学位論文　（要約）

MOLECULAR PHYLOGENETIC STUDIES ON JAPANESE CLAUSILIID LAND SNAILS

（日本産キセルガイ科の分子系統学的研究）

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第2章以外については、5年以内に雑誌等で刊行予定のため、非公開。

第2章の内容は、平成29年7月 Zoological Journal of the Linnean Society誌 181巻 795〜845頁「Molecular phylogeny, frequent parallel evolution and new system of Japanese clausiliid land snails (Gastropoda: Stylommatophora)」において公表済みである。（Min Wang, Rei Ueshimaと共著）

The content of Chapter 2 was already published in Zoological Journal of the Linnean Society Vol. 181, pages 795–845 “Molecular phylogeny, frequent parallel evolution and new system of Japanese clausiliid land snails (Gastropoda: Stylommatophora)” in July 2017, in collaboration with co-authors Min Wang and Rei Ueshima.

Chapter 2

Molecular phylogeny, frequent parallel evolution and new system of Japanese clausiliid land snails (Gastropoda: Stylommatophora)

Introduction

Clausiliidae is one of the most speciose families in the Japanese land snail fauna with more than 200 nominal endemic species and subspecies being recognized (Azuma, 1982; Minato, 1994). Clausiliidae occurs throughout the Japanese archipelago, ranging from Yonaguni Island to southern Hokkaido, and is found in various habitats such as leaf litter, tree trunks, and limestone areas. Clausiliidae is characterized and distinguished from other land snail family by having very complex structure inside the shell (Nordsieck, 2007). The complex structure, called clausilial apparatus (CA), is comprised of many folds and a clausilium which is a flexible door-like structure. CA morphology has long been regarded as the most important taxonomic characters for clausiliids, because the morphology is highly variable among taxa (Nordsieck, 2007).

The taxonomy of Japanese Clausiliidae has been based heavily on the CA morphology. Numbers of genera or subgenera of Japanese clausiliids were named based on some differences in the CA morphology. Although as many as 39 genera and subgenera have been proposed for Japanese taxa and all traditional systems of Japanese taxa are based on almost the same morphological characters, the generic classification is problematic, with the definition of each genus and the hierarchical ranking of subgenera being discordant among authors. For example, *Hemizaptyx takarai* (Kuroda, 1960) was initially placed in *Zaptyx* Pilsbry, 1900 and then transferred to *Tyrannozaptyx* Käufel, 1930 by Azuma (1982), then to *Hemizaptyx* Pilsbry, 1905 by Minato (1994), and finally placed in *Hemiphaedusa* Boettger, 1877 by Nordsieck (1998) who regarded *Hemizaptyx* as a subgenus of *Hemiphaedusa* (see Table 2.1 for many other examples of frequent changes of generic placement).

Despite this taxonomic confusion, no comprehensive molecular phylogenetic studies have been undertaken. In this chapter, I performed a molecular phylogenetic analysis on Japanese clausiliids based on nuclear and mitochondrial DNA (mtDNA) sequences. This is the first comprehensive molecular study on Japanese clausiliids which covers

198 nominal taxa endemic to Japan and encompasses all 39 genera and subgenera proposed for Japanese taxa. A new system of Japanese and Taiwanese clausiliids is also proposed based on the molecular phylogeny.

Materials and methods

Taxon sampling

In total, 303 clausiliid specimens of the subfamily Phaedusinae were used for the present study. The examined samples include 198 nominal taxa endemic to Japan (including subspecies and synonymized taxa), 14 taxa from Taiwan, 15 taxa from China, and eight taxa from other areas of Southeast Asia (Table 2.2). The samples encompass all 39 generic taxa proposed for Japanese clausiliids and all Japanese species-level taxa except 16 taxa that are endangered or endemic to a difficult to access locality. In this study, snails of each species or subspecies were collected from one to seven localities. For species with wide distribution ranges and/or with notable geographic variations, samples were collected from more localities than for narrowly endemic species. My taxon sampling effort was intended to cover not only as many valid taxa as possible, but also as many synonymized taxa as possible.

DNA extraction, PCR, and sequencing

Land snails were collected in the field and killed by immersing in hot water (80 ºC). Soft parts were extracted from the shell by water injection into a small hole that was opened near the apex with a fine needle. Soft parts were stored at –80 ºC until DNA extraction. Total DNA was extracted from foot tissue using the High Pure PCR Template Preparation Kit (Roche Diagnostic) according to the manufacturer’s protocol, or by the method described by Shimizu & Ueshima (2000).

For all samples, nuclear ribosomal *internal transcribed spacer* (*ITS*) *1* and *2* regions and a mitochondrial DNA segment encoding 3’-partial sequences of the *NADH dehydrogenase subunit 1* (*ND1*) gene, complete sequences of the *NADH-ubiquinone oxidoreductase chain 4L* (*ND4L*) gene, and 5’-partial sequences of the *Cytochrome b* (*Cytb*) gene, were amplified by polymerase chain reaction (PCR) using the primer pairs 18S-1666/28S-700R and ND1-2N/Cb268R, respectively (Table 2.3). Amplifications were performed in 20 µl volumes containing 10 µL Ampdirect Plus (Shimadzu) (including buffer and dNTPs), 0.5 U NovaTaq Hot Start DNA polymerase (Novagen), 0.5 μM of each primer, and approximately 2 ng template DNA under the following reaction conditions: initial denaturing at 94 °C for 5 min, 40 cycles at 94 °C for 30 s, annealing at 50 °C for 30 s (for *ITS*) or at 40 °C for 1 min (for mtDNA), extension at 72 °C for 2 min, and final extension at 72 °C for 5 min. 5 μL of the PCR products were incubated with 1 unit each of exonuclease I and shrimp alkaline phosphatase (USB Corp.) at 37 °C for 15 min and 98 °C for 5 min to degrade excess primers and nucleotides, and then directly sequenced using BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on an ABI 3130xl genetic analyzer (Applied Biosystems). Additional primers used for the sequencing (18S-1676, ls5. 8f, ls5.8r, ND1-3N, Cb264R, Cb366F) are also shown in Table 2.3.

Sequence alignment and phylogenetic analysis

Sequences were edited using CLC Main Workbench 6.7 (CLC bio). *ITS* sequences were initially aligned with MAFFT version 7 online server (http://mafft.cbrc.jp/alignment/server/) using default parameters and were refined manually in Se-Al v2.0a11 (Rambaut, 2002) to increase positional homology. Ambiguous regions in the *ITS* alignment were excluded using Gblocks v0.91b (Castresana, 2000) with the following settings: minimum number for a conserved position = 50%, minimum number of sequences for a flanking position = 85%, maximum number of contiguous non-conserved positions = 8, minimum length of a block = 2, and allowed gap positions = with half. mtDNA sequences were aligned manually for each gene (*ND1*, *ND4L*, *Cytb*) in Se-Al v2.0a11 guided by translated amino acid sequences, and the unambiguously alignable regions were used for phylogenetic analysis.

Three datasets were created for phylogenetic analysis: 884 bp of concatenated sequences of nuclear *ITS1* (519 bp) and *ITS2* (365 bp) regions, 1257 bp of concatenated mitochondrial sequences of the *ND1* (225 bp), *ND4L* (216 bp), and *Cytb* (816 bp) genes, and the concatenated sequences of all the nuclear and mitochondrial regions (2141 bp). These datasets were partitioned according to the genes and codon positions. Before conducting the model-based phylogenetic analysis, the best-fit model of nucleotide substitution was identified for each gene partition using PartitionFinder v1.1.1 (Lanfear et al., 2012) under the Bayesian Information Criterion (BIC). PartitionFinder selected

GTR+I+Γ model for *ITS1*, 1st codon positions of *ND1*, *ND4L,* and *Cytb*, and 2nd codon positions of *Cytb*; GTR+Γ model for 2nd codon positions of *ND1* and *ND4L*, and 3rd codon position of *ND1*; HKY+I+Γ model for 3rd codon positions of *Cytb*; HKY+Γ model for 3rd codon position of *ND4L*; and SYM+Γ model for *ITS2*. These selected evolutionary models were applied in the partitioned Bayesian inference.

Maximum Likelihood (ML) analyses were carried out using raxmlGUI v1.3.1 (Silvestro & Michalak, 2012), which includes RAxML v.8.0.2 (Stamatakis, 2014). I used PartitionFinder to estimate the best fitted models that are available in RAxML software according to the Akaike Information Criterion. PartitionFinder selected the GTR+I+ Γ model for nine out of eleven partitions. As RAxML does not permit the application of different models to different partitions, I applied the GTR+I+ Γ model to all partitions. Bootstrap support values were obtained from 1000 replicates using the rapid bootstrap algorithm. Bayesian inference using Markov chain Monte Carlo (MCMC) was implemented in MrBayes 3.2.5 (Ronquist et al., 2012) with substitution models selected by PartitionFinder. Two replicate runs with four independent chains were run, sampling every 100 generations, until the average standard deviation of split frequencies (ASDSF) fell below 0.01 (using the stoprule option), at which point chains were considered to have reached stationarity. The stationarity and convergence of chains were also checked using Tracer v1.6 (Rambaut et al., 2014) by plotting the log-likelihood values versus generation number. In this program, I ensured that the effective sample sizes for all parameters were >200 in all analyses, indicating the Markov chain had reached stationarity. The first 25% of the total samples were discarded as burn-in, and the remaining trees were used to generate a 50% majority rule consensus tree and calculate the posterior probabilities (PP).

In order to determine an appropriate outgroup for Japanese clausiliids belonging to the subfamily Phaedusinae, I initially carried out a preliminary ML phylogenetic analysis of *ND1*, *ND4L*, and *Cytb* genes using *Albinaria coerulea* (Deshayes, 1835) (GenBank ID X833901), a member of the different subfamily Alopiinae, as the outgroup. The methods of phylogenetic reconstution is same as those described above. The result of this preliminary analysis strongly suggests that *Synprosphyma* Wagner, 1920 is the most basal offshoot within the subfamily Phaedusinae (Fig. 2.1). This result is concordant with the most recent classification of the subfamily Phaedusinae based on anatomical differences in the bursa copulatrix (Nordsieck, 2007). I therefore used *Synprosphyma* species as outgroups for the phylogenetic analysis of Japanese clausiliids.

Among the generic/subgeneric classifications of Japanese clausiliids that differ substantially among taxonomists (see Table 2.1), I used the latest generic classification of Nordsieck (2007) as a working hypothesis for the phylogenetic analysis. All subgenera were treated equally as distinct generic taxa.

Character mapping

To test the phylogenetic significance of taxonomic characters that have been used in the traditional systems, 14 characters were selected as taxonomically important characters, due to them being used as key characters for supra-specific classification of Japanese clausiliids in Azuma (1982), Minato (1988), Nordsieck (1998), and Schileyko (2000), and were mapped onto the molecular phylogenetic tree obtained by this study. Characters with unique character states that are not shared by more than two taxa were excluded from the analysis. The characters used for the analysis include the following 12 morphological characters (11 shell characters and one anatomical character), one reproductive character, and one ecological character. Character 1 is the morphology of the superior lamella with two character states (developed or reduced). Character 2 is the morphology of the inferior lamella with two character states (spirally ascending or not). Character 3 is the morphology of the clausilium plate with three character states (wide, narrow, or with a distinctive projection such as a spine or a transverse plate). Character 4 is the location of the plicae and clausilium with two character states (lateral or ventral to ventro-lateral). Character 5 is the morphology of the lunella with three character states (present and axial, present and oblique, or absent). Character 6 is the morphology of the upper palatal plica in relation to the lunella with five character states (present and without a lunella, present and attached to the lunella, present and fused with the lunella, present and separated from the lunella, or absent). Character 7 is the morphology of the upper palatal plica with three character states (short, long and/or interrupted, or absent). Character 8 is the morphology of the middle palatal plica with three character states (present and developed, weakly developed and coalesced to a lunella-like structure, or absent). Character 9 is the morphology of the lower palatal plica in relation to the lunella with five character states (present and without a lunella, present and attached to the lunella, present and fused with the lunella, present and separated from the lunella, or absent). Character 10 is the presence or absence of the sutural plica with two character states (present or absent). Character 11 is the morphology of the shell apex with three character states (pointed, rounded, or decollated). Character 12 is the morphology of the diverticulum of the bursa copulatrix with two character states (developed or reduced). Character 13 is the mode of reproduction with two character states (oviparous or ovoviviparous). Character 14 is the type of habitat with two character states (terrestrial or arboreal). The character state of a character is usually fixed in each taxon. In a few exceptional cases where a character shows some intra-taxon variation, the character state was coded as polymorphic in the species or subspecies.

Results

Phylogenetic relationships among Japanese and Taiwanese clausiliids

Phylogenetic trees inferred from nuclear *ITS* and mtDNA are shown in Figs 2.2–2.5. The nuclear tree provides better resolution in basal branches and the mtDNA tree provides better resolution in terminal branches, reflecting the faster substitution rate of metazoan mtDNA over nuclear DNA (Moritz, Dowling, & Brown, 1987a; Ballard & Whitlock, 2004). Phylogenetic relationships among Japanese clausiliids were largely concordant between nuclear and mitochondrial trees except for two species, *Stereophaedusa stereoma* (Pilsbry, 1901) and *Mesophaedusa cymatodes* (Pilsbry, 1905) (Figs 2.3 and 2.4). The *ITS* and mitochondrial sequences of the remaining species were concatenated and used for subsequent phylogenetic analysis of the combined dataset. In the combined analysis, the mtDNA sequences of *S. stereoma* and *M. cymatodes* were excluded because incongruencies in phylogenetic positions between the nuclear and mitochondrial trees strongly suggest inter-specific mitochondrial introgressions for these species (see Discussion below). The phylogenetic tree based on the combined dataset (nuclear + mtDNA) is shown in Figs 2.2 and 2.5. Tree topologies obtained by the ML and Bayesian analyses were almost identical. In comparison to the trees based on each dataset alone, the resolution of the tree topology was improved at both terminal and basal branches in the combined tree. Therefore, I will discuss the phylogenetic relationships among Japanese clausiliids based on the combined tree.

All Taiwanese taxa except *Formosana* Boettger, 1877 and all Japanese taxa except *Mundiphaedusa miyoshii* Kuroda & Minato, 1979 constituted a large clade α, indicating their close phylogenetic affinity relative to foreign taxa. However, the Japanese species

M. miyoshii fell outside clade α and was recovered as a sister group to two Chinese species, *Selenophaedusa bavayi* (Nordsieck, 2002) and *Hemizaptyx minuta* (Yen, 1939). This is one of the most surprising findings of this study. *M. miyoshii* is distributed in a narrow area of Northern Honshu and has morphological features typical of the Japanese endemic genus *Mundiphaedusa* Minato, 1979. Despite the close morphological similarity to the other *Mundiphaedusa* species included within clade α, *M. miyoshii* was found to be unrelated to any other Japanese taxa.

Within the large clade α, Japanese and Taiwanese taxa were divided into seven clades (A–G). The monophyly of each clade is strongly supported by high statistical values. In addition, members of some of these clades share unique sets of deletions and fixed substitutions in a hyper variable region of *ITS2* (Fig. 2.6). Although the sequences of this hyper variable region was not included in the phylogenetic analysis, the sharing of such unique deletions and substitutions provide qualitative molecular markers that also support the monophyly of these clades.

Within the large clade α, clades A, B, and C constitute a well-supported clade. Clades D, E, and F form another well-supported clade in which F is a sister to the clade D+E. The phylogenetic relationships among and within these clades were substantially discordant with current morphology-based taxonomy. The following genera were dispersed across different clades and thus demonstrated to be polyphyletic: *Mundiphaedusa*, *Hemizaptyx*, *Mesophaedusa* Ehrmann, 1929, *Pseudophaedusa* Tomiyama, 1984, and *Pliciphaedusa* Nordsieck, 1998. Each of the other genera was contained within a certain clade, but most of these genera were recovered as non-monophyletic within each clade.

Clade A comprises Japanese taxa from Eastern Honshu to the Ryukyu Islands. Members of this clade were referred to the following generic taxa in Nordsieck (2007): *Hemiphaedusa*, *Hemizaptyx*, *Luchuphaedusa* Pilsbry, 1901, *Mesophaedusa*, *Nesiophaedusa* Pilsbry, 1905, *Phaedusa* A. Adams, 1855, *Pliciphaedusa*, *Pseudophaedusa*, and *Stereophaedusa* Boettger, 1877.

