous light-colored lines, confluent spots and vermiculations forming dense irregular reticulated marbling. However in some specimens (see KIZ06120, Fig. 25) light spots are so small and few that the animal appears almost uniformly dark with faint signs of light mottling on the dorsum. In a single male specimen (KIZ06136, see Fig. 25) the dorsum is covered with numerous irregular yellowish blotches, such a dorsal pattern is often found in *O. koreanus*, but in the latter species light ocelli are usually present, whereas in *O. zhangyapingi* we have never observed these light ocelli in the dorsal pattern. In a single young female (KIZ06124, see Fig. 25) the dorsal pattern consists of irregular confluent yellowish blotches, and can be mistaken for the pattern typical for *O. zhaoermii*. We recorded insignificant sexual variation in coloration: females in general tend to have denser marbling and smaller blotches than those of the males (see Figs. 22; 23), in males the blotches are usually larger and the reticulated dorsal pattern is sparser.

Color in preservative. Color patterns of the paratypes in preservative correspond well to those observed in life, although the bright tints fade from the original coloration; base color of dorsal surface fades to dark gray or brownish; dark brown and black is slightly less warm in tone turning grayish-brown; light pattern at the dorsal sides of head, body and tail turned gray-yellow to dark-beige; ventral sides change color to light beige or yellowish-gray in the same way as described for the holotype (see Fig. 22, C).

Osteology and anatomy. We are not aware of any specific works on the skeletal anatomy in *O. zhangyapingi*. Fei *et al.* (2006) provide a brief morphological description and a figure of the skull, this description seems to be based on material from Jilin Province and likely corresponds to *O. zhangyapingi*. Variation in the number of trunk vertebrae (TVN) and number of costal grooves (CGN) among the type series of *O. zhangyapingi* are presented in Table 6. Modal TVN-number in *O. zhangyapingi* is 18 for males, with a range of 17–19, mean is 17.8 0.75; and 18–19 for females, mean is 18.5 ± 0.53). The trunk–vertebrae numbers result in the respective costal groove counts: 12 (11–13) for males and 12–13 for females (based on 16 specimens, see Tab. 6).

Vomerine teeth morphology. Adult *O. zhangyapingi* have vomerine teeth in two transverse comparatively shallow, almost straight “^”-shaped series with inner and outer branches of the series usually being nearly the same length (in some specimens the outer tooth series branches are slightly longer) (Fig. 4, B). This pattern resembles that of *O. fischeri* sensu stricto (Fig. 4, A), however in *O. zhangyapingi* the vomerine tooth series are almost in contact with each other without a gap between them; whereas those gaps are always evident in *O. fischeri* sensu stricto. In the new species the outer branch of the vomerine tooth series is longer than that of *O. fischeri* sensu stricto: in *O. zhangyapingi* it reaches the level of the external edge of the naris (Fig. 4, B), whereas in *O. fischeri* sensu stricto it seldom reaches the level of the naris’ internal edge (Fig. 4, A). The outer branch of vomerine tooth series is slightly curved towards its external end, while the inner tooth series branch is nearly straight. The ends of the outer branches of the tooth series are located just about on the same level as the ends of the inner branches (see Fig. 4, B). Variation in the number of vomerine teeth (VTN) among the type series of the new species is given in Tab. 7. In our sample the number of vomerine teeth in the species was significantly higher than in *O. fischeri* sensu stricto: 15–18 (mean 16.9 0.92) teeth per each branch in males and 14–18 (mean 16.2 1.03) for females (based on 14 specimens, see Tab. 7).

Eggs and clutch. Data on clutches, egg laying, embryonic and larval development and metamorphosis in *O. zhangyapingi* are totally absent and no reproduction records are known to us. Most likely, egg clutch data in this species does not differ greatly from those described for other *Onychodactylus* species and consists of a pair of egg sacs, connected to each other by a gelatinous stalk which serves to attach the clutch to stones and other similar objects. Examination of ovaries in ten *O. zhangyapingi* females from the type series had shown that each female had from 16 to 21 eggs, from 7 to 12 eggs per ovary, which allow us to assume that the average clutch size is approximately 19 ± 1.73 eggs per egg sac pair; ca. 9.5 ± 1.65 eggs per egg sac. Thus, reproduction and embryonic development of *O. nipponoborealis* remains unknown and new studies in this area are warranted.

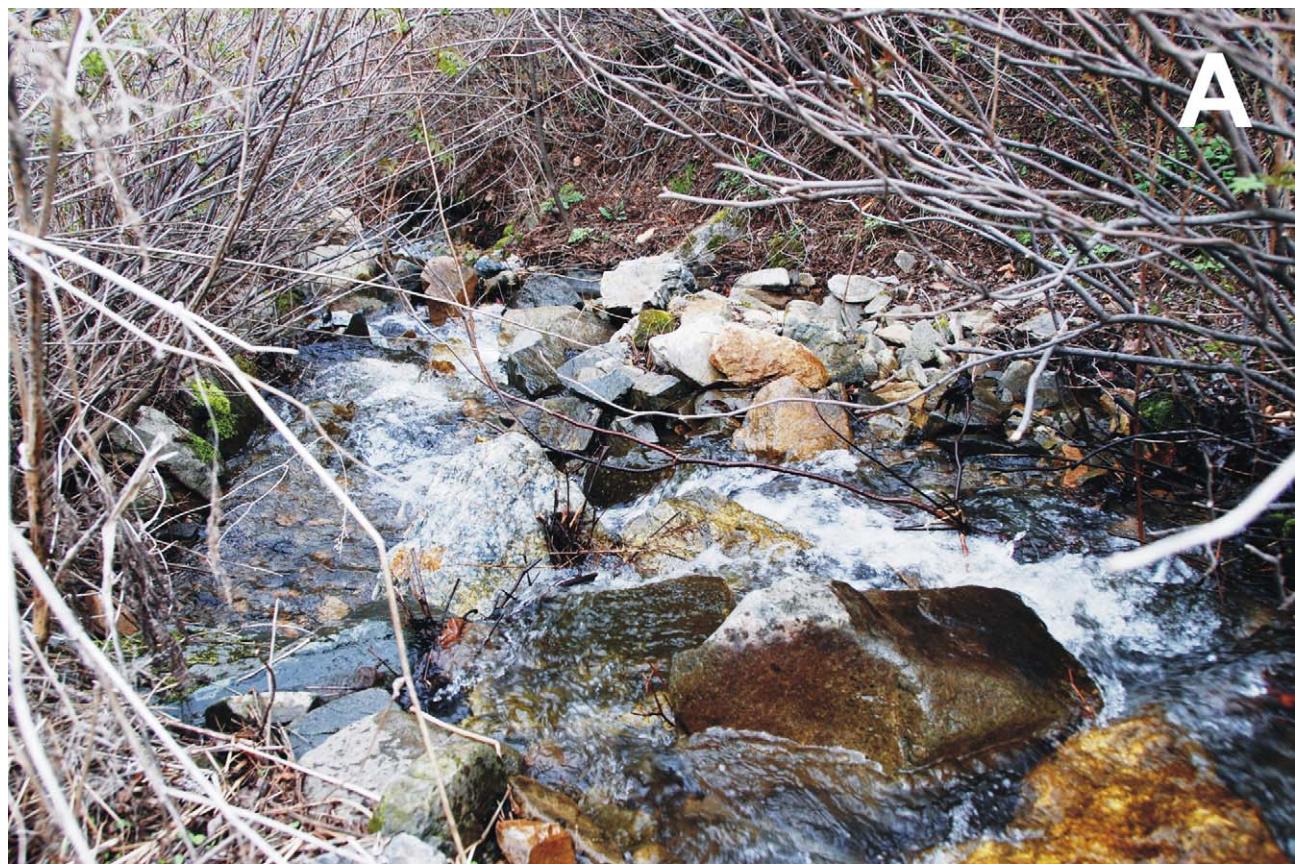


FIGURE 24. (A)—Breeding habitat of *Onychodactylus zhangyapini* (Xiaonangou environs, Linjiang County, Jilin Province, China); (B), (C)—Premetamorphic larvae of *Onychodactylus zhangyapini*, CIB-18336 (780114) (B) and CIB-18333 (780109) (C), from Shanchengzi environs, Jian County, Jilin Province, China, in preservative.

Larval morphology and metamorphosis. The smallest known larvae of *O. zhangyapingi* have well-developed fore- and hindlimbs, short gills and low tail fin folds; they appear in streams at a size of 30–40 mm in length (total length). The initial metamorphic events, including the development of adult dorsal pattern, occur when larval length reaches a total length ca. 40–50 mm. Metamorphosis is normally completed at a total length of 80–90 mm. *O. zhangyapingi* shows the typical combination of larval morphological characteristics for all *Onychodactylus* species (see Fig. 24, B, C): large, flattened and elongated rectangular-shaped head with an obtusely blunted snout; the head is slightly wider than the body; gills are short and their base is covered with an opercular skin fold, eyes slightly prominent, all digits on both fore- and hindlimbs bear dark-black, cone-shaped, horny claws. Both fore- and hindlimbs develop a dermal fold on their outer edges, which disappear during metamorphosis. The tail fin is low, consisting of low dorsal and ventral fins, dorsal fin is notably higher than the ventral fin. The tail fin runs along the back surface of the tail from the tail base of the tail (approximately above the cloaca) and disappears on the ventral side of the tail near the middle of its length. Tail tip is usually obtusely tapered but rounded at the very end. Coloration of the larvae is quite variable, variation is mostly pronounced on the dorsal pattern. The ground coloration in larvae is normally beige, yellow-brownish, ochre, but may be bright to almost orange. After the larvae begin to actively feed, they gradually develop a dark pigment, which first appears as numerous small black spots on the lateral sides of body and tail. Normally, dark spots are absent on the dorsum; the light ground color there forms a distinct narrow light dorsal stripe (Fig. 24, B), while the flanks are mottled with numerous dark (blackish or brownish) spots, or posses a diffused and unclear clouded pattern. As the larvae grow, the dark coloration on the flanks develop and becomes more contrasting, forming numerous irregular dark spots of different sizes where they often merge into each other and may form a reticulated pattern (Fig. 24, B) or sometimes large contrasting black blotches (Fig. 24, C). At this age the light dorsal stripe is usually not present. The ventral side is always lighter than the other body surfaces and completely lacks black spots. Normally, a light (yellowish to orange) dorsal stripe is seen on the back surface of the tail often bordered with two irregular dark lateral stripes. Closer to metamorphosis the larvae get darker, the light areas on dorsum and tail decrease and form a dense reticulated pattern similar to that described for the adults. Most likely, larvae metamorphose in the second or the third year; the lifespan of this species is unknown. More research in this area is needed.

Etymology. The specific epithet “*zhangyapingi*” is a patronymic noun in the genitive singular; derived from the name of Professor Zhang Ya-Ping, an academician of the Chinese Academy of Sciences, who contributed greatly to the promotion and development of biodiversity and evolutionary studies in China and to acknowledge his permanent support and encouragement as well as his substantial contributions to the development of molecular taxonomy in China. We suggest Jilin Clawed Salamander as the English common name of the species as a reference to species distribution. Recommended common names in Chinese, Russian, Korean and Japanese are given above.

Distribution. *Onychodactylus* were recorded for the first time from Jilin Province by Mori (1928), who reported a specimen from the Yanji district, however since that time no additional specimens from this region of Jilin have been found; our surveys in Yanji district in 2010 also failed to detect any *Onychodactylus*. To date, *O. zhangyapingi* is known only from Linjiang, Ji'an and Tonghua counties in Jilin Province of China though discoveries in neighboring areas of North Korea and, possibly, in Liaoning Province of China are anticipated. This species inhabits the mountainous forests in the Changbaishan mountain area in Jilin Province of China, the distribution range of *O. zhangyapingi* should include the regions of Tonghua, Baishan, and, possibly, Yanji districts along the Changbaishan mountains, and this range likely extends into Chagang-do and Yanggang-do provinces of North Korea. It is noteworthy that to date, no valid records of *Onychodactylus* are known from the extreme eastern region of Jilin Province (Dunhua, Longjing, Wangqi districts; a record by Mori (1928) was not confirmed by later surveys) and Mudanjiang County of Heilongjiang Province, although it was reported to inhabit those areas by some authors (see Fei, 1999; Kuzmin *et al.*, 2004; Sparreboom, 2012). During our regular fieldwork in these parts of Jilin and Heilongjiang provinces, we failed to find *Onychodactylus* populations. Thus, we assume that there is a gap between the distribution areas of *O. fischeri* sensu stricto and *O. zhangyapingi* in this area. Since no geographic barrier is known to separate the ranges of *O. zhangyapingi* and *O. zhaoermii* both species are currently documented from only a few localities, therefore the extent of the distribution of *O. zhangyapingi* in China and North Korea requires further investigation.