Within clade A, I recognized eight well-supported subclades, each comprising more than one taxon (subclades A1–8 in Fig. 2.5). Phylogenetic relationships among these subclades are poorly resolved with the exception of the sister group relationship between subclades A4 and A5. All generic taxa within the clade were found to be polyphyletic or paraphyletic. For example, *Stereophaedusa* species were recovered as three distinct lineages (subclades A1, A2, and a terminal branch of subclade A4). Within subclade A4, *Mesophaedusa* species were paraphyletic to *Stereophaedusa* species. *Luchuphaedusa* species were also recovered as diphyletic lineages with *Luchuphaedusa* species of one lineage constituting a subclade A5 together with *Nesiophaedusa* species and *Luchuphaedusa* species of the other lineage constituting a different subclade A7. Another unexpected finding is the placement of *Hemizaptyx caloptyx* (Pilsbry, 1902) within this clade. Although this species has been regarded as a member of *Hemizaptyx*, all other species of *Hemizaptyx* were placed in a different clade D. A similar example is the unexpected placement of the two *Pseudophaedusa* species, *P. neniopsis* (Pilsbry, 1902) and *P. tokunoshimaensis* (Minato, 1997). Although these two *Pseudophaedusa* species appear as two independent lineages within clade A, all other "congeneric" species were placed in a different clade F.

Clade B comprises Japanese endemic taxa from the main islands of Japan (Hokkaido, Honshu, Shikoku, and Kyushu). Members of the clade were referred to the following generic taxa in Nordsieck (2007): *Aulacophaedusa* Azuma, 1982, *Hemiphaedusa*, *Megalophaedusa* Boettger, 1877, *Mesophaedusa*, *Mundiphaedusa*, *Mesozaptyx* Kuroda, 1963 (= *Neophaedusa* Kuroda & Minato, 1975), *Pauciphaedusa* Minato & Habe, 1983, *Pinguiphaedusa* Azuma, 1982, *Placeophaedusa* Minato, 1994, *Pliciphaedusa*, and *Tyrannophaedusa* Pilsbry, 1900. Within this clade, I recognized nine well-supported subclades that include more than one taxon (subclades B1–9 in Fig. 2.5). Phylogenetic relationships among these subclades are poorly resolved with the exception of the sister group relationships between B1 and B2 and between B3 and B1+B2.

Of the traditional generic taxa included in this clade, only *Aulacophaedusa* and *Placeophaedusa* were recovered as monophyletic. All other genera were recovered as polyphyletic or paraphyletic. A notable example of polyphyly is *Mundiphaedusa*. Even with the exclusion of the solitary *M. miyoshii*, which was placed outside this clade, *Mundiphaedusa* was split into five distinct lineages within clade B.

Another example of polyphyly is *Tyrannophaedusa*. Although most *Tyrannophaedusa* species constitute a large subclade B4, some *Tyrannophaedusa* species were recovered as distinct subclades B2 and B5.

It is also notable that *Mesophaedusa ikenoi* Minato, 1980 is included in this clade, while all other congeners of *Mesophaedusa* were placed in the different clade A.

Clade C is a small clade comprising only two Japanese species: *Tosaphaedusa* *cincticollis* (Ehrmann, 1900) and *Mundiphaedusa akiratadai* (Minato, 1978). Both species are endemic to Shikoku. Although monophyly of the clade is strongly supported, the members differ substantially in morphology, i.e. in shell shape, the sculpture outside the aperture, and the location and morphology of the plicae.

Clade D mainly comprises species from Southern Japan (Kyushu and the Ryukyu Islands) and Taiwan, but also includes a few species from Honshu. The members of this clade share a strongly developed lunella. However, except for this synapomorphy, the morphology of plicae is highly variable within this clade. It is also noted that most of the members are zaptychoid taxa (small phaedusine clausiliids resembling *Zaptyx*) and that all species with sutural plicae are included in this clade exclusively. Within this clade, I recognized eight well-supported subclades that include more than one taxon (subclades D1–8 in Fig. 2.5). Subclades D1, D2, and D3 constitute a well-supported clade together with *Hemizaptyx* sp. cf. *pseudosheridani*.

The species included in clade D were referred to the following generic taxa in Nordsieck (2007): *Diceratoptyx* Pilsbry, 1905, *Hemiphaedusa*, *Hemizaptyx*, *Heterozaptyx* Pilsbry, 1906, *Metazaptyx* Pilsbry, 1905, *Oligozaptyx* Pilsbry, 1905, *Parazaptyx* Pilsbry, 1905, *Pulchraptyx* Minato, 1981, *Selenoptyx* Pilsbry, 1908, *Stereozaptyx* Pilsbry, 1905, *Thaumatoptyx* Pilsbry, 1908, *Tyrannozaptyx*, *Zaptychopsis* Ehrmann, 1927, and *Zaptyx*. Among these genera, *Pulchraptyx*, *Parazaptyx*, *Oligozaptyx*, and *Zaptychopsis* are monotypic genera, and *Heterozaptyx* is represented by a single species in this study. When excluding such genera, only *Selenoptyx*, *Stereozaptyx*, and *Tyrannozaptyx* were recovered as monophyletic lineages with high statistic supports. *Zaptyx* was found to be paraphyletic with respect to *Oligozaptyx* and *Metazaptyx*. *Hemizaptyx* was demonstrated to be a heterogeneous assemblage comprising five distinct lineages within this clade and an isolated lineage in the different clade A. It is remarkable that Taiwanese *Hemizaptyx* species are included in this clade, while a Chinese *Hemizaptyx* species, *Hemizaptyx minuta*, is distantly related to these species.

Clade E comprises Japanese species that have been referred to *Euphaedusa* Boettger, 1877 and *Tauphaedusa* Nordsieck, 2003, which was treated as a subgenus of the former in Nordsieck (2007). Members of this clade include species from the main islands of Japan (including Hokkaido) and the Southern Ryukyus.

Clade F comprises mainly Japanese endemic species, but also includes a Taiwanese species. All members of this clade are arboreal and ovoviviparous species with a spirally ascending inferior lamella. Most of the members have a characteristic shell colour with subaxial flammulations and exhibit a tendency of reduction of the superior lamella and the diverticulum of the bursa copulatrix. In this clade, I recognized three well-supported subclades, each comprising more than one taxon (subclade F1–3). Inter-relationships among these subclades are not resolved. It is remarkable that members of subclade F1 show extensive diversity in the morphology of the lamella and genitalia. The members of clade F were assigned to the following generic taxa in Nordsieck (2007): *Reinia* Kobelt, 1876, *Parareinia* Nordsieck, 1998, *Pictophaedusa* Azuma, 1982, *Phaedusa*, *Pseudophaedusa*, and *Proreinia* Thiele, 1931. Within clade F, none of these “generic” taxa were monophyletic except for the monotypic *Parareinia*. The very close phylogenetic affinity between *Reinia variegata* (A. Adams, 1868) and *R. ashizuriensis* (Azuma, 1968) is surprising. Although these have often been classified in different genera or subgenera (Kuroda, 1963; Azuma, 1982; Minato, 1994; Nordsieck, 1997), they constitute a single lineage with almost no genetic divergence.

Clade G is represented by a single species endemic to Taiwan, *Pseudophaedusa horikawai* (Kuroda, 1941). Although the species has been classified in *Stereophaedusa* or *Pseudophaedusa* (Chang & Maeda, 1984; Nordsieck, 1997; Hsieh, Wu, & Tsai, 2013), it was found to represent an isolated lineage unrelated to any other Taiwanese or Japanese taxa.

Some Japanese clausiliids have been assigned to genera that were proposed for foreign species, such as *Phaedusa* proposed for an Indonesian species, *Hemiphaedusa* for a Chinese species, and *Euphaedusa* for a Chinese species (Kuroda, 1963; Minato, 1994; Nordsieck, 1998; Schileyko, 2000; Nordsieck, 2007). However, results of the present study do not support such classifications. Although the Japanese taxa within clade E have been assigned to *Euphaedusa* (Kuroda, 1963; Azuma, 1982; Minato, 1994; Nordsieck, 1998, 2007), they were found to be only distantly related to *E. aculus* (Benson, 1842) [the senior synonym of *Euphaedusa shanghaiensis* (Pfeiffer, 1859), the type species of the genus]. In cases of *Phaedusa* and *Hemiphaedusa* [*sensu lato* in Nordsieck (2007)], “congeneric” species from areas close to the localities of the type species were found to be unrelated to the Japanese taxa. In addition, I found notable morphological differences between such Japanese taxa and the type species of these genera. For example, true *Phaedusa* species from Southeast Asia, including the type species, are characterized by having wavy ribs on the last whorl (Loosjes, 1953; Schileyko, 2000), but such a character state is never found in Japanese taxa. *Hemiphaedusa pluviatilis* (Benson, 1842), the type species of the genus, is characterized by a shell with a basal keel (Nordsieck, 2001), but none of the Japanese "*Hemiphaedusa*" species has a basal keel. Accordingly, the traditional systems under which some Japanese clausiliids have been assigned to foreign genera are no longer supported either by molecular phylogeny or by morphology.

Frequent parallel evolution of taxonomically important characters

In Fig. 2.7, the 14 taxonomic characters that have been used in traditional systems are mapped onto the molecular phylogeny. As is evident from the mosaic pattern of the character state distribution, homoplasy occurs frequently and repeatedly across different clades and within a clade in all the taxonomically important characters. Extensive homoplasies in the CA morphology (characters 1–10) are surprising, because the traditional systems have depended heavily on these characters. For example, a spirally ascending inferior lamella occurs in at least seven lineages within clade A, at least four lineages within clade D, at least two lineages within clade E, and the common ancestor of clade F. There is no character that is completely congruent with the phylogeny. Although some characters seem partially concordant with the molecular phylogeny, all characters show homoplasies and/or reversals. I could not find any tendency for a certain character to be less homoplastic than other characters. It is also remarkable that homoplasy occurs not only in a character, but also in a combination of different characters. A unique set of six character states that are characteristic to traditional *Luchuphaedusa* occurred in two lineages independently within clade A. Such parallel evolution of the same or very similar set of character states was recognized in various character combinations.

Another notable finding from the character mapping is that radical changes involving more than three characters occasionally occur within some closely related species. Notable examples are extensive morphological divergence within *Thaumatoptyx* species (clade D) and that within a subclade comprising of *Pliciphaedusa hemileuca* (Pilsbry, 1909) and *Pseudophaedusa neniopsis* (clade A). Sporadic divergence of two or three characters within sister taxa are more common.

The results of the character mapping analysis of Japanese clausiliids can be summarized in the following points: (1) similarities in morphological characters do not necessarily reflect a close phylogenetic affinity, due to frequent parallel evolution; (2) divergence in taxonomically important characters is not necessarily correlated with phylogenetic divergence, due to the differential rate of morphological, reproductive, and ecological changes among taxa; (3) some characters can occasionally, but not always, change in concert.

Congruence between molecular phylogeny and biogeography

Despite the substantial discordance between the molecular phylogeny and the morphology in Japanese and Taiwanese clausiliids, many of the tree topologies recovered by the molecular phylogeny were concordant with biogeography.

Notable examples are found in clade D. Subclade D1 exclusively comprises Taiwanese zaptychoid taxa that have been classified in two genera. Likewise, subclade D3 exclusively comprises taxa endemic to the Southern Ryukyus that have been classified in two genera. These are cases where locally endemic species constitute their own clades despite morphological divergence. More importantly, these zaptychoid subclades form a well-supported clade together with Taiwanese *Hemizaptyx* species. The phylogeographical affinity of all these taxa is reasonable because Taiwan and the Southern Ryukyus were land-connected until the Kuroshio sea current entered into the Yonaguni Gap at about 1.5 Ma (Osozawa et al., 2012). Another example of close phylogenetic affinity being reflected by biogeography is *Stereophaedusa*. Excluding a *Stereophaedusa* lineage (subclade A1), whose members were previously classified in *Breviphaedusa* Azuma, 1982 by Azuma (1982) and Minato (1994), there are two distinct lineages in the remaining *Stereophaedusa* species. One lineage (subclade A2) is exclusively represented by *Stereophaedusa* taxa endemic to the Ryukyu Islands. Meanwhile, the other *Stereophaedusa* lineage from the main islands of Japan constitutes a different subclade A4 together with *Mesophaedusa* species that are also distributed in the same area. A similar example is found in smaller *Mundiphaedusa* species from Western Japan. *Mundiphaedusa* species endemic to Kyushu constitute a subclade within clade B together with “*Mesozaptyx*” *ishikawai* Kuroda & Minato, 1975 which is also endemic to Kyushu. Meanwhile, a *Mundiphaedusa* species endemic to Shikoku constitutes a distinct clade C together with *Tosaphaedusa cincticollis*, which is also endemic to Shikoku.

The present study revealed non-monophyly of many traditional genera. When a traditional genus is divided into more than one distinct lineage, some of the lineages reflect the geographical distribution. For example, *Luchuphaedusa* species were divided into two distinct lineages. The distribution of one lineage (subclade A5) is restricted to the central Ryukyus, while the other lineage (subclade A7) is distributed in certain more northward reaching islands of Kyushu. A similar pattern is also found in the polyphyletic *Mundiphaedusa*. Three major lineages of *Mundiphaedusa* species, namely, subclades B3, B7, and B8, are mainly represented by taxa from Eastern, Central, and Western Honshu, respectively.

Furthermore, there are many examples where, within a subclade, species from the same area or neighboring areas are more closely related to each other than species from distant areas. These include certain species groups or species pairs within subclades A1, A4, A7, B1, B3, B4, B8, D3, D8, and F3.

Proposal of new generic and subgeneric classification of Japanese clausiliids and the related Taiwanese taxa

The present study revealed that the traditional morphology-based classifications of Japanese and Taiwanese clausiliids do not reflect the phylogenetic relationships. I therefore propose a new system of Japanese and the related Taiwanese clausiliids based primarily on molecular phylogeny. In the new system, I propose to rank the seven well-supported clades within the large clade α and the independent lineage of *Mundiphaedusa miyoshii* as genera (Fig. 2.8), and to rank some subclades within these clades as subgenera (Fig. 2.9). Generic and subgeneric names are determined by the oldest generic taxon whose type species is included within each clade or subclade. The clades A, B, C, D, E, and F are therefore assigned to the genus *Stereophaedusa*, *Tosaphaedusa* Ehrmann, 1929, *Megalophaedusa*, *Reinia*, *Tauphaedusa*, and *Zaptyx*, respectively. New genera *Solitariphaedusa* and *Changphaedusa* are proposed for *Mundiphaedusa miyoshii* and *Pseudophaedusa horikawai*, respectively. Well-supported subclades within a genus whose members share some morphological similarities are treated as subgenera. Some species representing unresolved lineages within a genus are provisionally placed in: *Genus* (*sensu lato*), for example, as in *Stereophaedusa* (*sensu lato*). Needless to say, this is a provisional taxonomic treatment until the phylogenetic positions within each genus are fully resolved by future molecular phylogenetic studies.

Such taxa may represent new subgenera of their own or may be included in a subgenus listed below when their phylogenetic positions are determined.

A total of 26 subgenera are recognized in my present system: subgenera *Breviphaedusa*, *Luchuphaedusa*, *Mesophaedusa*, *Oophaedusa*, *Pliciphaedusa*, and *Stereophaedusa*, in the genus *Stereophaedusa*; subgenera *Aulacophaedusa*, *Dimphaedusa* (subgen. nov.), *Megalophaedusa*, *Neophaedusa*, *Pauciphaedusa*, *Pinguiphaedusa*, *Tyrannophaedusa*, *Tyrannophaedusoides* (subgen. nov.), *Ventriphaedusa* Azuma, 1982, and *Vitriphaedusa* Azuma, 1982 in the genus *Megalophaedusa*; subgenera, *Hemizaptyx*, *Parazaptyx*, *Pulchraptyx*, *Selenoptyx*, *Stereozaptyx*, *Taiwanphaedusa* (subgen. nov.), *Thaumatoptyx*, *Tyrannozaptyx*, *Zaptychopsis*, and *Zaptyx* in the genus *Zaptyx*.

Although the new system seems partially concordant with the traditional ones, the diagnosis, the hierarchic ranking, and the taxonomic composition of each genus or subgenus differs largely from the traditional systems (see below). Due to the frequent parallel evolution seen in all taxonomic characters handled here, not all of the newly defined generic taxa can be diagnosed by morphological characters alone. Even so, most of the generic taxa can be diagnosed by a combination of morphological, reproductive, ecological, and molecular characters and geographic distribution. In two cases, newly defined genera can only be diagnosed by molecular characters.

Systematics

Note: Species with asterisks are provisionally included in a genus or a subgenus based on morphology and distribution.

Family Clausiliidae Gray, 1855
Subfamily Phaedusinae Wagner, 1922
Genus *Stereophaedusa* Boettger, 1877
(= Clade A)

Type species: Clausilia valida Pfeiffer, 1850

Synonyms: Breviphaedusa Azuma, 1982; *Luchuphaedusa* Pilsbry, 1901; *Mesophaedusa* Ehrmann, 1929; *Nesiophaedusa* Pilsbry, 1905; *Oophaedusa* Pilsbry, 1905; *Pliciphaedusa* Nordsieck, 1998; *Vastina* Ehrmann, 1929.

Diagnosis: Although *Stereophaedusa* redefined here cannot be diagnosed by morphology, its monophyly is strongly supported by molecular phylogeny. The presence of unique deletions and substitutions in the hyper variable region of *ITS2* (Fig. 2.6) is a molecular diagnostic character of the genus.

Morphology: Shell small to large. Apex usually pointed and preserved, rarely decollated in adult. Plicae and clausilium located laterally to ventrally. Superior lamella always developed. Inferior lamella variable, spirally or obliquely ascending and appearing at the aperture, or almost straightly ascending and receding within the aperture. Lunella present or absent. Principal plica developed. Middle palatal plica(e) present or absent, rarely coalesced into a lunella. Clausilium wide or narrow. Diverticulum of bursa copulatrix developed.

Reproduction: Oviparous or ovoviviparous.

Ecology: Mainly terrestrial, occasionally arboreal.

Distribution: Endemic to Japan (Honshu, Shikoku, Kyushu, and Ryukyu Islands).

Remarks: Stereophaedusa is redefined here to include a wide range of species that show extensive morphological diversity. In the newly defined genus, I recognize following subgenera: *Stereophaedusa*, *Breviphaedusa*, *Luchuphaedusa*, *Mesophaedusa*, *Oophaedusa*, and *Pliciphaedusa*.

Subgenus *Stereophaedusa* Boettger, 1877

(= Subclade A2)

Diagnosis: Shell large. Apical whorls decollated in adult. Inferior lamella spirally ascending, strongly developed and approaching to the superior lamellar near the aperture. Lunella absent. Clausilium wide. Reproduction ovoviviparous. Ecology arboreal. Distribution: endemic to the Ryukyu Islands (Okinawa-shima and Miyako Islands).

Morphology: Plicae and clausilium located laterally. Superior lamella developed. Principal plica developed. Upper and lower palatal plicae present. Middle palatal plica absent. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction, ecology, and distribution: As in Diagnosis.

Included taxa: S. (*S.*) *valida fasciata* (Skyes, 1893); *S.* (*S.*) *valida striatella* (Pilsbry, 1901); *S.* (*S.*) *valida valida* (Pfeiffer, 1850).

Remarks: The taxonomic composition of *Stereophaedusa* (*S.*) redefined here differs from those of *Stereophaedusa* (*S.*) of traditional systems by the members being restricted to the arboreal and decollated taxa endemic to the Ryukyu Islands.

Subgenus *Breviphaedusa* Azuma, 1982
(= Subclade A1)

Type species: Clausilia gouldi A. Adams, 1868

Diagnosis; Shell small to medium-sized. Inferior lamella spirally ascending, strongly developed and approaching to the superior lamella near the aperture. Lunella absent. Middle palatal plica(e) usually present, short. Clausilium wide. Reproduction ovoviviparous. Distribution: endemic to Japan (Eastern Honshu, Kyushu, and Northern Ryukyus).

Morphology: Apex pointed. Plicae and clausilium located laterally. Superior lamella developed. Principal plica developed. Upper and lower palatal plicae present. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction and distribution: As in Diagnosis.

Ecology: Terrestrial.

Included taxa: S. (*B.*) *addisoni* (Pilsbry, 1901); **S.* (*B.*) *addisoni plagioptyx* (Pilsbry, 1902); *S.* (*B.*) *gouldi* (A. Adams, 1868); *S.* (*B.*) *jacobiana* (Pilsbry, 1902); *S.* (*B.*) *jacobiella* (Pilsbry, 1909); *Breviphaedusa nugax* (Pilsbry, 1901); *S.* (*B.*) *stereoma* (Pilsbry, 1901); *S.* (*B.*) *tripleuroptyx* (Pilsbry, 1909); *S.* (*B.*) *tryoni* (Pilsbry, 1901); *S.* (*B.*) *tryoni miyakejimana* (Pilsbry, 1905).

Remarks: Nordsieck (1998, 2007) treated *Breviphaedusa* as a synonym of *Stereophaedusa*. However, *Breviphaedusa* is a distinct subgenus because *Breviphaedusa* and *Stereophaedusa* (*S.*) were recovered as distinct lineages within the genus.

Subgenus *Luchuphaedusa* Pilsbry, 1901
(= Subclade A5)

Type species: Clausilia callistochila Pilsbry, 1901

Synonym: Nesiophaedusa Pilsbry, 1905

Diagnosis: Shell medium-sized to large. Plicae and clausilium located ventrally to laterally. Inferior lamella developed, spirally ascending, broadened and/or slightly twisted near the aperture. Lunella present, oblique or vertical, attached to or fused with the lower palatal plica. Upper palatal plica separated from or united with the lunella. Lower palatal plica angled at the junction with lunella. Parietal margin of aperture frequently folded. Clausilium rather wide, with a small process at the baso-columellar edge. Distribution: endemic to the Ryukyu Islands (Okinawa-jima, Amami, and Tokuno-shima Islands).

Morphology: Apex pointed. Superior lamella present. Principal plica developed. Middle palatal plica(e) absent. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: S. (*L.*) *bernardii* (Pfeiffer, 1861); *S.* (*L.*) *callistochila* (Pilsbry, 1901); *S.* (*L.*) *inclyta* (Pilsbry, 1908); *S.* (*L.*) *nesiothauma* (Pilsbry, 1901); *S.* (*L.*) *oshimae degenerata* (Pilsbry, 1905); *S.* (*L.*) *oshimae oshimae* (Pilsbry, 1901).

Remarks: The taxonomic composition of *Luchuphaedusa* redefined here differs from that of *Luchuphaedusa* of traditional systems in the following points: 1) exclusion of *S.* (*Oophaedusa*.) *ophidoon* (Pilsbry, 1905), *S.* (*O.*) *azumai* (Pilsbry, 1905), *S.* (*O.*) *mima* (Pilsbry, 1901), and *S.* (*O.*) *una* (Pilsbry, 1902); and 2) inclusion of *S.* (*L.*) *bernardii* and hence synonymization of *Nesiophaedusa*.

Subgenus *Mesophaedusa* Ehrmann, 1929
(= Subclade A4)

Type species: Clausilia hickonis Boettger, 1877

Synonym: Vastina Ehrmann, 1929

Diagnosis: Shell medium-size to large, rarely small. Inferior lamella developed, variable, spirally ascending and approaching to the superior lamella near the aperture, or obliquely ascending, occasionally thickened near the aperture. Lunella absent. Middle palatal plica(e) present or absent, short to moderately long if present. Clausilium narrow or wide. Reproduction oviparous or ovoviviparous. Distribution: endemic to Japan (Kyushu, Shikoku, and Honshu).

Morphology: Apex pointed. Plicae and clausilium located laterally. Superior lamella developed. Principal plica developed. Upper and lower palatal plicae present. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: **S.* (*M.*) *affinis* (Minato & Tada, 1987); *S.* (*M.*) *aethiops* (Moellendorff 1882); *S.* (*M.*) *costifera* (Kuroda & Taki, 1944); *S.* (*M.*) *elongata* (Minato & Tada, 1979); *S.* (*M.*) *goniopoma* (Pilsbry, 1902); *S.* (*M.*) *hickonis* (Boettger, 1877); *S.* (*M.*) *hickonis fultoni* (Sykes, 1895); **S.* (*M.*) *higomonticola* (Minato & Tada, 1979); *S.* (*M.*) *hiraseana* (Pilsbry, 1901); *S.* (*M.*) *hooyoensis* (Minato & Tada, 1987); *S.* (*M.*) *ijimae* (Ehrmann, 1900); *S.* (*M.*) *interlamellaris* (Martens, 1876); *S.* (*M.*) *japonica* (Crosse, 1871); *S.* (*M.*) *koshikijimana* (Pilsbry, 1905); *S.* (*M.*) *mikawa* (Pilsbry, 1905); *S.* (*M.*) *moriyai* (Kuroda & Taki, 1944); *S.* (*M.*) *nishinoshimana* (Pilsbry, 1909); *S.* (*M.*) *oostoma chichibuensis* (Sorita & Azuma, 1982); *S.* (*M.*) *oostoma oostoma* (Moellendorff, 1882); *S.* (*M.*) *pallens* (Moellendorff, 1882); *S.* (*M.*) *tabukii* (Kuroda & Minato, 1985); *S.* (*M.*) *ujiguntoensis* (Minato, 1982); *S.* (*M.*) *ultima* (Pilsbry, 1909); *S.* (*M.*) *vasta* (Boettger, 1877); *S.* (*M.*) *viridiflava* (Boettger, 1877).

Remarks: The taxonomic composition of *Mesophaedusa* redefined here differs from those of *Mesophaedusa* of traditional systems in the following points: 1) inclusion of "*Stereophaedusa*" species from the main islands of Japan; 2) exclusion of *Megalophaedusa ikenoi* (Minato, 1980); 3) exclusion of *S. okimodoki* (Minato & Tada, 1990); and 4) inclusion of *S. koshikijimana*.

Subgenus *Oophaedusa* Pilsbry, 1905
(= Subclade A7)

Type species: Clausilia ophidoon Pilsbry, 1905

Diagnosis; Shell small to large. Apex pointed or rounded. Plicae and clausilium located ventrally or ventro-laterally. Inferior lamella spirally ascending, broadened and/or slightly twisted near the aperture. Lunella present, oblique or vertical, attached to the lower palatal plica. Upper palatal plica rather long, always separated from the lunella. Lower palatal plica angled at the junction with lunella. Parietal and columellar margin of aperture strongly folded. Clausilium rather wide, with a small process at the baso-columellar edge. Distribution: endemic to northern part of the Central Ryukyus (Amami and Tokuno-shima Islands) and western islands of Kyushu (Goto and Koshiki-jima Islands, with an exceptional isolate in Nagasaki).

Morphology: Superior lamella developed. Principal plica developed. Middle palatal plica(e) absent. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: S. (*O.*) *azumai* (Pilsbry, 1905); *S.* (*O.*) *mima* (Pilsbry, 1901); *S.* (*O.*) *ophidoon* (Pilsbry, 1905); *S.* (*O.*) *una* (Pilsbry, 1902).

Remarks: Oophaedusa Pilsbry, 1905 was originally proposed for only *S.* (*O.*) *ophidoon*, which is characterized by the unusually oval shell with a rounded apex, but is redefined here to include three additional species with a pointed apex. Although *Oophaedusa* has been treated as a synonym of *Luchuphaedusa* (Kuroda, 1963; Azuma, 1982; Minato, 1994; Nordsieck, 1998), *Oophaedusa* is restored here as an independent subgenus. Despite the very close morphological similarities, *Luchuphaedusa* and *Oophaedusa* are not sister groups in the molecular phylogeny.

Subgenus *Pliciphaedusa* Nordsieck, 1998

(= Subclade A6)

Type species: Clausilia tosana Pilsbry, 1901

Diagnosis: Shell small. Aperture protruded. Middle palatal plica(e) present, short, variable, separated or coalesced into a weak lunella. Distribution: endemic to Shikoku and Kyushu.

Morphology: Apex pointed. Plicae and clausilium located laterally. Superior lamella developed. Inferior lamella receding within the aperture. Lunella present or absent. Principal plica developed. Upper and lower palatal plicae present. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: S. (*Pliciphaedusa*) *tosana* (Pilsbry, 1901); several undescribed species.

Remarks: Pliciphaedusa sensu Nordsieck (1998) is polyphyletic. *Pliciphaedusa* is redefined here to include only *S.* (*Pliciphaedusa*) *tosana* and its relatives.

Stereophaedusa (*sensu lato*)

The following *Stereophaedusa* taxa that cannot be assigned to the subgenera listed above are provisionally placed in *Stereophaedusa* (*sensu lato*): *S. caloptyx caloptyx* (Pilsbry, 1902); *S. caloptyx subtilis* (Kato, 1979); *S. cymatodes* (Pilsbry, 1905); *S. hemileuca hemileuca* (Pilsbry, 1909); *S. hemileuca takii* (Kuroda, 1936); *S. neniopsis* (Pilsbry, 1902); *S. okimodoki* (Minato & Tada, 1990); *S. tokunoshimaensis* (Minato, 1997). The taxonomic status of these taxa must be revised after their phylogenetic relationships within the genus have been resolved definitely.

Genus *Megalophaedusa* Boettger, 1877

(= Clade B)

Type species: Clausilia yokohamensis Crosse, 1873 (= *Clausilia martensi* Martens, 1860)

Synonyms: Aulacophaedusa Azuma, 1982; *Mundiphaedusa* Minato, 1979; *Neophaedusa* Kuroda & Minato, 1975; *Pauciphaedusa* Minato & Habe, 1983; *Pinguiphaedusa* Azuma, 1982; *Tyrannophaedusa* Pilsbry, 1900; *Ventriphaedusa* Azuma, 1982; *Vitriphaedusa* Azuma, 1982.

Diagnosis: Although *Megalophaedusa* redefined here cannot be diagnosed by morphology, its monophyly is strongly supported by molecular phylogeny. The presence of long hyper variable sequences of *ITS2* (Fig. 2.6) without deletion is diagnostic of the genus. Although the absence of apomorphic deletions may be the retention of a plesiomorphic character state shared with outgroups, the retention of the long sequences is unique among Japanese clausiliids.

Morphology: Shell small to very large. Plicae and clausilium located laterally to ventrally. Superior lamella developed. Inferior lamella receding within or appearing at the aperture, obliquely or straightly ascending. Lunella developed or absent. Principal plica developed. Upper and lower palatal plicae present. Middle palatal plica(e) present or absent, occasionally replaced by a lunella. Clausilium narrow. Diverticulum of bursa copulatrix developed.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: Endemic to the main islands of Japan (Hokkaido, Honshu, Shikoku, and Kyushu).

Remarks: Megalophaedusa is redefined here to include a very wide range of species exhibiting extensive morphological diversity. *Megalophaedusa* as redefined here is somewhat similar to *Megalophaedus sensu* Nordsieck (1998) in that it includes *Mundiphaedusa*, *Vitriphaedusa*, *Mesozaptyx* (=*Neophaedusa*), and *Pauciphaedusa*.

However, the taxonomic composition of *Megalophaedusa* redefined here differs from that of *Megalophaedusa sensu* Nordsieck (1998) by the exclusion of *Mesophaedusa* species and inclusion of many more species that have been assigned to various genera, such as *Tyrannophaedusa* and *Pinguiphaedusa*. Under the newly defined *Megalophaedusa*, I recognize the following subgenera: *Megalophaedusa*, *Aulacophaedusa*, *Dimphaedusa* (subgen. nov.), *Neophaedusa*, *Pauciphaedusa*, *Pinguiphaedusa*, *Tyrannophaedusa*, *Tyrannophaedusoides* (subgen. nov.), *Ventriphaedusa*, and *Vitriphaedusa*.

Subgenus *Megalophaedusa* Boettger, 1877
(= Subclade B7)

Synonym: Mundiphaedusa Minato, 1979

Diagnosis: Shell medium-sized to very large. Apex rounded. Middle palatal plica(e) present, short, more than one, rarely replaced by lunella. Distribution: endemic to Japan (Eastern and Central Honshu and Shikoku).

Morphology: Superior lamella developed. Inferior lamella receded within the aperture. Principal plica developed. Plicae and clausilium located laterally. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*M.*) *dorcas* (Pilsbry, 1902); *M.* (*M.*) *ducalis* (Kobelt, 1876); *M.* (*M.*) *martensi* (Martens, 1860); **M.* (*M.*) *mitsukurii* (Pilsbry, 1902); *M.* (*M.*) *pilsbryi* (Nordsieck, 1997).

Remarks: Mundiphaedusa has been treated as a distinct genus (Kuroda, 1963; Azuma, 1982; Minato, 1994) or a subgenus of *Megalophaedusa* (Nordsieck, 1998). The present study revealed the polyphyly of *Mundiphaedusa* in the traditional sense. Among the heterogeneous lineages of *Mundiphaedusa*, *Megalophaedusa ducalis* (the type species of *Mundiphaedusa*) and its relatives constitute a subclade together with *Megalophaedusa martensi* (the senior synonym of the type species of *Megalophaedusa*). *Mundiphaedusa* is therefore treated as a junior synonym of *Megalophaedusa* (*Megalophaedusa*), while most species formerly included in *Mundiphaedusa* are excluded from the subgenus (see below).

Subgenus *Aulacophaedusa* Azuma, 1982
[= Subclade B6 + *M.* (*A.*) *aratrum* (Pilsbry, 1903)]

Type species: Clausilia gracilispira Moellendorff, 1882

Diagnosis: Shell small and thin. Parietal margin of the aperture with a longitudinal groove just beside the superior lamella or not. Plicae and clausilium located laterally to ventro-laterally. Lunella present or absent. Upper and lower palatal plicae always present. Distribution: endemic to Western Honshu and Shikoku.

Morphology: Apex pointed. Superior lamella developed. Inferior lamella receded. Principal plica developed. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*A.*) *aratrum* (Pilsbry, 1903); **M.* (*A.*) *aulacophora* (Pilsbry, 1900); *M.* (*A.*) *gracilispira* (Moellendorff, 1882); *M.* (*A.*) *matsumurai* (Minato, 2014); *M.* (*A.*) *morisakii* (Kuroda & Habe, 1980).