Comparisons. *O. zhangyapingi* can be distinguished from the other salamanders in the region, including two sympatric hynobiids, *Hynobius leechii* and *Salamandrella tridactyla*, by its slender body, smooth skin with distinct costal grooves on the flanks, very long tail, almost cylindrical at the base, slightly compressed in the middle and

flattened towards its end, small and somewhat elongated head with rounded snout, and a combination of morphological features characteristic of *Onychodactylus*, such as absence of lungs, breeding males develop dermal flaps on the outer surface of the hindlimbs, both sexes during the reproductive season possess black horny claws on both fingers and toes, vomerine teeth in two short transverse arch-shaped series, premaxillary fontanelle large fully separating nasals, caudal ribs numerous and present on more than 5–6 postsacral tail vertebrae.

From other congeners *O. zhangyapingi* is different in the average number of trunk vertebrae (20) and costal grooves (14), and the typical coloration of juveniles (contrast bright confluent spots and blotches on a dark ground color) and adults—dark ground color with numerous light confluent spots and vermiculations, forming a reticulated pattern with no distinct dorsal band.

O. zhangyapingi (Houttuyn, 1782) can be further distinguished from other *Onychodactylus* species by a following combination of morphological attributes:

O. zhangyapingi can be distinguished from *O. fischeri* (Boulenger, 1886) by the following combination of morphological attributes: lower trunk vertebrae number (TVN = 18–19) and costal groove count (CGN = 12–13) (versus TVN = 20–21 and CGN = 14–15 in *O. fischeri*) (Tab. 6); left and right vomerine tooth series in contact with no gap noticeable between them, Fig. 4, B (versus a distinct gap is present between the vomerine tooth series in *O. fischeri*; Fig. 4, A); vomerine teeth numerous, VTN = 16.4 ± 1.03 (per row) in *O. zhangyapingi* (versus VTN = 11.5 ± 1.23 in *O. fischeri*) (Tab. 7); and dorsal coloration: no prominent dorsal stripe, background color of dorsal surface is dark; back side of body is covered with numerous contrast light lines and vermiculations forming a marbling or a dense reticulate pattern, Fig. 5, B (versus light dorsal stripe present, indistinct with unclear edges in *O. fischeri*, Fig. 5, A). *O. zhangyapingi* further differs from *O. fischeri* in following morphometric features (see Tabs. 4; 5 for details): smaller SVL in males, comparatively longer tail in both sexes, comparatively longer hindlimbs in both sexes and forelimbs in males, comparatively larger eyes in both males and females, and comparatively longer snout in both sexes.

O. zhangyapingi differs from the members *O. japonicus* species complex, *O. japonicus* (Houttuyn, 1782) and *O. nipponoborealis*, in dorsal pattern: no prominent dorsal stripe present in *O. zhangyapingi*, background color of dorsum is dark; normally back side of body is covered with numerous light lines and vermiculations forming a dense reticulated pattern, Fig. 5, B (versus light-colored dorsal stripe usually present in members of *O. japonicus* species complex, background color of dorsal surface is lighter than color of body sides, Fig. 5, E-G). It also differs from the members of *O. japonicus* complex in the shape of vomerine tooth series: comparatively shallow, almost straight and not curved tooth series in *O. zhangyapingi*, Fig. 4, B (versus deep notably curved vomerine tooth series in *O. japonicus*, Fig. 4, E and *O. nipponoborealis*, Fig. 4, F) and by having a greater vomerine tooth count (VTN) than in *O. japonicus* (but not in *O. nipponoborealis*): VTN = 16.4 ± 1.03 in *O. zhangyapingi* (versus VTN = 11.4 ± 1.16 in *O. japonicus*) (Tab. 7). It is also different from *O. japonicus* in having a greater trunk vertebrae number (TVN): 18–19, normally 18 in *O. zhangyapingi* (versus 17–18, usually 17 in *O. japonicus*) and a greater costal groove count (CGN): 12–13, more often 12 (versus 11–13, usually 11 in *O. japonicus*) (Tab. 6) (but no differences with *O. nipponoborealis*). *O. zhangyapingi* is also different from *O. nipponoborealis* in absence of gap between the vomerine tooth series (versus usually a pronounced gap is present between the vomerine tooth series in *O. nipponoborealis*). Finally, *O. zhangyapingi* further differs from *O. japonicus* some important morphometric ratios (see Tabs. 4; 5 for details): wider heads in both sexes, comparatively larger eyes than in *O. japonicus*, and comparatively shorter fore- and hindlimbs in both sexes. Males of *O. zhangyapingi* have significantly longer tails than in male *O. nipponoborealis*, and shorter axilla-groin distances in both sexes. In comparison with in *O. nipponoborealis*, *O. zhangyapingi* has smaller male SVL, narrower heads and comparatively shorter fore- and hindlimbs, smaller internarial and interorbital distances for both males and females.

For a more detailed comparison of *O. zhangyapingi* with the two other new species of *Onychodactylus* described from continental Northeast Asia in this paper, see “Comparisons” sections in taxonomic accounts for *O. koreanus* and *O. zhaoermii* given above.

Karyotype. $2n = 78$, NF = 102. Chromosomal formula: 6M+6SM+10ST+14T+42a. The karyotype of *O. zhangyapingi* (as *O. fischeri*) is reported by Zhao *et al.* (1991) based on a specimen from “Jilin Province, Tonghua County” and is typical for the genus with $2n = 78$ including 18 pairs of macrochromosomes and 21 pairs of microchromosomes.

Genome size. Our estimate of *O. zhangyapingi* genome size is 94.0 pg per diploid nucleus; CV = 47.0 (DNA flow cytometry; one specimen from the type locality (Heisonggou environs, Linjiang County, Jilin Province, China); J. Che, pers. obs.; peripheral red blood cells of the Goldfish, *Carassius auratus* (Cyprinidae), were used as

a reference standard for genome size measurements. Due to different reference species used this genome size estimate is cannot be compared with the data reported for *O. fischeri*, *O. japonicus*, *O. nipponoborealis* and *O. koreanus*).