Remarks: Although *Aulacophaedusa* has been treated as a subgenus of *Tyrannophaedusa* (Minato, 1994; Nordsieck, 1998), the present study revealed that the former represents a distinct lineage from the latter. Accordingly, *Aulacophaedusa* is treated as a subgenus independent from *Tyrannophaedusa*. *Megalophaedusa* (*A.*) *aratrum*, which has been included in *Vitriphaedusa* or *Mundiphaedusa* in the traditional systems, is transferred to *Aulacophaedusa* for the first time because its close phylogenetic affinity to *Aulacophaedusa* (in the traditional sense) is strongly supported by ML analysis. The most basal position of this species within *Aulacophaedusa* suggests that the absence of the characteristic groove at the parietal margin of the aperture represents a plesiomorphic character state of this subgenus.

Subgenus *Dimphaedusa* Motochin & Ueshima **subgen. nov.**

(= Subclade B5)

Type species: Clausilia (*Megalophaedusa*) *ducalis decapitata* Pilsbry, 1902

Diagnosis: Shell large to small. Apex rounded or pointed, decollated or not. Lunella absent. Middle palatal plica(e) present, more than one, short or rather long. Distribution: endemic to Western Honshu.

Morphology: Plicae and clausilium located laterally. Principal plica developed. Upper and lower palatal plicae present. Superior lamella developed. Inferior lamella receded within the aperture. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*D.*) *decapitata* (Pilsbry, 1902); *M.* (*D.*) *kurozuensis* (Pilsbry, 1902); *M.* (*D.*) *kyotoensis* (Kuroda, 1936).

Remarks: The new subgenus is proposed for "*Mundiphaedusa*" species from Western Honshu because they represent a distinct linage independent from other subgenera within *Megalophaedusa*.

Etymology: The subgeneric name is derived from an anagram of parts of the letters "Mundi" in allusion to the members being a part of *Mundiphaedusa* in the traditional systems.

Subgenus *Neophaedusa* Kuroda & Minato, 1975
[= Subclade B9 + *M. albela* (Minato, 1976)]

Type species: Neophaedusa ishikawai Kuroda & Minato, 1975

Synonym: Mesozaptyx Kuroda, 1963 (*nomen nudum*)
Diagnosis: Shell small. Apex rounded. Inferior lamella spirally ascending or not. Middle palatal plica(e) present or absent, occasionally replaced by a lunella. Distribution: endemic to Kyushu.

Morphology: Plicae and clausilium located laterally to ventrally. Superior lamella developed. Lunella present or absent. Principal plica developed. Clausilium wide or narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*N.*) *albela* (Minato, 1976); *M.* (*N.*) *ishikawai* (Kuroda & Minato, 1975); *M.* (*N.*) *masotokandai masatokandai* (Minato, 1978); **M.* (*N.*) *masotokandai shiroi* (Minato, 1978); **M.* (*N.*) *spelaeonis* (Kuroda & Minato, 1975).

Remarks: The taxonomic composition of *Neophaedusa* redefined here differs from that of *Neophaedusa sensu* Minato (1994) by the exclusion of *Tosaphaedusa akiratadai* (Minato, 1978). Although the inclusion of *M.* (*N.*) *albela* is congruent with biogeography and morphology, the close phylogenetic affinity of this species to the subclade B9 [*M.* (*N.*) *ishikawai* + *M.* (*N.*) *masotokandai masatokandai*] was well-supported only by the Bayesian analysis. *M.* (*N.*) *spelaeonis* and *M.* (*N.*) *masotokandai shiroi* are provisionally placed in this subgenus and their taxonomic positions need to be tested by future molecular phylogenetic analysis.

Subgenus *Pauciphaedusa* Minato & Habe, 1983

Type species: Pauciphaedusa toshiyukii Minato & Habe, 1983

Diagnosis: Shell small, glossy. Plica simple, comprised of only principal plica. Palatal plica and lunella absent.

Morphology: Apex pointed. Plicae and clausilium located laterally. Superior lamella developed. Inferior lamella receded. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*Pauciphaedusa*) *toshiyukii* (Minato & Habe, 1983).

Remarks: Pauciphaedusa is treated here as a monotypic subgenus due to its possible basal position within the genus and the unique morphology.

Subgenus *Pinguiphaedusa* Azuma, 1982
(= Subclade B1)

Type species: Clausilia platydera Martens, 1876

Synonym: Placeophaedusa Minato, 1994

Diagnosis: Shell small to large, fusiform, frequently with thin apical whorls and broadened middle whorls. Inferior lamella moderately developed within the aperture or receded. Lunella well developed, curved or straight, usually attached to the lower palatal plica. Upper palatal plica distinct and attached to the lunella, or indistinct and fused with the lunella. Lower palatal plica usually present, frequently angled at the junction with the lunella. Distribution: endemic to Honshu, Shikoku, and Kyushu.

Morphology: Apex pointed. Plicae and clausilium located laterally. Superior lamella developed. Principal plica developed. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*Pinguiphaedusa*) *attrita attrita* (Boettger, 1877); *M.* (*P.*) *attrita infausta* (Pilsbry, 1902); *M.* (*P.*) *awajiensis* (Pilsbry, 1900); *M.* (*P.*) *expansilabris* (Boettger, 1878); *M.* (*P.*) *hakonensis* (Pilsbry, 1900); **M.* (*P.*) *ignobilis* (Sykes, 1895); *M.* (*P.*) *kubinaga* (Kuroda, 1936); *M.* (*P.*) *pinguis pinguis* (A. Adams, 1868); *M.* (*P.*) *pinguis platyauchen* (Martens, 1877); *M.* (*P.*) *pinguis platydera* (Martens, 1876); *M.* (*P.*) *schmackeri* (Sykes, 1895).

Remarks: The taxonomic composition of *Pinguiphaedusa* redefined here differs from those of *Pinguiphaedusa sensu* Minato (1994) and *sensu* Nordsieck (1998) by inclusion of *M.* (*Pinguiphaedusa*) *expansilabris* and *M.* (*Pinguiphaedusa*) *awajiesis*, and hence by synonymization of *Placeophaedusa*. The current taxonomic composition also differs from that of Nordsieck (1998) by exclusion of *M.* (*Tyrannophaedusoides*) *kawamotoi* (Kuroda & Taki, 1944). Although *Pinguiphaedusa* has been treated as a subgenus of *Hemiphaedusa* (Kuroda, 1963; Nordsieck, 1998) or a full genus (Azuma, 1982; Minato, 1994), *Pinguiphaedusa* is treated here as a subgenus of *Megalophaedusa* for the first time.

Subgenus *Tyrannophaedusa* Pilsbry, 1900
(= Subclade B4)

Type species: Clausilia mikado Pilsbry, 1900

Synonyms: Decolliphaedusa Azuma, 1982; *Spinulaphaedusa* Minato, 1994

Diagnosis: Apex usually pointed, occasionally rounded, rarely decollated. Plicae and clausilium located laterally to ventrally. Lunella usually present. Upper palatal plica present, distinct and attached to the lunella, or fused with lunella. Lower palatal plica present, attached to the lunella. Distribution: endemic to Japan (Western Honshu, Shikoku, Kyushu, and Osumi Islands with an exceptional isolate in an island of Hokkaido).

Morphology: Shell small to large. Superior lamella developed. Inferior lamella receded. Principal plica developed. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*Tyrannophaedusa*) *aurantiaca* (Boettger, 1877); *M.* (*T.*) *bilabrata* (Smith, 1876); *M.* (*T.*) *dalli* (Pilsbry, 1902); *M.* (*T.*) *fukudainadai* (Minato, 2014); *M.* (*T.*) *iotaptyx* (Pilsbry, 1900); **M.* (*T.*) *iyoensis* (Minato & Tada, 1977); *M.* (*T.*)

kanjiookuboi Minato, 1980; *M.* (*T.*) *mikado* (Pilsbry, 1900); *M.* (*T.*) *miyazakii* (Minato & Tada, 1977); *M.* (*T.*) *moellendorffi* (Nordsieck, 2003); *M.* (*T.*) *nankaidoensis nankaidoensis* (Kuroda, 1955); **M.* (*T.*) *nankaidoensis yanoi* (Minato, 1978); *M.* (*T.*) *oxycyma* (Pilsbry, 1902); *M.* (*T.*) *plicilabris* (A. Adams, 1868); *M.* (*T.*) *puellaris* (Minato & Tada, 1978); *M.* (*T.*) *sugimotonis misaki* (Minato & Tada, 1978); *M.* (*T.*) *sugimotonis sugimotonis* (Minato & Tada, 1978); *M.* (*T.*) *surugensis* (Pilsbry, 1902); *M.* (*T.*) *tanegashimae* (Pilsbry, 1901); *M.* (*T.*) *tosaensis* (Pilsbry, 1903).

Remarks: The taxonomic composition of *Tyrannophaedusa* as redefined here is somewhat similar to that of *Tyrannophaedusa* (*sensu lato*) of Kuroda (1963) and Minato (1994) and that of *Tyrannophaedusa* (*T.*) of Nordsieck (1998), but differs in the following points: 1) exclusion of *M.* (*Tyrannophaedusoides*) *pilsbryana* (Ancey, 1904) and *M.* (*Tyrannophaedusoides*) *kawamotoi*; 2) exclusion of *Ventriphaedusa* species; 3) exclusion of *Aulacophaedusa* species; and 4) synonymization of *Decolliphaedusa* and *Spinulaphaedusa*. *Decolliphaedusa sensu* Minato (1994) is polyphyletic. *Decolliphaedusa* and *Spinulaphaedusa* are treated as junior synonyms because the type species of these generic taxa are nested within the subclade of *Tyrannophaedusa*.

Subgenus *Tyrannophaedusoides* Motochin & Ueshima **subgen. nov.**

(= Subclade B5)

Type species: Tyrannophaedusa kawamotoi Kuroda & Taki, 1944

Diagnosis: Shell small to medium-size. Apex pointed. Plicae and clausilium located laterally or ventro-laterally. Subcolumellar lamella emerging at the aperture. Lunella developed. Upper palatal plica fused with the lunella. Lower palatal plica present, attached to the lunella, angled at the junction with the lunella. Baso-columellar margin of the aperture weakly folded or not. Distribution westernmost Honshu (Yamaguchi) and Kyushu.

Morphology: Shell small to large. Superior lamella developed. Inferior lamella receded within the aperture, obliquely ascending. Principal plica developed. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*Tyrannophaedusoides*) *kawamotoi* (Kuroda & Taki, 1944); *M.* (*Tyrannophaedusoides*) *pilsbryana* (Ancey, 1904).

Remarks: Although the morphological features of *M.* (*Tyrannophaedusoides*) *kawamotoi* and *M.* (*Tyrannophaedusoides*) *pilsbryana* coincide with those of *Tyrannophaedusa* (including *Decolliphaedusa*), they represent a distinct lineage independent from the subgenus *Tyrannophaedusa* in the molecular phylogeny. A new subgenus is proposed here based on the phylogenetic position.

Subgenus *Ventriphaedusa* Azuma, 1982
(= Subclade B2)

Type species: Clausilia platyderula Pilsbry, 1903

Diagnosis: Shell small to medium-sized. Plicae and clausilium located ventrally. Lunella present or absent. Upper palatal plica present, attached to or fused with lunella, if the lunella is present. Lower palatal plicae always present. Middle palatal plica(e) occasionally developed when the lunella is absent. Distribution: endemic to Western Honshu and Shikoku.

Morphology: Apex pointed. Superior lamella developed. Inferior lamella receded within the aperture. Principal plica developed. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*Ventriphaedusa*) *platyderula* (Pilsbry, 1903); *M.* (*V.*) *proba* (A. Adams, 1868); *M.* (*V.*) *ventriluna* (Pilsbry, 1905).

Remarks: Ventriphaedusa has been treated as a subgenus or synonym of *Tyrannophaedusa* (Kuroda, 1963; Minato, 1994; Nordsieck, 1998). *Ventriphaedusa*, however, cannot be placed under *Tyrannophaedusa* because *Ventriphaedusa* is a sister to *Pinguiphaedusa*, not to *Tyrannophaedusa*. *Ventriphaedusa* is redefined here as a distinct subgenus of *Megalophaedusa*.

Subgenus *Vitriphaedusa* Azuma, 1982
(= Subclade B3)

Type species: Clausilia opeas Moellendorff, 1885 (= *Clausilia subulina* Moellendorff, 1882)

Diagnosis: Shell small to medium-sized. Apex mostly rounded, occasionally pointed. Lunella present or absent. Middle palatal plica(e) present or absent, short when present. Distribution: endemic to Eastern Honshu with an isolate at Wakayama.

Morphology: Superior lamella developed. Inferior lamella receded. Principal plica developed. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: M. (*Vitriphaedusa*) *decussata* (Martens, 1877); *M.* (*V.*) *hosayaka* (Pilsbry, 1905); *M.* (*V.*) *iijimakuniakii* (Minato & Habe, 1983); *M.* (*V.*) *kawasakii* (Kuroda, 1936); *M.* (*V.*) *kuninoae* (Pilsbry, 1936); *M.* (*V.*) *micropeas* (Moellendorff, 1882); *M.* (*V.*) *rhopalia* (Pilsbry, 1902); *M.* (*V.*) *stenospira* (A. Adams, 1868); *M.* (*V.*) *sublunellata* (Moellendorff, 1885); *M.* (*V.*) *subulina* (Moellendorff, 1882); *M.* (*V.*) *yagurai* (Kuroda, 1936).

Remarks: Vitriphaedusa sensu Minato (1994) is polyphyletic. *Vitriphaedusa* has been treated as a subgenus or a synonym of *Mundiphaedusa* (Minato, 1994; Nordsieck, 1998). However, *Vitriphaedusa* cannot be placed under *Mundiphaedusa* because the type species of these "genera" belong to the different subclades B3 and B7, respectively. The taxonomic composition of *Vitriphaedusa* redefined here differs from those of *Vitriphaedusa* of traditional systems in the following points: 1) exclusion of *M.* (*A.*) *aratrum* and *M. aenea* (Pilsbry, 1903); and 2) inclusion of smaller and medium-sized "*Mundiphaedusa*" species from Eastern Honshu and *M. stenospira*.

Megalophaedusa (*sensu lato*)

The following *Megalophaedusa* species that cannot be assigned to the subgenera listed above are provisionally placed in *Megalophaedusa* (*sensu lato*): *M. aenea* (Pilsbry, 1903); *M. ikenoi* (Minato, 1980); *M. pachyspira* (Pilsbry, 1902); *M. rex* (Pilsbry, 1905). The taxonomic status of these species must be revised after their phylogenetic relationships within the genus have been resolved definitely.

Genus *Tosaphaedusa* Ehrmann, 1929

(= Clade C)

Type species: Clausilia cincticollis Ehrmann, 1900

Diagnosis: Although *Tosaphaedusa* redefined here cannot be diagnosed by morphology, its monophyly is strongly supported by molecular phylogeny. The presence of unique deletions and substitutions in the hyper variable region of *ITS2* (Fig. 2.6) is a molecular diagnostic character of the genus. The distribution is endemic to Shikoku.

Morphology: Shell small to medium-sized. Apex rounded or somewhat pointed. Plicae and clausilium located ventrally or laterally. Superior lamella developed. Inferior lamella receded. Lunella present or absent. Principal plica developed. Upper and lower palatal plicae present. Middle palatal plica(e) present or absent. Dorsal crest present or absent. Clausilium wide or narrow. Diverticulum of bursa copulatrix developed.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: T. akiratadai (Minato, 1978); *T. cincticollis* (Ehrmann, 1900).

Remarks: Tosaphaedusa has been known as a monotypic taxon (Minato, 1994; Nordsieck, 1998) and was treated as a subgenus or a synonym of *Tyrannophaedusa* (Kuroda, 1963; Nordsieck, 1998). *Tosaphaedusa* is redefined here as a distinct genus that includes not only the type species but also *Tosaphaedusa akiratadai*. The presence of a strong dorsal crest, on which the traditional generic or subgeneric diagnosis has been based, was demonstrated to be an autapomorphy of the type species, not a synapomorphy of the genus.

Genus *Reinia* Kobelt, 1876
(= Clade F)

Type species: Balea variegata A. Adams, 1868

Synonyms: Parareinia Nordsieck, 1998; *Pictophaedusa* Azuma, 1982; *Proreinia* Thiele, 1931; *Pseudophaedusa* Tomiyama, 1984.

Diagnosis: Shell small to very small, frequently thin-walled, frequently with subaxial and whitish flammulation, occasionally with a light-coloured band below the suture. Superior lamella frequently reduced to various degrees, occasionally developed. Inferior lamella usually developed, spirally ascending and approaching to the superior lamella. Plicae present except for *R. variegata* (A. Adams, 1868). Principal plica usually developed, but occasionally shortened or reduced. Upper and lower palatal plicae usually present. Lunella always absent. Clausilium present except for *R. variegata*, wide. Diverticulum of bursa copulatrix frequently reduced to various degrees. Ecology arboreal. Reproduction ovoviviparous. Presence of unique deletions in the hyper variable region of *ITS2* (Fig. 2.6) is a molecular diagnostic character of the genus.

Morphology: Apex pointed. Plicae and clausilium located laterally if present. See also Diagnosis.

Reproduction and ecology: As in Diagnosis.

Distribution: Southern Hokkaido, Honshu, Shikoku, Kyushu, Ryukyu Islands, Taiwan, Korea, and Southern China.

Included taxa: R. arborea (Tomiyama, 1984); *R. ashizuriensis* Azuma, 1968; **R. changi* Nordsieck, 2003; *R. eastlakeana* (Moellendorff, 1882); *R. echo* (Pilsbry, 1909); *R. elegans* (Habe, 1962); *R. euholostoma* (Pilsbry, 1901); *R. holotrema* (Pilsbry, 1902); *R. hungerfordiana hungerfordiana* (Moellendorff, 1882); **R. hungerfordiana okayamensis* (Kuroda & Azuma, 1982); *R. hungerfordiana tokushimensis* Kuroda & Abe, 1980; *R. masaoi* (Habe, 1940); *R. monelasmus* (Pilsbry, 1909); *R. nakadai* (Pilsbry, 1902); *R. sieboldtii* (Pfeiffer, 1848); *R. tayalis* (Kuroda, 1941); *R. variegata* (A. Adams, 1868).

Remarks: Reinia is redefined here to include a wider range of species than in the traditional systems. It is notable that two species with a well-developed inferior lamella and thicker shell, *R. arborea* and *R. sieboldtii*, are included in this genus for the first time. Although the traditional "genera" or "subgenera" were characterized by the reduction of some diagnostic features, such as the superior lamella, plicae, clausilium, and diverticulum of bursa copulatrix, my molecular phylogeny strongly suggests the occurrence of frequent parallel evolution and/or reversal in these characters. I therefore refute subgeneric division within this genus. The genus is widely distributed not only in

Japan and Taiwan but also in continental China (Nordsieck, 2012) and Korea (Kuroda & Hukuda, 1944; Min et al., 2004).

"*Phaedusa*" *hayashii* Kuroda, 1941 is an arboreal clausiliid endemic to Taiwan. Judging from the morphology and ecology, this species may be a member of *Reinia* or *Stereophaedusa*. The phylogenetic position of this species needs to be examined based on molecular data.

Genus *Tauphaedusa* Nordsieck, 2003

(= Clade E)

Type species: Clausilia tau Boettger, 1877

Diagnosis: Superior lamella usually present, occasionally reduced. Inferior lamella spirally ascending and approaching to the superior lamella, or obliquely ascending and receding within the aperture. Lunella absent or very weakly developed. Upper and lower palatal plicae present. Middle palatal plica(e) absent. Clausilium wide. Reproduction ovoviviparous. Presence of unique deletions and substitution in the hyper variable region of *ITS2* (Fig. 2.6) that are shared only with *Zaptyx* is a molecular diagnostic character of the genus.

Morphology: Shell small to large. Apex pointed. Plicae and clausilium located laterally. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: As in Diagnosis.

Ecology: Terrestrial.

Distribution: Hokkaido, Honshu, Shikoku, Kyushu, Southern Ryukyus, and probably Taiwan and Korea.

Included taxa: T. comes (Pilsbry, 1900); *T. dignoptyx* (Boettger, 1877); **T. eumegetha* (Schmacker & Boettger, 1891); **T. rowlandi* (Pilsbry, 1902); **T. senkakuensis* (Kuroda, 1960); **T. sheridani* (Pfeiffer, 1866); *T. stearnsii iriomotensis* (Kuroda, 1960); *T.*

stearnsii stearnsii (Pilsbry, 1894); *T. subaculus* (Pilsbry, 1902); *T. tau* (Boettger, 1877).

Remarks: Tauphaedusa was originally proposed as a subgenus of *Euphaedusa* by Nordsieck (2003). *Tauphaedusa* is raised to full genus status here because it is not related to the type species of *Euphaedusa*. Some Taiwanese and Korean taxa assigned to *Euphaedusa* should be placed in this genus.

Genus *Zaptyx* Pilsbry, 1900
(= Clade D)

Type species: Clausilia hirasei Pilsbry, 1900

Synonyms: Diceratoptyx Pilsbry, 1905; *Hemizaptyx* Pilsbry, 1905; *Heterozaptyx* Pilsbry, 1906; *Idiozaptyx* Pilsbry, 1909; *Oligozaptyx* Pilsbry, 1905; *Metazaptyx* Pilsbry, 1905; *Paganizaptyx* Azuma, 1982; *Parazaptyx* Pilsbry, 1905; *Pulchraptyx* Minato, 1981; *Selenoptyx* Pilsbry, 1908; *Stereozaptyx* Pilsbry, 1901; *Thaumatoptyx* Pilsbry, 1908; *Tyrannozaptyx* Käufel, 1930; *Zaptychopsis* Ehrmann, 1927.

Diagnosis: Shell mostly small and slender, but becoming large only in a few subgenera. Plicae and clausilium located laterally to ventrally. Sutural plica present or absent. Lunella always present, strongly developed. Upper palatal plica usually present, mostly attached to the lunella, variable in the length. Presence of unique deletions and substitution in the hyper variable region of *ITS2* (Fig. 2.6) that are shared only with *Tauphaedusa* is a molecular diagnostic character of the genus.

Morphology: Apex pointed. Lower palatal plica frequently absent. Middle palatal plica absent. Superior lamella usually developed, rarely reduced. Inferior lamella variable, spirally ascending and appearing at the aperture, or almost straightly ascending and receding within the aperture. Clausilium wide or narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous or ovoviviparous.

Ecology: Terrestrial.

Distribution: Honshu, Shikoku, Kyushu, Ryukyu Islands, and Taiwan.

Remarks: Zaptyx is redefined here to include a wide range of species that encompass not only all "zaptychoid genera" but also Taiwanese "*Hemiphaedusa*" species. Despite the extensive morphological diversity among the members, all member species share a well-developed lunella. All Japanese and Taiwanese taxa with sutural plicae are included in the genus. I recognized the following subgenera under the redefined genus: *Zaptyx*, *Hemizaptyx*, *Parazaptyx*, *Pulchraptyx*, *Selenoptyx*, *Stereozaptyx*, *Taiwanphaedusa* (subgen. nov.), *Thaumatoptyx*, *Tyrannozaptyx*, and *Zaptychopsis*. Several species of *Hemizaptyx* (as a subgenus of *Hemiphaedusa*) are recorded from continental China and Vietnam (Nordsieck, 2003, 2012), and two species of *Prozaptyx* are recorded from the Philippines (Loosjes, 1950; Nordsieck, 2003). Although the shell morphologies of these taxa are somewhat similar to those of *Zaptyx* redefined here, their actual phylogenetic positions must be tested by molecular phylogenetic analysis. A Chinese species, "*Hemizaptyx*" *minuta* (Yen, 1939), is found to be unrelated to *Z.* (*Hemizaptyx*) by the present study.

Subgenus *Zaptyx* Pilsbry, 1900
(= Subclade D8)

Synonyms: Metazaptyx Pilsbry, 1905; *Diceratoptyx* Pilsbry, 1905; *Idiozaptyx* Pilsbry, 1909.

Diagnosis: Shell small, slender. Superior lamella usually developed, rarely reduced. Inferior lamella variable, spirally ascending and appearing at the aperture, or almost straightly ascending and receded within the aperture. Sutural plica always present, one or two. Lunella present, usually developed, rarely shortened in an exceptional case. Upper palatal plica present, usually short, rarely long and/or interrupted. Lower palatal plica usually absent. Clausilium wide or narrow. Reproduction oviparous or ovoviviparous. Distribution: endemic to the Ryukyu Islands and southern Kyushu.

Morphology: Apex pointed. Plicae and clausilium located laterally. Principal plica developed. Middle palatal plica absent. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction and distribution: As in Diagnosis.

Ecology: Terrestrial.

Included taxa: Z. (*Zaptyx*) *cladoptyx* (Pilsbry, 1905); *Z.* (*Z.*) *daemonorum* (Pilsbry, 1902); **Z.* (*Z.*) *daitojimana* (Kuroda, 1960); *Z.* (*Z.*) *dolichoptyx* (Pilsbry, 1908); *Z.* (*Z.*) *hachijoensis* (Pilsbry, 1901); *Z.* (*Z.*) *hirasei* (Pilsbry, 1900); *Z.* (*Z.*) *hyperoptyx* (Pilsbry, 1900); *Z.* (*Z.*) *kikaiensis* (Pilsbry, 1905); *Z.* (*Z.*) *nakanoshimana* (Pilsbry, 1909); *Z.* (*Z.*) *pattalus* (Pilsbry, 1905); *Z.* (*Z.*) *sarissa* (Pilsbry, 1905); *Z.* (*Z.*) *yaeyamensis* (Pilsbry, 1905).

Remarks: Zaptyx (*Z.*) is redefined here to include *Metazaptyx* and *Diceratoptyx*. The presence of sutural plicae is a synapomorphy of the newly defined *Zaptyx* (*Z.*). *Idiozaptyx*, which was proposed based on a variant morph of *Z* (*Z.*) *kikaiensis* as noted by Nordsieck (1998), is treated here as a junior synonym of *Zaptyx* (*Z.*).

Subgenus *Hemizaptyx* Pilsbry, 1905

(= Subclade D5)

Type species: Clausilia pinto Pilsbry, 1901

Diagnosis: Shell small, slender, glossy, transparent. Sutural plica absent. Lunella developed, attached to the upper palatal plica. Upper palatal plica short. Lower palatal plica present or absent. Distribution: endemic to the Northern Ryukyus and Izu Islands.

Morphology: Apex pointed. Plicae and clausilium located laterally. Principal plica developed. Middle palatal plica(e) absent. Superior lamella developed. Inferior lamella receded. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: Z. (*Hemizaptyx*) *pinto* (Pilsbry, 1901); *Z.* (*H.*) *purissima* (Pilsbry, 1905).

Remarks: Although *Hemizaptyx* has occasionally been treated as a subgenus of *Hemiphaedusa* (Nordsieck, 1997, 1998, 2007; Schileyko, 2000), *Hemizaptyx* is redefined here as a subgenus of *Zaptyx*. The taxonomic composition of the redefined *Hemizaptyx* differs from that of *Hemizaptyx* of traditional systems by its members being restricted to only the type species and *Z.* (*H.*) *purissima*. Eight Japanese taxa formerly assigned to *Hemizaptyx* are transferred to *Zaptyx* (*s. lato*), *Z.* (*Tyrannozaptyx*), and *Stereophaedusa*. Close phylogenetic affinities of *Paganizaptyx* species and Z. *tantilla* (Pilsbry, 1902) to the redefined *Hemizaptyx* are weakly supported. *Hemizaptyx* may be expanded to include these species if statistical support for affinity is greatly increased in a future analysis using more data.

Subgenus *Parazaptyx* Pilsbry, 1905

Type species: Clausilia thaumatopoma Pilsbry, 1905

Diagnosis: Shell small, slender. Inferior lamella receded, but developed inside the aperture, obliquely ascending. Sutural plica absent. Lunella oblique, separated from the upper palatal plica. Principal plica developed, long. Lower palatal plica absent. Clausilium wide, with a short transverse plate on the outer side. Reproduction ovoviviparous. Distribution: endemic to Kerama Islands in the central Ryukyus.

Morphology: Apex pointed. Plicae and clausilium located laterally. Superior lamella developed. Inferior lamella receded. Upper palatal plica present. Middle palatal plica(e) absent. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction and distribution: As in Diagnosis.

Ecology: Terrestrial.

Included taxa: Z. (*Parazaptyx*) *thaumatopoma* (Pilsbry, 1905).

Subgenus *Pulchraptyx* Minato, 1981

Type species: Clausilia longiplicata Pilsbry, 1908

Diagnosis: Shell small, slender. Sutural plica absent. Lunella oblique, short, separated from the upper palatal plica. Upper palatal plica very long, extended near the aperture. Lower palatal plica absent. Distribution endemic to Tokashiki Islands in the central Ryukyus.

Morphology: Apex pointed. Superior lamella developed. Inferior lamella receded. Plicae and clausilium located laterally. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: Z. (*Pulchraptyx*) *longiplicata* (Pilsbry, 1908).

Subgenus *Selenoptyx* Pilsbry, 1908
(= Subclade D4)

Type species: Clausilia noviluna Pilsbry, 1908

Diagnosis: Shell small, slender. Plicae and clausilium located ventrally. Sutural plica absent. Lunella oblique, fused with the upper palatal plica. Principal plica developed. Lower palatal plica absent. Clausilium concave at the palatal side. Distribution: endemic to Okinawa-jima, Iheya-jima, and Kume-jima Islands.

Morphology: Apex pointed. Superior lamella developed. Inferior lamella receded. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: Z. (*Selenoptyx*) *inversiluna* (Pilsbry, 1908); *Z.* (*Selenoptyx*) *noviluna* (Pilsbry, 1908).

Subgenus *Stereozaptyx* Pilsbry, 1901
(= Subclade D6)

Type species: Clausilia entospira Pilsbry, 1901

Synonym: Oligozaptyx Pilsbry, 1905

Diagnosis: Shell small, slender, glossy. Superior lamella developed or weakened. Inferior lamella developed, appearing at the aperture or receded but developed inside the aperture, obliquely ascending. Clausilium and plicae located laterally or ventro-laterally. Sutural plica present or absent. Lunella developed. Upper palatal plica short, attached to or fused with the lunella. Lower palatal plica present or absent, attached to the lunella if present. Clausilium wide, with or without a terminal notch. Distribution: endemic to the Northern Ryukyus.

Morphology: Apex pointed. Principal plica developed. Middle palatal plica(e) absent. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: Z. (*Stereozaptyx*) *entospira* (Pilsbry, 1901); *Z.* (*Stereozaptyx*) *exulans* (Pilsbry, 1908); *Z.* (*Stereozaptyx*) *exodonta* (Pilsbry, 1909); *Z.* (*Stereozaptyx*) *hedleyi* (Pilsbry, 1905).

Remarks: Stereozaptyx is redefined here to include *Oligozaptyx* species for the first time.

Subgenus *Taiwanphaedusa* Motochin & Ueshima **subgen. nov.**

(= Subclade D2)

Type species: Clausilia similaris H. Adams, 1866

Diagnosis: Shell small to large, thick. Apex pointed or rounded. Inferior lamella usually receded and obliquely ascending, rarely spirally ascending. Sutural plica absent. Lunella always developed, usually straight, occasionally oblique or curved. Upper palatal plica present, attached to the lunella, rarely fused with the lunella. Lower palatal plica present or absent, attached to or fused with the lunella if present. Distribution: endemic to Taiwan.

Morphology: Superior lamella developed. Plicae and clausilium located laterally. Principal plica developed. Middle palatal plica(e) absent. Clausilium usually narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous, rarely ovoviviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: **Z.* (*Taiwanphaedusa*) *amphileuca* (Chang, 1978); **Z.* (*T.*) *antuensis antuensis* (Chang, Tada & Ookubo, 1995); **Z.* (*T.*) *antuensis chichiensis* (Nordsieck, 2005); **Z.* (*T.*) *arikangensis* (Chang, 1992); **Z.* (*T.*) *arikangensis longiplicata* (Nordsieck, 2005); **Z.* (*T.*) *baibaraensis* (Chang, Toda, Hwang & Ookubo, 1998); **Z.* (*T.*) *buduiensis* (Chang & Ookubo, 1997); **Z.* (*T.*) *exilis* (H. Adams, 1866) **Z.* (*T.*) *exilis janshanensis* (Chang & Wu, 1979); **Z.* (*T.*) *gochishanensis* (Chang, 1999); **Z.* (*T.*) *hemmeni hemmeni* (Nordsieck, 2005); **Z.* (*T.*) *hemmeni yucola* (Nordsieck, 2005); *Z.* (*T.*) *kanaganensis* (Chang, 1980); *Z.* (*T.*) *kosakai* (Kuroda, 1941); **Z.* (*T.*) *kuanmini* (Lee & Wu, 2003); **Z.* (*T.*) *lini* (Chang & Tada, 2000); **Z.* (*T.*) *litouensis* (Chang & Ookubo, 2004); *Z.* (*T.*) *lushanensis* (Chang & Maeda, 1982); **Z.* (*T.*) *maanliauensis* (Chang & Wu, 1978); **Z.* (*T.*) *magaensis* (Chang, 1991); **Z.* (*T.*) *myersi* (Schmacker & Böettger, 1891); **Z.* (*T.*) *nigricans* (Nordsieck, 1998); **Z.* (*T.*) *odontochila* (Schmacker & Böttger, 1891); **Z.* (*T.*) *odontochila clava* (Chang & Ookubo, 1994); **Z.* (*T.*) *odontochila fulvicollis* (Zilch, 1954); **Z.* (*T.*) *ooi* (Kuroda, 1941); *Z.* (*T.*) *similaris* (H. Adams, 1866); **Z.* (*T.*) *similaris ventriosa* (Schmacker & Boettger, 1891); **Z.* (*T.*) *similaris clava* (Schmacker & Boettger, 1891); **Z.* (*T.*) *taibuensis* (Chang & Tada, 2005); **Z.* (*T.*) *tantaensis* (Chang & Wu, 1977).