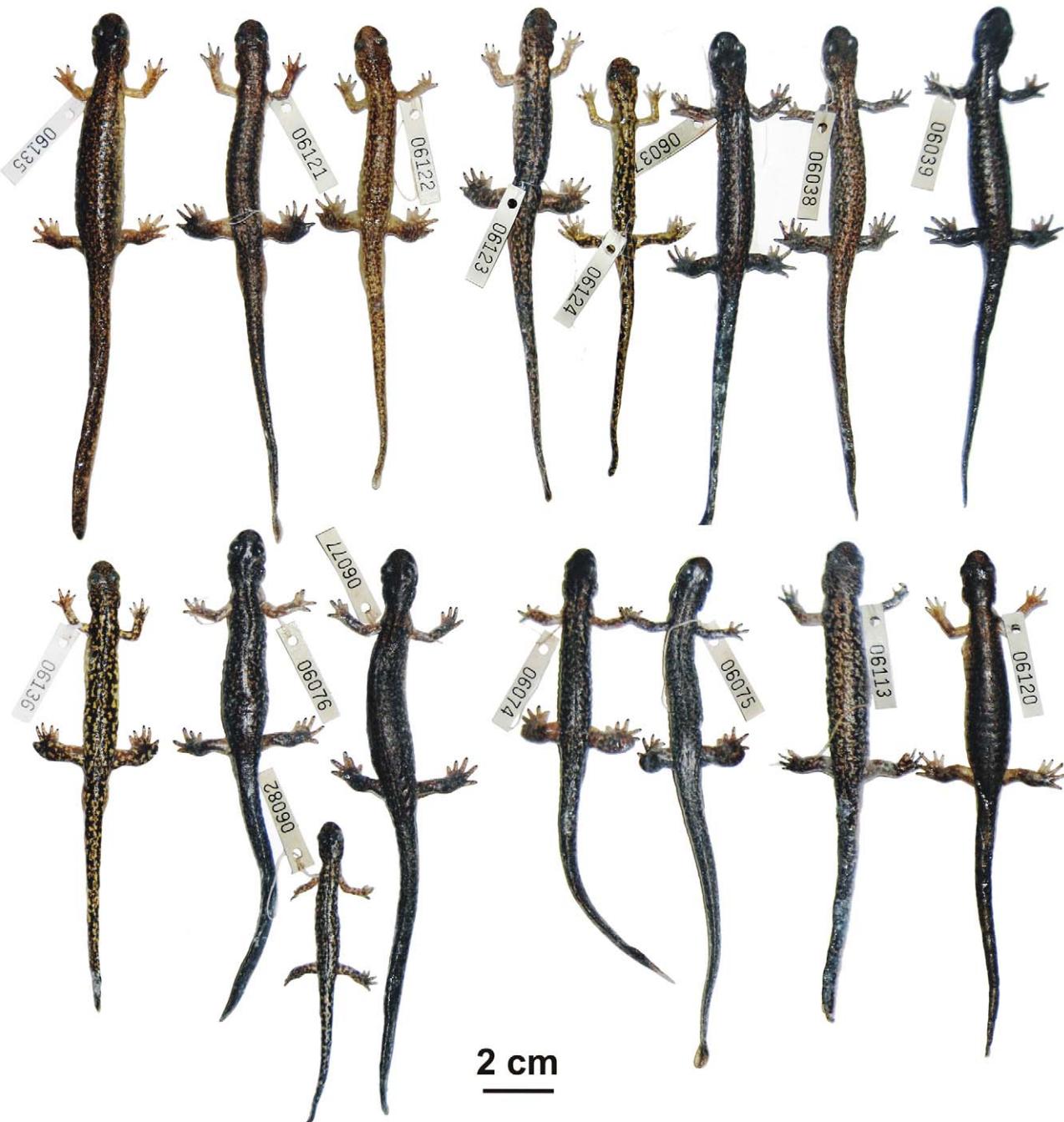


FIGURE 25. The type series of *Onychodactylus zhangyapingi*, showing variation in dorsal coloration: KIZ06074-06075; KIZ06121-06123; KIZ06136 (six adult males from the type locality, Heisonggou environs, Linjiang County, Jilin Province, China); KIZ06076-06077; KIZ06082 (three adult females from the type locality); KIZ06037-06039; KIZ06113; KIZ06120; KIZ06124 (six adult females from Xiaonangou environs, Linjiang County, Jilin Province, China); KIZ06135 (one adult female from Laolitougou environs, Linjiang County, Jilin Province, China). Scale bar is 2 cm. Photos by J. Che.

Phylogenetic position. According to the results of our phylogenetic analyses, *O. zhangyapingi* is more closely related to the *Onychodactylus* species inhabiting the Japanese islands rather than to other *Onychodactylus* species from mainland northeast Asia (see Fig. 3). The divergence between *O. zhangyapingi* and all other *Onychodactylus* species ranges from 7.5 to 12.2% in COI and from 2.0 to 5.3% in 16S rRNA in uncorrected genetic distances (Tab. 3).

Habitats and natural history. The natural history record for *O. zhangyapingi* is rather poor. *O. zhangyapingi* inhabits moist, cool and shady places in mountainous mixed and evergreen forests of the Changbaishan Mountain area. It is adapted to the upper reaches of small mountain streams under the canopy in mixed forests of broad-leaved deciduous trees and cedar pines. In the Jilin Province it usually occurs from an elevation of 300 m; our series was collected at 330–560 m a.s.l. Since *O. zhangyapingi* is a strict specialist, adapted to cool mountain streams, it is like to be found at higher elevations of over 1.000 m a.s.l. as well, although any such documented records are absent to date. As with other *Onychodactylus* species, *O. zhangyapingi* is associated with the running springs and upper current waterways of small mountain brooks. This habitat is usually overgrown with mixed forests of deciduous trees and cedars; preferred streambeds that have a thick layer of pebbles, moss-covered rocks and rich vegetation, which provides high humidity and dense shadows along the stream margins with numerous hiding places; temperatures ranging from 6 to 14°C. Photo of the typical habitat is illustrated in Fig. 24, A. Adults prefer areas of the of streams with minimal direct sunlight, abundant hiding places (crevices under logs, stones etc.), unfrozen stream pools and underground springs. During the breeding season animals migrate to these streams, and outside of the breeding season salamanders can be found under rocks, stones, fallen trees and logs but they usually remain close to springs and permanent streams. Reproduction of *O. zhangyapingi* has not been observed in the wild or under captive conditions. Specimens were collected by searching after dark with flashlights along the Changbaishan region in Jilin Province since 2007. Usually, specimens were found after 18:00; adult specimens were found on the stream-sides and in the water, salamanders often hide under rocks in the running streams. Larvae are easily observed between stones and pebbles in shallow areas on the bottom of the stream, where they are mostly active in the evening and at night, however, they also can be found at daytime under stones and in other shelters in streams. In the study area, *O. zhangyapingi* are sometimes found to be sympatric with *Hynobius leechii*, however habitat preferences in these species are different and they were not observed in the same biotope. Other sympatric amphibian species include *Rana dybowskii* (our data) and, possibly, *Salamandrella tridactyla*, *Rana amurensis*, *Bombina orientalis*, *Bufo gargarizans* and *Hyla ussuriensis*.