Remarks: This subgenus includes most of the Taiwanese taxa formerly assigned to *Hemiphaedusa*. Although Nordsieck (1997) placed these Taiwanese "*Hemiphaedusa*" species in the subgenus *Hemizaptyx*, they are not closely related to the type species of *Hemizaptyx* in the molecular phylogeny. Although many Taiwanese species are provisionally placed in this subgenus based on morphology, their taxonomic position should be tested by molecular phylogeny. *Zaptyx pseudosheridani* (Zilch, 1954) may be transferred to a new subgenus together with its relatives.

Subgenus *Thaumatoptyx* Pilsbry, 1908

(= Subclade D1)

Type species: Clausilia bivincta Pilsbry, 1908

Diagnosis: Shell small, slender. Superior lamella variable, developed or reduced to various degrees. Plicae and clausilium located variably, ventral to dorso-lateral. Sutural plica absent. Lunella present, attached to or fused with the upper palatal plica. Upper palatal plica present, highly variable, short to very long, occasionally interrupted. Additional palatal plica occasionally present between the principal plica and upper palatal plica. Lower palatal plica present or absent. Distribution: endemic to Taiwan.

Morphology: Apex pointed. Inferior lamella receded within the aperture. Principal plica developed. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: *Z. (*Thamatoptyx*) alloptyx* (Nordsieck, 2003); *Z.* (*T.*) *aptyx* (Nordsieck, 2003); **Z.* (*T.*) *bagsana* (Schmacker & Boettger, 1891); *Z.* (*T.*) *bivincta* (Pilsbry, 1909); **Z.* (*T.*) *changi* (Nordsieck, 2003); **Z.* (*T.*) *costellata* (Nordsieck, 2005); *Z.* (*T.*) *crassilamellata* Kuroda, 1941; **Z.* (*T.*) *diacoptyx hassenensis* Kuroda, 1941; *Z.* (*T.*) *diacoptyx* (Pilsbry, 1909); **Z.* (*T.*) *euptyx* (Nordsieck, 2003); *Z.* (*T.*) *kotoshoensis* Kuroda, 1932; *Z.* (*T.*) *gonyptyx* (Nordsieck, 2003); **Z.* (*T.*) *gonyptyx lacuphila* (Nordsieck, 2005; **Z.* (*T.*) *ilanensis* (Nordsieck, 2003); **Z.* (*T.*) *montuosa* (Nordsieck, 2003); **Z.* (*T.*) *oligoptyx* (Nordsieck, 2003); **Z.* (*T.*) *orthoptyx* (Nordsieck, 2003); **Z.* (*T.*) *paraptyx* (Nordsieck, 2003); **Z.* (*T.*) *santiaoensis* Chang, 1982; **Z.* (*T.*) *takahasii* Kuroda, 1932; **Z.* (*T.*) *uraniscoptyx* (Schmacker & Böttger, 1891); **Z.* (*T.*) *uraniscoptyx diploptyx* (Nordsieck, 2005); **Z.* (*T.*) *ypsilonptyx* (Nordsieck, 2003).

Remarks: Thaumatoptyx is redefined here to include a wide range of species that were formerly assigned to *Zaptyx*, *Heterozaptyx*, *Hemizaptyx*, and *Hemiphaedusa*. The morphology of the redefined *Thaumatoptyx* shows extensive variation in various shell characters, such as the morphology and location of plicae, degrees of development of superior lamella, presence or absence of constriction on the last whorls, general shell shape, and shell colour. *Thaumatoptyx* provides a remarkable example of how taxonomically important characters can change substantially and rapidly within a single lineage.

Subgenus *Tyrannozaptyx* Käufel, 1930
(= Subclade D3)

Type species: Tyrannozaptyx adulta Käufel, 1930

Diagnosis: Shell small, slender. Plicae and clausilium located ventrally to laterally. Sutural plica absent. Upper palatal plica moderately long, attached to the lunella. Lunella developed. Lower palatal plica absent. Distribution: endemic to the Southern Ryukyus.

Morphology: Apex pointed. Superior lamella developed. Inferior lamella receded within the aperture. Principal plica developed. Middle palatal plica(e) absent. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: Z. (*Tyrannozaptyx*) *adulta* (Käufel, 1930); *Z.* (*T.*) *deminuta* (Käufel, 1930); *Z.* (*T.*) *polita* Käufel, 1930; *Z.* (*T.*) *takarai* Kuroda, 1960.

Remarks: Z. (*Tyrannozaptyx*) *polita* and *Z.* (*Tyrannozaptyx*) *takarai* have been placed in *Hemizaptyx* because of the laterally located plicae (Minato, 1994; Nordsieck, 1998).

Tyrannozaptyx is redefined here to include these species.

Subgenus *Zaptychopsis* Ehrmann, 1927

Type species: Clausilia buschi Küster, 1844

Diagnosis: Shell medium-sized to rather large, glossy. Plica very simple, almost missing except for a lunella. Sutural plica absent or vestigial. Principal plica and palatal plica absent or vestigial. Lunella strongly developed. Distribution: endemic to Eastern Honshu.

Morphology: Apex pointed. Superior lamella developed. Inferior lamella receded within the aperture. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxa: Z. (*Zaptychopsis*) *buschi* (Küster, 1844).

Zaptyx (*sensu lato*)

The following *Zaptyx* species that cannot be assigned to the subgenera listed above are provisionally placed in *Zaptyx* (*sensu lato*): *Z. asperata* (Pilsbry, 1905); **Z. hyperaptyx* (Pilsbry, 1905); **Z. kusakakiensis* (Minato, 1982); *Z. minutus* (Chang & Tada, 2006); *Z. munus* (Pilsbry, 1901); **Z. oxypomatica* (Pilsbry, 1908); *Z. pseudosheridani* (Zilch, 1954); *Z. ptychocyma* (Pilsbry, 1901); *Z. stimpsoni* (A. Adams, 1868); *Z. strictaluna* (Boettger, 1877); **Z. subignobilis* (Pilsbry, 1902); *Z. tantilla* (Pilsbry, 1902); **Z. wenderi* (Lee & Wu, 2005); *Z. yukitai* (Uozumi & Yamamoto, 1993).

Heterozaptyx Pilsbry, 1906 and *Paganizaptyx* Azuma, 1982 are provisionally treated as junior synonyms of *Zaptyx* (*sensu lato*) due to the poorly resolved phylogenetic status. The taxonomic positions of these species must be revised after their phylogenetic relationships within the genus have been resolved definitely. A new subgenus should be erected for *Z.* sp. cf. *pseudosheridani* after the species identity has been determined.

Genus *Changphaedusa* Motochin & Ueshima **gen. nov.**

Type species: Phaedusa (*Stereophaedusa*) *horikawai* Kuroda, 1941

Diagnosis: Shell large. Lunella absent. Inferior lamella developed, spirally ascending, approaching to the superior lamella near the aperture, somewhat thickened at the aperture. Clausilium rather wide. Reproduction ovoviviparous. Ecology arboreal. Distribution: endemic to Taiwan.

Morphology: Shell large. Apex pointed. Plicae and clausilium located at left lateral side. Principal plica present, long. Upper palatal plica present, short. Lower palatal plica present, short. Middle palatal plica absent. Superior lamella developed, continuous with the spiral lamella. Subcolumellar lamella not emerging at the aperture. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction, ecology, and distribution: As in Diagnosis.

Included taxa: C. horikawai (Kuroda, 1941); **C. horikawai ishizakii* (Kuroda, 1941).

Remarks: C. horikawai has been classified in *Stereophaedusa* or *Pseudophaedusa* (Chang & Maeda, 1984; Nordsieck, 1997; Hsieh et al., 2013). A new genus is erected for this species because it is not related to any other Taiwanese or Japanese taxa.

Etymology: The new generic name is dedicated to Kuan Min Chang, a Taiwanese malacologist, who made great contributions to the taxonomy of Taiwanese clausiliids.

Genus *Solitariphaedusa* Motochin & Ueshima **gen. nov.**

Type species: Mundiphaedusa miyoshii Kuroda & Minato, 1979

Diagnosis: Shell medium-sized. Apex rounded. Middle palatal plica(e) present, one or two, short. Lunella absent. Distribution: endemic to Northern Honshu (Akita, Iwate, Yamagata).

Morphology: Shell colour dark brown. Shell surface smooth, glossy in fresh specimen. Plicae and clausilium located at left lateral side. Principal plica present, long. Upper palatal plica present, short. Lower palatal plica short. Superior lamella developed, separated from the spiral lamella. Inferior lamella receded within the aperture, almost straightly ascending. Subcolumellar lamella not emerging at the aperture. Clausilium narrow. Diverticulum of bursa copulatrix developed. See also Diagnosis.

Reproduction: Oviparous.

Ecology: Terrestrial.

Distribution: As in Diagnosis.

Included taxon: S. miyoshii (Kuroda & Minato, 1979).

Remarks: Although the morphological features of the genus are identical to those of *Mundiphaedusa*, *Solitariphaedusa miyoshii* represents a distinct lineage independent from all other Japanese and Taiwanese clausiliids. The distribution of the type species, the only member of the genus, is restricted to a very narrow range of Northern Honshu, while the main islands of Japan are dominated by clausiliids of other lineages. *S. miyoshii* may be a relic of an old lineage that was almost swept out of Japan by major lineages. No clausiliid with morphology similar to *Solitariphaedusa* is known to date from China and Korea.

Etymology: The new generic name is derived from the Latin *solitarius* in reference to the phylogenetic position that is distantly isolated from all other Japanese clausiliids.

Discussion

Hereinafter, my newly proposed system for Japanese and Taiwanese clausiliids shall be used to denote taxa unless otherwise specified by the use of “traditional” genera.

Minor cases of mitochondrial introgression

Although phylogenetic relationships among Japanese clausiliids were largely concordant between nuclear and mitochondrial trees, exceptional cases of incongruity were found in the two species, *Stereophaedusa* (*Breviphaedusa*) *stereoma* (Pilsbry, 1901) and *Stereophaedusa* (*s. l.*) *cymatodes* (Pilsbry, 1905) (formerly, *Mesophaedusa cymatodes*). In the nuclear tree (Fig. 2.3), *S.* (*B.*) *stereoma* is included in a subclade exclusively comprising *Breviphaedusa* species within clade A, while *S.* (*s. l.*) *cymatodes* is placed outside but is related to the *Breviphaedusa* subclade, and the two species are neither sister species nor related to *Mesophaedusa* species. However, in the mtDNA tree (Fig. 2.4), *S.* (*B.*) *stereoma* and *S.* (*s. l.*) *cymatodes* appear as sister species within a subclade comprised of *Mesophaedusa* species, rather than the *Breviphaedusa* subclade. The phylogenetic positions of these species are therefore inconsistent between nuclear and mtDNA trees not only in their mutual phylogenetic relationship, but also in their phylogenetic affinity to *Breviphaedusa* or *Mesophaedusa*. It is notable that these problematic species are distributed within or near the area where the distribution ranges of *Breviphaedusa* and *Mesophaedusa* overlap (Fig. 2.10).

The observed conflict between nuclear and mitochondrial phylogenies, together with the geographic distribution, strongly suggests a hybrid origin of these species. It is generally accepted that in interspecific hybridization, mitochondrial introgression occurs more easily and persists for more generations than in the nuclear genome because of maternal inheritance and smaller effective population size (Ballard & Whitlock, 2004; Toews & Brelsford, 2012). Replacement of the authentic mitochondrial genome by introgressed mtDNA through past interspecific hybridization is reported in various animals including land snails (e.g. Shimizu & Ueshima, 2000; Hailer et al., 2012; Toews & Brelsford, 2012). The observed conflict must have been caused by past inter-subclade hybridization and subsequent mitochondrial introgressions because the presumably introgressed mtDNAs constitute a distinct lineage that is somewhat divergent from both “parental” mtDNAs. Two hypotheses may be raised to explain the process. One is that *Mesophaedusa*-type mtDNA introgressed independently into these species from the same donor species. The other hypothesis is that *Mesophaedusa*-type mtDNA introgressed into *S.* (*s. l.*) *cymatodes* and then further introgressed into *S.* (*B.*) *stereoma* from the former species, or vice versa. In either case, mitochondrial introgression is most likely to have occurred at least twice. The morphological features of *S.* (*B.*) *stereoma* are characteristic of *Breviphaedusa* and this is concordant with the *ITS* tree, supporting the view that the nuclear genome rather than mtDNA reflects the true evolutionary history of the species.

It is also notable that probable cases of mtDNA introgression were detected only in two species out of the 198 nominal Japanese clausiliids examined here. Inter-species mitochondrial introgression is a rare event in Japanese clausiliids, supporting the validity of the phylogenetic reconstruction based on combined data of mtDNA and nuclear *ITS* sequences.

Causes of conflict between the molecular phylogeny and traditional systems

The results of my molecular phylogenetic analysis were substantially discordant with all traditional morphology-based systems proposed to date (Figs 2.2–2.5, Table 2.1). The conflict is attributable to the following causes: 1) frequent homoplasy in characters previously thought to be taxonomically important, 2) rapid morphological changes in certain lineages, and 3) over-splitting of generic taxa. These issues are discussed below.

Traditional systems of Japanese clausiliids were either typological or based on a hypothesis of morphological evolution. In either case, the previous systems did not assume homoplastic evolutions of certain morphological characters, in particular, the morphologies of the lamellae, plicae, and clausilium. However, the present study revealed frequent parallel evolution in all the taxonomic characters in the Japanese and Taiwanese clausiliids (Fig. 2.7). More surprisingly, parallel evolution of a set of character states that characterize generic taxa also occurred repeatedly, resulting in non-monophyly of traditional genera (Fig. 2.7).

A notable example is the polyphyly of the traditional *Phaedusa* (*sensu lato*) according to Minato (1994) and Nordsieck (1998) which includes the traditional *Stereophaedusa*, *Breviphaedusa*, and *Pseudophaedusa* as subgenera. The diagnostic characters of the traditional *Phaedusa* (*sensu lato*) are: a spirally ascending inferior lamella that approaches the superior lamella near the aperture, absence of a lunella, a wide clausilium, and ovoviviparity (Nordsieck, 1998). This set of character states, however, has evolved independently and repeatedly in various lineages: at least once in clade E, once followed by multiple apomorphic changes or twice independently in clade F, and possibly five times in clade A. It is also notable that such *Phaedusa*-like character states are strongly associated with an arboreal habitat in the clausiliids examined. Almost all arboreal Japanese and Taiwanese clausiliids show such a combination of character states. These findings strongly suggest that some taxonomic characters may have changed in concert and that certain morphological characters may have evolved convergently under selection favoring a certain ecological condition and/or reproductive strategy. With the polyphyletic traditional *Hemizaptyx*, the occurrence of the *Hemizaptyx*-type plica in various lineages might be explained by the retention of plesiomorphic character states and/or independent reversal to a simple morphology of the plica. Although reconstruction of the detailed evolutionary process of each taxonomic character is beyond the scope of this study, there is no doubt that frequent parallel evolution in characters previously thought to be taxonomically important is a major cause for the conflict between the molecular phylogeny and the traditional systems in Japanese and Taiwanese clausiliids.

Frequent parallel evolution of the G-type CA has been demonstrated in many European clausiliids (Douris et al., 1998b; van Moorsel et al., 2000; Uit de Weerd et al., 2004; Hausdorf & Nägele, 2016). Transformation to the G-type CA from the ancestral type involves simultaneous morphological changes in many different shell characters. These include: enlargement of the clausilium plate, reduction of the principal plica and spiral lamella, occurrence of novel lamellae such as lamella fulcans, and shifting of certain plicae (Nordsieck, 2007). Repeated parallel evolutions of the G-type CA in the subfamily Alopiinae (Douris et al., 1998b; van Moorsel et al., 2000; Uit de Weerd et al., 2004) and the subfamily Clausiliinae (Hausdorf & Nägele, 2016) are remarkable examples showing that the same set of shell characters can change in concert and independently within related lineages and among unrelated lineages. It is thus highly possible for a different set of shell characters to change simultaneously and in parallel in Japanese clausiliids. The CA is a very complex structure and rich in taxonomic characters. However, I should be careful when using these characters for phylogenetic reconstruction because some of them are correlated with each other and apt to change in the same direction.

Another problem that also misleads morphology-based classification is sporadic and rapid morphological divergence occurring exclusively in certain lineages. For example, traditional *Diceratoptyx* was characterized by having a reduced lunella, a long principal plica, a short lower palatal plica that is widely separated from the lunella, a ventrally shifted clausilium, and a notched clausilium plate (Pilsbry, 1905). However, whereas all of these distinctive character states are autapomorphies of a single species, *Zaptyx* (*Z.*) *cladoptyx* (Pilsbry, 1905), within subclade D8, the plesiomorphic states of these characters are retained in the other members of this subclade. The acquisition of the suite of *Phaedusa*-type character states in "*Stereophaedusa*" species within subclade A4 is another example of rapid morphological changes that occurred only in a single lineage within a specious clade. Generic separation of such species based on the many autapomorphies results in paraphyly of the related taxa, and thus cannot be supported in view of phylogenetic classification. Morphological divergence in many different characters does not necessarily support a deep phylogenetic divergence of clausiliid snails.

The last problem in the traditional classifications of Japanese clausiliids is the over-splitting of generic taxa. This issue includes the over-splitting of genera or subgenera based on trivial differences and the over-ranking of supra-specific taxa. Some of the traditional genera, such as *Paganizaptyx* and *Vastina*, were not defined explicitly and by demonstrating clear differences from other genera (e.g. Azuma, 1982). Other traditional genera, such as *Spinulaphaedusa* and *Placeophaedusa*, were described based on a single character or character state that is variable in other genera (Minato, 1994). Nordsieck (1998) stated that the Japanese clausiliid genera and subgenera correspond only to subgenera and species groups of Western Palaearctic clausiliids, respectively.

Phylogeographic implications

Many of the tree topologies recovered by the molecular phylogenetic analysis showed strong correlation between phylogeny and biogeography rather than morphology. Such patterns of phylogeography are highly possible in terrestrial animals with low dispersability, like land snails. It has also been increasingly evident in European clausiliids that phylogenetic relationships revealed by molecular analyses are often more congruent with biogeography than morphology (Douris et al., 1998a, 2007; Uit de Weerd et al., 2004; Uit De Weerd & Gittenberger, 2005; Hausdorf & Nägele, 2016). As

I demonstrated with Japanese and Taiwanese clausiliids, frequent parallel evolutions of CA morphology have also occurred in European taxa (Douris et al., 1998b; van Moorsel et al., 2000; Uit de Weerd et al., 2004; Hausdorf & Nägele, 2016). Therefore, endemic speciation associated with parallel morphological changes is a dominant pattern of clausiliid evolution.

Another biogeographical point to be mentioned is the close phylogenetic relationships between some clausiliids endemic to Hachijo Islands and those endemic to the Northern Ryukyus. The Hachijo Islands are located 950 km east from the Northern Ryukyus. Despite the long geographical distance, close phylogenetic affinities between land snails respectively endemic to these island groups have been suggested for various land snail families including Clausiliidae (Habe, 1977). In fact, my molecular phylogeny revealed very close phylogenetic affinities between some clausiliids from those islands. These include the species pairs of *Reinia echo* (Pilsbry, 1909) and *R. nakadai* (Pilsbry, 1902), *Zaptyx* (*Z.*) *hachijoensis* (Pilsbry, 1901) and *Z.* (*Z.*) *daemonorum* (Pilsbry, 1902), and *Z.* (*Hemizaptyx*) *purissima* (Pilsbry, 1905) and *Z.* (*H.*) *pinto* (Pilsbry, 1901). Such a phylogeographical pattern, together with the low level of genetic divergence between these species pairs, strongly suggests recent over-sea dispersal between these islands, probably via sea currents.

Supra-generic classification of Phaedusinae

Minato (1994) did not provide any argument on phylogenetic relationships among clausiliid genera. Supra-generic classifications of Japanese clausiliids were proposed by Zilch (1959), Nordsieck (1998), Schileyko (2000), and Nordsieck (2007) (see Table 2.4).

Zilch (1959) classified Japanese taxa into three tribes, Megalophaeduseae, Phaeduseae, and Zaptycheae, while Nordsieck (1998) and Schileyko (2000) classified them into two tribes, Megalophaedusini and Phaedusini. Nordsieck's (1998) system is based on his own hypothesis on evolutionary changes of morphology of plicae. This system is unique in his argument of polyphyletic origin of zaptychoid genera. Schileyko's (2000) system is a modified version of Nordsieck (1998) with some genera being transferred between the two tribes. None of these systems is supported by this study because all the proposed tribes were revealed to be non-monophyletic. More recently, Nordsieck (2007) proposed that the subfamily Phaedusinae should be re-organised into two tribes:

Synprosphymini, which includes only the genus *Synprosphyma*, and Phaedusini, which includes all other genera of the subfamily. Although the result of my study is concordant with Nordsieck's (2007) system, the supra-generic classification of the subfamily Phaedusinae needs to be revised based on a more comprehensive molecular phylogenetic analysis covering more phaedusine taxa from China and Southeast Asia and many genera formerly included in the subfamily Serrulininae because the latter subfamily should be integrated with Phaedusinae (Uit de Weerd & Gittenberger, 2013).

Although the main focus of this study is the phylogeny of Japanese clausiliids, my data provides new insights for taxonomy of clausiliid taxa from other countries/regions. Phylogenetic relationships among some Chinese and Vietnamese clausiliids revealed by the molecular phylogeny are incongruent with Nordsieck's (2007) system in the following points. *Papilliphaedusa* Nordsieck, 2003 and *Margaritiphaedusa* Nordsieck, 2001 were recovered as non-monophyletic in my tree. Although Nordsieck (2007) regarded *Pseudonenia* Boettger, 1877 and *Acrophaedusa* Boettger, 1877 as synonyms of *Oospira* (*Oospira*) Blanford, 1872, and treated *Formosana*, *Atractophaedusa* Ehrmann, 1927, and *Formosanella* Nordsieck, 2003 as subgenera of *Oospira*, the examined species of these genera were not related to each other. The *Papilliphaedusa* species examined were not closely related to *Euphaedusa*, although the former genus was treated as a subgenus of the latter (Nordsieck, 2007). A Chinese "zaptychoid" species, "*Hemizaptyx*" *minuta* was not related to the true *Hemizaptyx* represented by the type species. Whereas *Selenophaedusa* Lindholm, 1924 and *Margaritiphaedusa* have been treated as subgenera of *Hemiphaedusa* (Nordsieck, 2007), examined species of these genera were not closely related to each other in my analysis. The taxonomy of these genera or subgenera must be revised by further molecular phylogenetic analysis using all the type species of these generic taxa.

Tables

Table 2.1. Historical changes of generic and subgeneric classifications of Japanese clausiliids.

Species and subspecies	Kuroda, 1963	Azuma, 1982	Minato, 1994	Nordsieck, 1998	Nordsieck, 2007
addisoni Pilsbry, 1901	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
adulta Käufel, 1930	*Zaptyx* (*Tyrannozaptyx*)	*Tyrannozaptyx*	*Tyrannozaptyx*	*Tyrannozaptyx*	*Tyrannozaptyx*
aenea Pilsbry, 1903	*Mundiphaedusa* (*Vitriphaedusa*)	*Vitriphaedusa*	*Mundiphaedusa* (*Vitriphaedusa*)	*Pliciphaedusa*	*Pliciphaedusa*
aethiops Moellendorff, 1882	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
affinis Minato & Tada, 1987	–	–	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
akiratadai Minato, 1978	–	*Neophaedusa*	*Neophaedusa*	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
albela Minato, 1976	–	*Neophaedusa*	*Neophaedusa*	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
aratorum Pilsbry, 1903	*Mundiphaedusa* (*Vitriphaedusa*)	*Vitriphaedusa*	*Mundiphaedusa* (*Vitriphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
arborea Tomiyama, 1984	–	*Phaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Pseudophaedusa*)	*Phaedusa* (*Pseudophaedusa*)
ashizuriensis Azuma, 1968	*Reinia* (*Proreinia*)	*Proreinia*	*Proreinia*	*Reinia* (*Proreinia*)	*Reinia* (*Reinia*)
asperata Pilsbry, 1905	Zaptyx (*Hemizaptyx*)	*Hemizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
attrita attrita Boettger, 1877	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
attrita infausta Pilsbry, 1902	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
aulacophora Pilsbry, 1900	*Mundiphaedusa* (*Aulacophaedusa*)	*Aulacophaedusa*	*Tyrannophaedusa* (*Aulacophaedusa*)	*Tyrannophaedusa* (*Aulacophaedusa*)	*Tyrannophaedusa* (*Aulacophaedusa*)
aurantiaca Boettger, 1877	*Tyrannophaedusa* (*Ventriphaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
azumai Pilsbry, 1905	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
bernardii Pfeiffer, 1861	*Tyrannophaedusa* (*Nesiophaedusa*)	*Nesiophaedusa*	*Nesiophaedusa*	*Luchuphaedusa* (*Nesiophaedusa*)	*Luchuphaedusa* (*Nesiophaedusa*)
bilabrata Smith, 1876	*Tyrannophaedusa* (*Decolliphaedusa*)	*Decolliphaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
buschi Küster, 1844	*Zaptychopsis*	*Zaptychopsis*	*Zaptychopsis*	*Zaptychopsis*	*Zaptychopsis*
callistochila Pilsbry, 1901	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
caloptyx caloptyx Pilsbry, 1902	Zaptyx (*Hemizaptyx*)	*Hemizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
caloptyx subtilis Kato, 1979	–	*Hemizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
caryostoma Moellendorff, 1882	*Tyrannophaedusa* (*Ventriphaedusa*)	*Ventriphaedusa*	–	–	–
cincticollis Ehrmann, 1900	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tosaphaedusa*	*Tyrannophaedusa* (*Tosaphaedusa*)	*Tyrannophaedusa* (*Tosaphaedusa*)
cladoptyx Pilsbry, 1905	*Zaptyx* (*Diceratoptyx*)	*Diceratoptyx*	*Diceratoptyx*	*Diceratoptyx*	*Diceratoptyx*

Table 2.1. *Continued*

comes Pilsbry, 1901	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*		–	*Euphaedusa* (*Tauphaedusa*)
costifera Kuroda & Taki, 1944	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
cymatodes Pilsbry, 1905	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
daemonorum Pilsbry, 1902	Zaptyx (*Metazaptyx*)	*Metazaptyx*	*Metazaptyx*	*Metazaptyx*	*Metazaptyx*
daitojimana Kuroda, 1960	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
dalli Pilsbry, 1902	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
decapitata Pilsbry, 1902	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
decussata Martens, 1877	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
deminuta Käufel, 1930	*Zaptyx* (*Tyrannozaptyx*)	*Tyrannozaptyx*	*Tyrannozaptyx*	*Tyrannozaptyx*	*Tyrannozaptyx*
digonoptyx Boettger, 1877	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*	*Euphaedusa*	*Euphaedusa*	*Euphaedusa* (*Tauphaedusa*)
dolichoptyx Pilsbry, 1908	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
dorcas Pilsbry, 1902	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
ducalis Kobelt, 1876	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
echo Pilsbry, 1909	*Reinia* (*Proreinia*)	*Proreinia*	*Proreinia*	*Reinia* (*Proreinia*)	*Reinia* (*Reinia*)
elegans Habe, 1962	*Reinia* (*Proreinia*)	*Proreinia*	*Proreinia*	*Reinia* (*Proreinia*)	*Reinia* (*Reinia*)
elongata Minato & Tada, 1979	–	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
entospira Pilsbry, 1901	*Zaptyx* (*Stereozaptyx*)	*Stereozaptyx*	*Stereozaptyx*	*Stereozaptyx*	*Stereozaptyx*
euholostoma Pilsbry, 1901	*Reinia* (*Pictophaedusa*)	*Pictophaedusa*	*Pictophaedusa*	*Reinia* (*Parareinia*)	*Reinia* (*Parareinia*)
exodonta Pilsbry, 1909	*Zaptyx* (*Stereozaptyx*)	*Stereozaptyx*	*Stereozaptyx*	*Stereozaptyx*	*Stereozaptyx*
expansilabris Boettger, 1878	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Placeophaedusa*	*Hemiphaedusa* (*Placeophaedusa*)	*Hemiphaedusa* (*Placeophaedusa*)
exulans Pilsbry, 1908	*Zaptyx* (*Stereozaptyx*)	*Stereozaptyx*	*Stereozaptyx*	*Stereozaptyx*	*Stereozaptyx*
fukudainadai Minato, 2014	–	–	–	–	–
goniopoma Pilsbry, 1902	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
gouldi A. Adams, 1868	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
gracilispira Mollendorff, 1882	*Mundiphaedusa* (*Aulacophaedusa*)	*Aulacophaedusa*	*Tyrannophaedusa* (*Aulacophaedusa*)	*Tyrannophaedusa* (*Aulacophaedusa*)	*Tyrannophaedusa* (*Aulacophaedusa*)
hachijoensis Pilsbry, 1901	Zaptyx (*Metazaptyx*)	*Metazaptyx*	*Metazaptyx*	*Metazaptyx*	*Metazaptyx*
hakonensis Pilsbry, 1900	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
hedleyi Pilsbry, 1905	Zaptyx (*Oligozaptyx*)	*Oligozaptyx*	*Oligozaptyx*	*Oligozaptyx*	*Oligozaptyx*

Table 2.1. *Continued*

hemileuca hemileuca Pilsbry, 1909	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Placeophaedusa*	*Pliciphaedusa*	*Pliciphaedusa*
hemileuca takii Kuroda, 1936	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Placeophaedusa*	*Pliciphaedusa*	*Pliciphaedusa*
hickonis fultoni Sykes, 1895	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
hickonis hickonis Boettger, 1877	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
higomonticola Minato & Tada, 1979	–	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
hiraseana Pilsbry, 1901	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
hirasei Pilsbry, 1900	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
holotrema Pilsbry, 1902	*Reinia* (*Pictophaedusa*)	*Pictophaedusa*	*Pictophaedusa*	*Reinia* (*Pictophaedusa*)	*Reinia* (*Pictophaedusa*)
hooyoensis Minato & Tada, 1987	–	–	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
hosayaka Pilsbry, 1905	*Tyrannophaedusa* (*Decolliphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
hungerfordiana Moellendorff, 1882	*Reinia* (*Pictophaedusa*)	*Pictophaedusa*	*Pictophaedusa*	*Reinia* (*Pictophaedusa*)	*Reinia* (*Pictophaedusa*)
hungerfordiana tokushimensis Kuroda & Abe, 1980	*Reinia* (*Pictophaedusa*)	*Pictophaedusa*	*Pictophaedusa*	*Reinia* (*Pictophaedusa*)	*Reinia* (*Pictophaedusa*)
hyperaptyx Pilsbry, 1905	Zaptyx (*Heterozaptyx*)	*Heterozaptyx*	*Heterozaptyx*	*Heterozaptyx*	*Heterozaptyx*
hyperoptyx Pilsbry, 1900	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
idioptyx Pilsbry, 1909	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
ignobilis Sykes, 1895	*Hemiphaedusa* (*Pinguiphaedusa*)	*Tyrannophaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
iijimakuniakii Minato & Habe, 1983	–	–	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
ijimae Ehrmann, 1900	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
ikenoi Minato, 1980	–	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
inclyta Pilsbry, 1908	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
interlamellaris Martens, 1876	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
inversiluna Pilsbry, 1908	*Zaptyx* (*Selenoptyx*)	*Selenoptyx*	*Selenoptyx*	*Selenoptyx*	*Selenoptyx*
iotaptyx Pilsbry, 1900	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
ishikawai Kuroda & Minato, 1975	Zaptyx (*Mesozaptyx*)	*Neophaedusa*	*Neophaedusa*	*Megalophaedusa* (*Mesozaptyx*)	*Megalophaedusa* (*Mesozaptyx*)
iyoensis Minato & Tada, 1977	–	*Tyrannophaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)