Conservation status. Because of the small range in China, restricted to mountainous areas in the northeast of the country, *O. fischeri* was listed as an endangered species in the Red Data Book of China (Zhao, 1998). Our results presented in this paper suggest that Chinese populations of *Onychodactylus* belong to two distinct species, with *O. zhangyapingi* having a very small known range: up to now it is documented from just two counties of Jilin Province (Linjiang and Tonghua). The extent of the new species distribution in China and North Korea and its population status is not known. As a strict specialist species, adapted to clean mountain forest streams, *O. zhangyapingi* is greatly threatened by habitat destruction due to logging and other anthropogenic activities in the area of its distribution. The species inhabits the National Forest Park in Ji'an County of Jilin Province. The extent of this species with regard to its population status needs to be studied in greater detail, and due to its very limited distribution and ecological vulnerability we recommend to include *O. zhangyapingi* to the China Red Data Book of Endangered Animals and suggest that its IUCN red list conservation status is Vulnerable (Vu2a) according to IUCN criteria.

Key for identification of *Onychodactylus* species

- | | | |
|---|---|---|
| 1 | Prominent light-colored dorsal stripe present (although it may have serrated edges or be covered with dark spots), background color of dorsal surface is lighter than the color of the sides of the body | 2 |
| - | No prominent dorsal stripe, background color of dorsal surface is dark; usually the posterior region of the body is covered with numerous small contrasting light spots or variegations forming a reticulate pattern | 5 |
| 2 | Costal grooves 14–15, trunk (presacral) vertebrae 20–21. Light dorsal stripe present but is indistinct and has unclear edges, more noticeable in juveniles. In life the dorsal stripe is light-brownish, golden or ochre colored and is covered with numerous black irregular spots or variegations of various sizes which may also be present on the sides of the body (Fig. 5, A). Found only in Russian Far East: southern parts of Sikhote-Alin mountain ridge in Primorye (Maritime) territory northwards reaching the Zerkalnaya River Valley— <i>O. fischeri</i> | |
| - | Less than 14 costal grooves (usually 11–13), trunk vertebrae, correspondingly, less than 20 (usually 17-19). Light dorsal band is normally distinct and bright with robust edges. Coloration in life of dorsal band varies from vermillion red to copper orange or golden-orange. Edges and body sides usually lack numerous black spots and variegations. Japanese islands— <i>O. japonicus</i> species complex | 3 |
| 3 | Rows of vomerine teeth are prominently curved forming «  »-shaped figure; posterior ends of their inner branches are recurved and located on the same level as the posterior ends of the outer branches. Vomerine teeth usually more | |

than 16 per each row. Costal grooves usually 12–13, trunk vertebrae—18–19. Tail is relatively short, in adult males TL/SVL ratio usually around 1.18. Light dorsal band normally distinct but sometimes with relatively jagged edges (Fig. 5, E). Found in Tohoku district encompassing north-eastern part of Honshu from prefecture Aomori in the north to prefectures Yamagata and Miyagi in the south—*O. nipponoborealis*

- Vomerine teeth in two slightly curved rows forming «»-shaped figure; posterior ends of their inner branches are minimally curved and located slightly more anteriorly towards the posterior ends of the outer branches. Vomerine teeth usually less than 15 per each row. Costal grooves usually 11–12, trunk vertebrae—17–18. Tail relatively long, in adult males TL/SVL ratio is usually around 1.3. Light dorsal band is normally distinct with sharp contrast edges. Honshu and Shikoku islands of Japan southwards from Yamagata and Miyagi prefectures 4
- 4 Light dorsal stripe usually wide with straight, unbroken edges and almost no or few black spots on it (Fig. 5, G). Typical color of the dorsal stripe—copper to orange, sides of body usually dark-brown, grayish or plumbeous. Central and south-western Honshu southwards from Yamagata and Miyagi prefectures in the north-east to Hiroshima and Shimane prefectures in the south-west—*O. japonicus*
- Coloration very bright and with high contrast. Light dorsal stripe often broken with clear, robust but meandering edges, sometimes forming black transverse bands or stripes (usually in the sacral area and on the tail). On the dorsal surface of the head, posteriorly beyond the eyes a dark “Y”-shaped figure is present. Light dorsal stripe is very bright, usually vermillion red or orange-red, often with a thin black dorsomedial stripe along the midline of the body (Fig. 5, F). Body sides are very dark, almost black with a purple tint. Shikoku Island, also found in Honshu in Hiroshima Prefecture sympatrically with *O. japonicus*, may be found on Kii Peninsula in Wakayama and Nara prefectures—*O. cf. japonicus*
- 5 Vomerine teeth rows are almost straight with the inner branch length nearly the same length as outer branch or longer. Dark background color of the dorsal surface is covered with numerous light (yellowish, pinkish) lines or variegations of irregular shape, usually tending to merge and form a marbling or dense reticulate pattern (Fig. 5, B); light-colored ocelli on the dorsal surface of the body and limbs are absent. Mountain areas of north-eastern China (Jilin Province), probably also in adjacent regions of North Korea—*O. zhangyapini*
- Rows of vomerine teeth are slightly curved with the outer branch usually being noticeably longer than the inner branch. Dark background color of the dorsal surface is covered with numerous light (bright-yellow, orange, golden) spots, which may be confluent forming thick variegations (on a cross-section of the dorsal surface in middle of the dorsum usually from 4 to 7 light spots) (Fig. 5, C, D); on the dorsal surface of body and limbs light-colored ocelli with dark centers are often found—*O. koreanus species complex* 6
- 6 Modal costal groove number—11 for males (trunk vertebrae—17), 12 for females (trunk vertebrae—18). Dark background color of dorsal surface is covered with numerous light (orange to copper-red) irregular confluent spots and dots, sometimes forming a sparse reticulate pattern (Fig. 5, C). Claws are well-developed on both fore- and hindlimbs in both sexes. Mountain areas of north-eastern China (Liaodong peninsula, Liaoning Province, S Jilin Province), probably also in adjacent regions of North Korea—*Onychodactylus zhaoermii*
- Modal costal groove number—13, trunk vertebrae—19 for both males and females. Dark background color of dorsal surface is covered with numerous light, (bright-yellow to golden) not confluent, relatively regular round or oval spots and dots, not forming a reticulate pattern (Fig. 5, D). Claws are absent in animals out of the breeding season, usually found in males on hindlimbs. Mountain areas of continental South Korea (almost the entire country) also may be found in adjacent regions of North Korea—*O. koreanus*

Species diversity within *Onychodactylus*

Here, we followed an integrative taxonomic approach to review the genus *Onychodactylus* and clarify its taxonomy. We provide new data on the morphological and genetic diversity within this genus and summarized it with the previously available literature. Historically, the taxonomy of *Onychodactylus* was based on morphological characters that allowed distinguishing two species (Dunn, 1923; Sato, 1943; Kuzmin, 1995, etc.), but also was hampered by a lack of a complete sampling that could have allowed to better understanding the geographic variation within this genus. Some remote areas in the Far East were only possible to sample in recent years, while there are still big gaps in regions such as North Korea that have very limited access to scientists from foreign countries. This, together with the increase of herpetological work in the Eastern Asia in recent years led to a significant increase in the discovery of cryptic diversity and description of many new species of Asian salamanders, mainly salamandrids (Shen *et al.*, 2008; Hou *et al.*, 2009; Nishikawa *et al.*, 2009, 2011a, 2011b; Wu *et al.*, 2010a, 2010b and references therein) and hynobiids (Kim *et al.*, 2003; Shen *et al.*, 2004; Matsui *et al.*, 2004; Zhou *et al.*, 2006; Xu *et al.*, 2007; Fu & Zeng, 2008; Matsui *et al.*, 2008; Poyarkov & Kuzmin, 2008; Lai & Lue, 2008; Wei *et al.*, 2009; Li *et al.*, 2010). Among the most striking recent discoveries in herpetology and for the region is the existence of the first Asian plethodontid salamander, *Karsenia koreana* in South Korea (Min *et al.*, 2005), which turned out to be a distinct new genus and a key piece to understanding the historical biogeographic connections in the region (Vieites *et al.*, 2007). These discoveries suggest that many new species of salamanders are expected to be discovered in Asia, which is also the case within *Onychodactylus*.

From our analyses and results, we recovered several new lineages within the genus *Onychodactylus* that diverge both morphologically and genetically from the two currently described species, four of those we here describe as new species. We followed an integrative taxonomic approach in defining species that considers not only species as distinct evolutionary lineages from a molecular perspective, but that show diagnostic characters in their morphology. Both lines of evidence have the same weight and are used in combination to study the variation within this genus (e.g. Dayrat, 2005) following a principle of congruency between them (Padial *et al.*, 2009, 2010; Vieites *et al.*, 2009). From this approach, molecular data were the first step in identifying potential candidate species across the range of the genus (*sensu* Vieites *et al.*, 2009), which was followed by a thorough morphological analysis. These two lines of evidence were proposed as suitable for species delimitation in amphibians (Glaw *et al.*, 2010). The combination of these data suggests the existence of at least six species within *Onychodactylus*: *O. fischeri*, *O. japonicus*, and four confirmed candidate species that are described here: *O. nipponoborealis*, *O. koreanus*, *O. zhaoermii* and *O. zhangyapingi*, based on their distinct morphology and genetic divergence. From three to four other forms, such as *Onychodactylus* sp. from Yangsan, Korea and three *O. cf. japonicus* lineages from the Japanese islands show a high degree of genetic divergence yet our morphological data and materials at hand are not sufficient to distinguish them from other species. On this basis, we consider these lineage as unconfirmed candidate species, following Vieites *et al.* (2009), which need further investigation to clarify their taxonomic status. For one of those lineages from western Japan (*O. cf. japonicus* from Chugoku and Kinki regions of Honshu and Shikoku) reproductive isolation with sympatric *O. japonicus* has been proven by recent allozyme electroporetic studies (Yoshikawa *et al.*, 2010a, 2010b), which confirms the assumptions on its specific status; whereas systematic relationships of the other forms are still to be studied. Thus, the diversity of the genus *Onychodactylus* is still far from complete and new discoveries and taxonomic reassessments are expected. The limits of the discussed species and lineages are still unclear, especially in areas such as North Korea where they may become in contact, suggesting that more fieldwork as well more data on divergent lineages such as the unconfirmed candidate species designated in the present paper are needed to complete the knowledge of the genus *Onychodactylus*.

Acknowledgements

We are grateful to numerous friends and colleagues who supported and helped during collection of materials in the field, assisted with molecular work in the lab, provided their own research materials, literature and constructive comments on the manuscript. In particular we are grateful to Yasutaka Abe, Kraig Adler, Masato Akiyama, Natalia B. Ananjeva, Pim (J.W.) Arntzen, Alex V. Borisenko, Evgeniy A. Dunayev, Alexandr S. Grafodatskiy, Nataly Ivanova, Jie-Qiong Jin, Tim Johnson, Steve Karsen, Reiko Katakura, Hiroyuki Koishi, Sophia M. Kolchanova, Sergius L. Kuzmin, Mu-Yeong Lee, Iñigo Martinez-Solano, Glib O. Mazepa, Anna K. Mihalskaya, Tadashi Nakazato, Roman A. Nazarov, Alejandra Nieto-Román, Nikolai L. Orlov, Valentina F. Orlova, Jong-Bun Park, Andrey D. Poyarkov, Anna V. Rasskazova, Evdokiya S. Reshetnikova, Svetlana A. Romanenko, Satoshi Sakuma, Karen S. Sarkisian, Taku Shibata, Yudai Shiraiwa, Irina A. Serbinova, Sergey V. Smirnov, Evgeniya N. Solovyeva, Masahiko Sotokawa, Anna B. Vassilieva, Boris D. Vassiliev, David B. Wake, Marvalee H. Wake, Yue-Zhao Wang, Feng Xie, Jian-Li Xiong, Junxiao Yang, Xiao-Mao Zeng, Peng Zhang, Xiao-Dong Zhang, Wei-Wei Zhou and Ya-Ping Zhang. NAP thanks Masato Aoyama, Yu-Hao Chang, Paul Freed, Tetsuya-Thomas Kusunoki, Ayako Tanabe, Ning Wang, Meng Zhang and Fedor S. Zhirov for their patience and kind help with translations and proof-reading the manuscript. We are also grateful to the curators and collections of the following museums that provided access to their materials: CIB, EWNHM, KIZ, MVZ, NSMT, RMNH, ZFMK, ZISP, and ZMMU. This work was partially supported by the Martin Fellowship (Naturalis, the Netherlands) and by the Russian Foundation of Basic Research (Grant Nos. RFFI-12-04-01552-a, RFFI-12-04-33150-mol_a_ved) to NAP; grants from the Ministry of Science and Technology of China (MOST Grant 2011FY120200), the National Natural Science Foundation of China (31090100), the Chinese Academy of Sciences (KSCX2-YW-Z-0807, KSCX2-EW-Z-2) and the Bureau of Science and Technology of Yunnan province to JC; a Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology (MEST) (No. 2009-0067686) to MMS; the National Science Foundation (grant EF-0334939) through the AmphibiaTree project, and a Spanish Ministry of Science and Innovation grant (CGL2009-10198) to DRV. Finally, we would like to thank Kraig Adler (Cornell University, Ithaca, NY, USA), Sergius L. Kuzmin (A.N. Severtsov Institute of Ecology and Evolution RAS, Moscow, Russia) and the third anonymous reviewer for proof reading and commenting on a previous version of the manuscript.

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APPENDIX 1. Specimens used in morphological analysis. See text for abbreviations of institutions and museums.

Populations used in morphological analysis

(Note – population numbers do not correspond to those in the Table 1)

Onychodactylus fischeri s. str.

Pop. 1: Russia, Primorye territory, Anuchinskiy distr., Serebryanyi spring (ZMMU A2742); **Pop. 2:** Russia, Primorye territory, Partizansk (ZMMU A1900); **Pop. 3:** Russia, Primorye territory, Shkotovsky distr., Anisimovka, Sukhodel River (MVZ 217440, MVZ 217441); **Pop. 4:** Russia, Primorye territory, Ussuriysk district, Ussuriyskiy Nature Reserve (MVZ 217442; MSUZP-Herp-A115-1-A115-7); **Pop. 5:** Russia, Primorye territory, Nakhodka region, Pedan mt. (ZMMU A1934); **Pop. 6:** Russia, Primorye territory, Partizansk distr., environs of Tirkovoi station (ZMMU A2208; MVZ 200602-200605; MSUZP-Herp-A146-1-A146-5); **Pop. 7:** Russia, Primorye territory, Partizansk distr., ~8-10 km S from Tirkovoi, Litovka mt. (ZMMU A4162); **Pop. 8:** Russia, Primorye territory, Olga distr., Mineralnaya River, 15 km NE from Gorno-Vodnoye village (ZMMU A3118; ZMMU A3152); **Pop. 9:** Russia, Primorye territory, Suputinskiy Nature Reserve (ZMMU A1348); **Pop. 10:** Russia, Primorye territory, Serebrianka river (ZMMU A2300); **Pop. 11:** Russia, Primorye territory, Suputinskiy Nature Reserve (ZMMU A1348; ZMMU A1973); **Pop. 12:** Russia, Primorye territory, Bolshekamensk distr. (ZMMU A1795).

Onychodactylus nipponoborealis

Pop. 13: Japan, Aomori Prefecture, environs of Hirakawa town, near the top of Yasute Mt. (**holotype:** NSMT H5710, 1 male; **paratypes:** NSMT H5711–5712, 2 adult males; NSMT H5713–5714, 2 adult females; ZMMU A4295-1–4295-4, 4 adult males from the same locality; ZMMU A4295-5–4295-7, 3 adult females from the same locality); **Pop. 14:** Japan, Aomori Prefecture, environs of Hirosaki city (**paratype:** ZMMU A4297-1, 1 adult female).

Onychodactylus japonicus s. str.

Pop. 15: Japan, Fukushima Prefecture, Minamiaizu district, Hinoemata-mura (ZMMU A4296; ZFMK 30797; ZFMK 30798; MVZ 233579); **Pop. 16:** Japan, Tochigi Prefecture, Kinugawa-koen st. (ZMMU A4294); **Pop. 17:** Japan, Tochigi Prefecture, vicinity of Nikko (MVZ 129397-129402; MVZ 231874; MVZ 184879); **Pop. 18:** Japan, Gunma Prefecture, Kusatsu (ZISP5090-1–5090-5); **Pop. 19:** Japan, Honshu (formerly Hondo), Kyoto environs (ZFMK 27696). **No specific locality recorded:** “Japon”: (*Salamandra unguiculata* Temminck & Schlegel, 1838: **lectotype:** RMNH 2292-A, adult male; **paralectotypes:** RMNH 2292-B, 2292-D, 2 adult females; RMNH 2292-C, adult male; specimens not designated as members of the type series, but possibly coming from the same locality of origin: RMNH 2289, 15 adult females, 2 adult males, 3 juveniles; RMNH 2290, 5 adults, 3 juveniles; RMNH 2291, 7 larvae; RMNH 18560, complete skeleton. From the same sample come MNHNP 4692, 6 adults (lectotype and 5 paralectotypes), and MCZ 21320). “Japan, unknown locality”: (ZFMK 27695; ZFMK 32179; ZFMK 32180; ZFMK 36283; MVZ 185186; MVZ 185187).

Onychodactylus koreanus

Pop. 20: Korea, Gangwon-do, Samcheok-shi, Singi-myeon (**holotype:** EWNHM 80316, adult male; **paratypes:** EWNHM 80317–80318, adult males; EWNHM 80315, adult female); **Pop. 21:** Korea, Gyeongsangbuk-do, Sangju-shi, Songni-san, Daemok-ri environs (EWNHM 80319–80320 (MMS1548-1549); MVZ DRV-5056); **Pop. 22:** Korea, Gangwon-do, Hwajon-ri, Nam-myon, Hongcheon-gun [Hongchon-gun] (MVZ 233472; MVZ 233473); **Pop. 23:** Korea, Gyeonggi-do, Yangpyeong-gun, Danwol-myon, Hyangso-ri (MVZ 233474; MVZ 233475); **Pop. 24:** Korea, Daejeon, Seo-gu, Jangan-dong, Jangtaesan (EWNHM 80321–80322); **Pop. 25:** Korea, Chungcheongnam-do, Nonsan-shi, Beolkok-myeon (EWNHM 80323–80325); **Pop. 26:** Korea, Chungcheongbuk-do, Cheongju-shi, Gadeok-myeon (EWNHM 80327–80328); **Pop. 27:** Korea, Jeollanam-do, Damyang-shi, Naejangsan NP (Sinung environs) (MVZ DRV-5050–5051); **Pop. 28:** Korea, Jeollabuk-do, Jeonju-shi, Kunghangsan environs (MVZ DRV-5057); **Pop. 29:** Korea, Jeollanam-do, Jangseong-gun, Bukii-myon, Baekyang-sa Temple (MVZ 233476); **Pop. 30:** Korea, Jeollabuk-do, Jeongsan [= Jeong Sun] (MVZ 163735); **Pop. 31:** Korea, Gyeongsangbuk-do, Kwangdeoksan (EWNHM 80326 (MMS1557)); **Pop. 32:** Korea, Gyeongsangnam-do, Sancheong, Jirisan NP, Jirisan environs (**paratypes:** ZMMU A-4064-1–4064-2, 2 juveniles; ZMMU A-4064-3–4064-7, 5 larvae). **No specific locality recorded:** “Korea, unknown locality”: (MVZ 173513).

Onychodactylus zhangyapingi

Pop. 33: China, Jilin Province, Linjiang County (KIZ06037-KIZ06039; KIZ06074-KIZ06077; KIZ06082; KIZ06113; KIZ06120-KIZ06124; KIZ06135-KIZ06136); **Pop. 34:** China, Jilin Province, Tonghua County, Laoling environs (CIB-18348 (750152)/ CIB 00141 1479, adult male; CIB-18347 (750155), larva); **Pop. 35:** China, Jilin Province, Jian County, Shanchengzi environs (CIB-18333 (780109), CIB-18335 (780110), CIB-18336 (780114), larvae).

Onychodactylus zhaoermii

Pop. 36: China, Liaoning Province, Xiuyan environs (KIZ06056-KIZ06058; KIZ06129-KIZ06133); **No specific locality recorded:** “China, Liaodong peninsula, unknown locality”: (MSUZP-Herp-A201).

APPENDIX 2. Studied morphological characters (see also Fig. 2, Fig. 4; Fig. 5 and Tab. 4 for details).

Character definitions

Metric characters

SVL—snout-vent length (measured on straighten body from snout to the anterior end of the vent); TL—tail length (measured on straighten tail from the tip of the tail to the anterior end of the vent); GA—gleno-acetabular distance (minimum distance between axilla and groin measured on a straighten body; measured separately for left and right body sides); FLL—forelimb length (length of the straighten forelimb measured from axilla to tip of the longest finger of forelimb; measured separately for left and right body sides); HLL—hindlimb length (length of the straighten hindlimb from groin to tip of the longest toe of hindlimb; measured separately for left and right body sides); HL—head length (measured from the tip of the snout to the gular fold); HW—head width (widest measurement of the head across the eyes anterior the level of parotid glands; does not include head broadening beyond the eyes in breeding males); EL, eye length (minimum distance from the anterior corner of the eye to the posterior corner of the eye; measured separately for left and right body sides); IN—internarial distance (minimum distance between the external nares); ON—orbitonarial distance (minimum distance between external nares and the anterior corner of the eye on the same side of the head; measured separately for left and right body sides); IO—interorbital distance (minimum distance between the upper eyelids); CW—chest width (minimum distance between left and right axillae); OR—orbitorostral distance, snout length (measured as minimum distance from tip of snout to the anterior corner of the eye; measured separately for left and right body sides); IC—intercanthal distance (measured as minimum distance between anterior corners of the eyes).

Meristic characters

TVN—trunk vertebrae number (number of presacral vertebrae); CGN—costal grooves number (number of costal grooves between the fore- and hindlimbs, excluding axillary and inguinal grooves, following Misawa, 1989; counted separately for left and right body sides); VTN—vomerine teeth number (number of plato-vomerine teeth; counted separately for left and right platovomerine tooth series).

Coloration characters and their states

1. Dorsal ground color of trunk and head (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange). 2. Dorsal marking of trunk (0: absent; 1: small round or oval spots (size ~ SVL/40-SVL/20); 2: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5)). 3. Light dorsal band (0: absent; 1: indistinct with no clear borders; 2: distinct with unclear borders, consisting of spots and variegations; 3: distinct broad band with clearly defined borders; 4: distinct discontinuous band with broken borders). 4. Dark dorsomedial stripe (0: absent; 1: present, continuous; 2: present, discontinuous). 5. Color of dorsal marking of trunk (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange). 6. Dorsal ground color of tail (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange). 7. Dorsal marking of tail (0: absent; 1: small round or oval spots (size ~ SVL/40-SVL/20); 2: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5)). 8. Light dorsal band on the tail (0: absent; 1: indistinct with no clear borders; 2: distinct with unclear borders, consisting of spots and variegations; 3: distinct broad band with clearly defined borders; 4: distinct discontinuous band with broken borders). 9. Color of dorsal marking of tail (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange). 10. Markings on dorsal and lateral surface of head (0: absent; 1: dots, or small round or oval spots (size ~ SVL/40-SVL/20); 2: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5); 4: large light confluent spots and bars (size ~ SVL/20-SVL/5)). 11. Color of head markings (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange). 12. Lateral ground color of trunk (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange; 6: plumbeous; grayish; off-white or whitish). 13. Markings on lateral surface of trunk (0: absent; 1: small dots (size < SVL/30); 2: small round or oval spots (size ~ SVL/30-SVL/20); 3: small vermiculations and confluent spots (size ~ SVL/40-SVL/20); 4: large dark variegations and spots (size ~ SVL/20-SVL/5); 5: large light confluent spots and bars (size ~ SVL/20-SVL/5)). 14. Color of lateral trunk markings (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange; 7: bluish, whitish or light-gray). 15. Lateral ground color of tail (0: black or dark-brown; 1: reddish-brown; 2: gray-brown; 3: ochre or yellow-brown; 4: golden, yellowish or pinkish; 5: bright red or orange; 6: plumbeous; grayish; off-white or whitish). 16. Markings on lateral surface of tail (0: absent; 1: dots, small round or oval spots (size ~ SVL/30-SVL/20); 2: small vermiculations and

confluent spots (size ~ SVL/40-SVL/20); 3: large dark variegations and spots (size ~ SVL/20-SVL/5); 5: large light confluent spots and bars (size ~ SVL/20-SVL/5); 6: continuous lines and variegations). 17. Color of lateral tail markings (0: absent markings; 1: black or dark-brown; 2: reddish-brown; 3: gray-brown; 4: ochre or yellow-brown; 5: golden, yellowish or pinkish; 6: bright red or orange; 7: bluish, whitish or light-gray). 18. Ventral ground color of trunk and head (0: dark-gray; 1: gray, plumbeous-gray; 2: brownish; 3: light reddish-purple). 19. Ventral markings on trunk and head (0: absent or faintly spotted; 2: small spots and vermiculations (size ~ SVL/40-SVL/20); 3: large variegations and spots (size ~ SVL/20-SVL/5)). 20. Color of ventral markings on trunk and head (0: absent markings; 1: black; 2: white or bluish; 3: yellowish or ochre; 4: reddish). 21. Ventral ground color of tail (0: dark-gray; 1: gray, plumbeous-gray; 2: brownish; 3: light reddish-purple; 4: reddish, orange or yellow). 22. Ventral markings on tail (0: absent or faintly spotted; 2: small spots and vermiculations (size ~ SVL/40-SVL/20); 3: large variegations and spots (size ~ SVL/20-SVL/5)). 23. Color of ventral markings on tail (0: absent markings; 1: black; 2: white or bluish; 3: yellowish or ochre; 4: reddish).