Table 2.1. *Continued*

jacobiana Pilsbry, 1902	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
jacobiella Pilsbry, 1909	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
japonica Crosse, 1871	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
kamoharai Kuroda, 1936	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Placeophaedusa*	–	*Pliciphaedusa*
kanjiookuboi Minato, 1980	–	*Tyrannophaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
kawamotoi Kuroda & Taki, 1944	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
kawasakii Kuroda, 1936	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
kikaiensis Pilsbry, 1905	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
koshikijimana Pilsbry, 1905	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Placeophaedusa*	*Pliciphaedusa*	*Pliciphaedusa*
kubinaga Kuroda, 1936	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
kuninoae Kuroda, 1936	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
kurozuensis Pilsbry, 1902	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
kusakakiensis Minato, 1982	–	–	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
kyotoensis Kuroda, 1936	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
longiplicata Pilsbry, 1908	Zaptyx (*Heterozaptyx*)	*Heterozaptyx*	*Pulchraptyx*	*Pulchraptyx*	*Pulchraptyx*
martensi Martens, 1860	*Megalophaedusa*	*Megalophaedusa*	*Megalophaedusa*	*Megalophaedusa* (*Megalophaedusa*)	*Megalophaedusa* (*Megalophaedusa*)
masaoi Habe, 1940	*Reinia* (*Pictophaedusa*)	*Pictophaedusa*	*Pictophaedusa*	*Reinia* (*Pictophaedusa*)	*Reinia* (*Pictophaedusa*)
masatokandai masatokandai Minato, 1978	–	*Neophaedusa*	*Neophaedusa*	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
masatokandai shiroi Minato, 1978	–	*Neophaedusa*	*Neophaedusa*	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
matsumurai Minato, 2014	–	–	–	–	–
micropeas Moellendorff, 1882	*Mundiphaedusa* (*Vitriphaedusa*)	*Vitriphaedusa*	*Mundiphaedusa* (*Vitriphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
mikado Pilsbry,1900	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
mikawa Pilsbry, 1905	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
mima Pilsbry, 1901	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
mitsukurii Pilsbry, 1902	*Megalophaedusa*	*Megalophaedusa*	*Megalophaedusa*	*Megalophaedusa* (*Megalophaedusa*)	*Megalophaedusa* (*Megalophaedusa*)
miyazakii Minato & Tada 1977	–	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)

Table 2.1. *Continued*

miyoshii Kuroda & Minato, 1979	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
moellendorffi Nordsieck, 2003	*Tyrannophaedusa* (*Ventriphaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	–
monelasmus Pilsbry, 1900	*Reinia* (*Pictophaedusa*)	*Pictophaedusa*	*Pictophaedusa*	*Reinia* (*Pictophaedusa*)	*Reinia* (*Pictophaedusa*)
morisakii Kuroda & Habe, 1980	–	*Aulacophaedusa*	*Tyrannophaedusa* (*Aulacophaedusa*)	*Tyrannophaedusa* (*Aulacophaedusa*)	*Tyrannophaedusa* (*Aulacophaedusa*)
moriyai Kuroda & Taki, 1944	*Megalophaedusa* (*Vastina*)	*Vastina*	*Mesophaedusa*	–	*Megalophaedusa* (*Mesophaedusa*)
munus Pilsbry, 1901	Zaptyx (*Heterozaptyx*)	*Heterozaptyx*	*Heterozaptyx*	*Heterozaptyx*	*Heterozaptyx*
nakadai Pilsbry, 1902	*Reinia* (*Proreinia*)	*Proreinia*	*Proreinia*	*Reinia* (*Proreinia*)	*Reinia* (*Reinia*)
nakanoshimana Pilsbry, 1909	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
nankaidoensis nankaidoensis Kuroda, 1955	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Spinulaphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
nankaidoensis yanoi Minato, 1987	–	–	*Tyrannophaedusa* (*Spinulaphaedusa*)	–	*Tyrannophaedusa* (*Tyrannophaedusa*)
neniopsis Pilsbry 1902	*Phaedusa* (*Pseudonenia*)	*Phaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Pseudophaedusa*)	*Phaedusa* (*Pseudophaedusa*)
nesiothauma Pilsbry, 1901	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Nesiophaedusa*)	*Luchuphaedusa* (*Nesiophaedusa*)
nishinoshimana Pilsbry, 1909	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
noviluna Pilsbry, 1908	*Zaptyx* (*Selenoptyx*)	*Selenoptyx*	*Selenoptyx*	*Selenoptyx*	*Selenoptyx*
nugax Pilsbry 1901	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
okimodoki Minato & Tada, 1990	–	–	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
oostoma Moellendorff, 1882	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	–	*Phaedusa* (*Stereophaedusa*)
ophidoon Pilsbry, 1905	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
oshimae degenerata Pilsbry, 1905	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
oshimae oshimae Pilsbry, 1901	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
oxycyma Pilsbry, 1902	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
oxypomatica Pilsbry, 1908	Zaptyx (*Heterozaptyx*)	*Heterozaptyx*	*Heterozaptyx*	*Heterozaptyx*	*Heterozaptyx*
pachyspira Pilsbry, 1902	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
pallens Moellendorff, 1882	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	–	*Phaedusa* (*Stereophaedusa*)
pattalus Pilsbry, 1905	Zaptyx (*Metazaptyx*)	*Metazaptyx*	*Metazaptyx*	*Metazaptyx*	*Metazaptyx*
pilsbryana Ancey, 1904	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)

Table 2.1. *Continued*

pilsbryi Nordsieck, 1997	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
pinguis A.Adams, 1868	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
pinto Pilsbry, 1901	Zaptyx (*Hemizaptyx*)	*Hemizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
plagioptyx Pilsbry, 1902	*Stereophaedusa* (*Breviphaedusa*)	*Breviphaedusa*	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
platyauchen Martens, 1877	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
platydera Martens, 1876	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
platyderula Pilsbry, 1903	*Tyrannophaedusa* (*Ventriphaedusa*)	*Ventriphaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
plicilabris A. Adams, 1868	*Tyrannophaedusa* (*Ventriphaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
polita Käufel, 1930	Zaptyx (*Hemizaptyx*)	*Hemizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
proba A.Adams, 1868	*Tyrannophaedusa* (*Ventriphaedusa*)	*Ventriphaedusa*	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
ptychocyma Pilsbry, 1901	Zaptyx (*Hemizaptyx*)	*Hemizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
puellaris Minato & Tada 1978	–	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
purissima Pilsbry, 1905	Zaptyx (*Hemizaptyx*)	–	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
rex Pilsbry, 1905	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
rhopalia Pilsbry, 1902	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
rowlandi Pilsbry & Gulick, in Pilsbry, 1902	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*	*Euphaedusa*	*Euphaedusa*	*Euphaedusa* (*Tauphaedusa*)
sarissa Pilsbry, 1905	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	–	*Zaptyx* (*Zaptyx*)
schmackeri Sykes, 1895	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Pinguiphaedusa*	*Hemiphaedusa* (*Pinguiphaedusa*)	*Hemiphaedusa* (*Pinguiphaedusa*)
senkakuensis Kuroda, 1960	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*	*Euphaedusa*	*Euphaedusa*	*Euphaedusa* (*Tauphaedusa*)
shikokuensis Moellendorff, 1901	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Placeophaedusa*	*Hemiphaedusa* (*Placeophaedusa*)	*Hemiphaedusa* (*Placeophaedusa*)
sieboldtii Pfeiffer, 1848	*Phaedusa* (*Pseudonenia*)	*Phaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Pseudophaedusa*)	*Phaedusa* (*Pseudophaedusa*)
spelaeonis Kuroda & Minato, 1975	–	*Neophaedusa*	*Neophaedusa*	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
stearnsii iriomotensis Kuroda, 1960	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*	*Euphaedusa*	*Euphaedusa*	*Euphaedusa* (*Tauphaedusa*)
stearnsii Pilsbry, 1894	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*	*Euphaedusa*	*Euphaedusa*	*Euphaedusa* (*Tauphaedusa*)
stenospira A. Adams, 1868	*Tyrannophaedusa* (*Decolliphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
stereoma Pilsbry, 1901	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)

Table 2.1. *Continued*

stimpsoni ikiensis Pilsbry, 1905	*Zaptyx* (*Paganizaptyx*)	*Paganizaptyx*	*Hemizaptyx*	–	*Hemiphaedusa* (*Hemizaptyx*)
stimpsoni stimpsoni A. Adams, 1868	*Zaptyx* (*Paganizaptyx*)	*Paganizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
striatella Pilsbry, 1901	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
strictaluna Boettger, 1877	*Zaptyx* (*Paganizaptyx*)	*Paganizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
subaculus Pilsbry, 1902	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*	*Euphaedusa*	*Euphaedusa*	*Euphaedusa* (*Tauphaedusa*)
subignobilis Pilsbry, 1902	*Zaptyx* (*Paganizaptyx*)	–	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
sublunellata Moellendorff, 1885	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
subulina Moellendorff, 1882	*Mundiphaedusa* (*Mundiphaedusa*)	–	–	–	–
sugimotonis misaki Minato & Tada, 1978	–	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
sugimotonis sugimotonis Minato & Tada, 1978	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
surugensis Pilsbry, 1902	*Tyrannophaedusa* (*Decolliphaedusa*)	*Decolliphaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
tabukii Kuroda & Minato, 1985	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
takarai Kuroda, 1960	*Zaptyx* (*Tyrannozaptyx?*)	*Tyrannozaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
tanegashimae Pilsbry, 1901	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
tantilla Pilsbry, 1902	*Zaptyx* (*Paganizaptyx*)	*Paganizaptyx*	*Hemizaptyx*	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)
tau Boettger, 1877	*Phaedusa* (*Euphaedusa*)	*Euphaedusa*	*Euphaedusa*	*Euphaedusa*	*Euphaedusa* (*Tauphaedusa*)
thaumatopoma Pilsbry, 1905	*Zaptyx* (*Parazaptyx*)	*Parazaptyx*	*Parazaptyx*	*Parazaptyx*	*Parazaptyx*
tokunoshimaensis Minato, 1997	–	*Phaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Pseudophaedusa*)	*Phaedusa* (*Pseudophaedusa*)
tosaensis Pilsbry, 1903	*Tyrannophaedusa* (*Decolliphaedusa*)	*Decolliphaedusa*	*Tyrannophaedusa* (*Decolliphaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)	*Tyrannophaedusa* (*Tyrannophaedusa*)
tosana Pilsbry, 1901	*Hemiphaedusa* (*Pinguiphaedusa*)	*Pinguiphaedusa*	*Placeophaedusa*	*Pliciphaedusa*	*Pliciphaedusa*
toshiyukii Minato & Habe, 1983	–	–	*Pauciphaedusa*	*Megalophaedusa* (*Pauciphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
tripleuroptyx Pilsbry, 1909	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
tryoni miyakejimana Pilsbry, 1905	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
tryoni Pilsbry, 1901	*Stereophaedusa* (*Breviphaedusa*)	*Stereophaedusa* (*Breviphaedusa*)	*Phaedusa* (*Breviphaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
ujiguntoensis Minato, 1982	–	–	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)

Table 2.1. *Continued*

ultima Pilsbry, 1909	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
una Pilsbry, 1902	*Tyrannophaedusa* (*Luchuphaedusa*)	*Luchuphaedusa*	*Luchuphaedusa*	*Luchuphaedusa* (*Luchuphaedusa*)	*Luchuphaedusa* (*Luchuphaedusa*)
valida Pfeiffer, 1850	*Stereophaedusa*	*Stereophaedusa*	*Phaedusa* (*Phaedusa*)	*Phaedusa* (*Stereophaedusa*)	*Phaedusa* (*Stereophaedusa*)
variegata A. Adams, 1868	*Reinia* (*Reinia*)	*Reinia*	*Reinia*	*Reinia* (*Reinia*)	*Reinia* (*Reinia*)
vasta Boettger, 1877	*Megalophaedusa* (*Vastina*)	*Vastina*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
viridiflava Boettger, 1877	*Mundiphaedusa* (*Mesophaedusa*)	*Mesophaedusa*	*Mesophaedusa*	*Megalophaedusa* (*Mesophaedusa*)	*Megalophaedusa* (*Mesophaedusa*)
yaeyamensis Pilsbry, 1905	*Zaptyx* (*Zaptyx*)	*Zaptyx*	*Zaptyx*	*Zaptyx*	*Zaptyx* (*Zaptyx*)
yagurai Kuroda, 1936	*Mundiphaedusa* (*Mundiphaedusa*)	*Mundiphaedusa*	*Mundiphaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)	*Megalophaedusa* (*Mundiphaedusa*)
yukitai Uozumi & Yamamoto, 1993	–	–	–	*Hemiphaedusa* (*Hemizaptyx*)	*Hemiphaedusa* (*Hemizaptyx*)

Table 2.2. List of taxa examined in this study. Unless otherwise stated, all samples were collected from Japan. Asterisks indicate that the sample was collected from or near the type locality of each taxon.

Species and subspecies	Synonymized taxa	Locality
Acrophaedusa sp.		Pagar Alam, South Sumatra, Indonesia
Atractophaedusa antibouddah (Nordsieck, 2003)		Cam Pha , Quảng Ninh Prov., Vietnam
Aulacophaedusa gracilispira (Mollendorff, 1882) 1		Mt. Otaki, Shionoe, Kagawa Pref.
Aulacophaedusa gracilispira (Mollendorff, 1882) 2		Shingu, Tatsuno, Hyogo Pref.
Aulacophaedusa gracilispira (Mollendorff, 1882) 3	*graciae* Pilsbry, 1902	Hukatani, Tanabe, Wakayama Pref.
Aulacophaedusa matsumurai Minato, 2014		*Mt. Kongo, Minamikawachi, Osaka Pref.
Aulacophaedusa morisakii (Kuroda & Habe, 1980)		Mt. Otaki, Mima, Tokushima Pref.
Dentiphaedusa spinula (Heudo, 1882) 1		Qingchengshan, Dujiangyan, Sichuan Province, China
Dentiphaedusa spinula (Heudo, 1882) 2		Qingchengshan, Dujiangyan, Sichuan Province, China
Diceratoptyx cladoptyx (Pilsbry, 1905)		*Mt. Tampatsu, Tokuno-shima Is., Kagoshima Pref.
Euphaedusa aculus (Benson, 1842)		Ertang, Pingle, Guangxi Province, China
Formosana splendens (Nordsieck, 2005)		Longsheng Hot Springs National Forest Park, Multinational Autonomous County of Longsheng, Guangxi Zhuang Autonomous Region, China
Formosana swinhoei Pfeiffer, 1865		Wutuku, Taipei, Taiwan
Formosanella bensoni (H. Adams, 1870)		Qingchengshan, Dujiangyan, Sichuan Province, China
Formosanella recedens (Boettger & Schmacker, 1894)		Shangqing Palace, Qingchengshan, Dujiangyan, Sichuan Province, China
Hemizaptyx asperata (Pilsbry, 1905)		*Sebi, Shimo-Koshiki Is., Kagoshima Pref.
Hemizaptyx caloptyx caloptyx (Pilsbry, 1902)		*Yakushima Is., Kagoshima Pref.
Hemizaptyx caloptyx subtilis Kato, 1979		*Yakushima Is., Kagoshima Pref.
Hemizaptyx kanaganensis Chang, 1980		Heping Station, Hualien, Taiwan
Hemizaptyx kosakai Kuroda, 1941		Taroko, Hualien, Taiwan
Hemizaptyx lushanensis Chang & Maeda, 1982 1		Meifeng, Nantou, Taiwan
Hemizaptyx lushanensis Chang & Maeda, 1982 2		Tsuifeng, Nantou, Taiwan
Hemizaptyx minuta (Yen, 1939)		Longsheng Hot Springs National Forest Park, Multinational Autonomous County of Longsheng, Guangxi Zhuang Autonomous Region, China
Hemizaptyx pinto (Pilsbry, 1901) 1		*Tanegashima Is., Kagoshima Pref.
Hemizaptyx pinto (Pilsbry, 1901) 2	*spicata* Pilsbry, 1909	*Akuseki Is., Kagoshima Pref.
Hemizaptyx polita (Käufel, 1930) 1		Mt. Urabudake, Yonaguni Is., Okinawa Pref.
Hemizaptyx polita (Käufel, 1930) 2		Yonaguni, Yonaguni Is., Okinawa Pref.
Hemizaptyx ptychocyma (Pilsbry, 1901) 1	*yakushimae* Pilsbry, 1901	*Yakushima Is., Kagoshima Pref.
Hemizaptyx ptychocyma (Pilsbry, 1901) 2		*Minamitane, Tanegashima Is., Kagoshima Pref.
Hemizaptyx purissima (Pilsbry, 1905)		*Kamitsuki, Miyake Is., Tokyo Pref.
Hemizaptyx similaris (H. Adams, 1866)		Sihchong River, Pingtung, Taiwan
Hemizaptyx sp. aff. *magaensis* Chang, 1991		Nantou, Taiwan
Hemizaptyx sp. cf. *pseudosheridani* (Zilch, 1954)		Hengchun Peninsula, Pingtung, Taiwan
Hemizaptyx stimpsoni (A. Adams, 1868)		*Tsushima Is., Nagasaki Pref.

Table 2.2. *Continued*

Hemizaptyx strictaluna (Boettger, 1877) 1		Nishino-shima Is., Oki, Shimane Pref.
Hemizaptyx strictaluna (Boettger, 1877) 2	*harimensis* Pilsbry, 1901	Yoshii, Ibara, Okayama Pref.
Hemizaptyx strictaluna (Boettger, 1877) 3		Shunan, Yamaguchi Pref.
Hemizaptyx strictaluna (Boettger, 1877) 4		Miyaura, Imabari, Ehime Pref.
Hemizaptyx takarai (Kuroda, 1960)		*Uotsuri Is., Senkaku Isls., Okinawa Pref.
Hemizaptyx tantilla (Pilsbry, 1902) 1		*Fukue Is., Goto, Nagasaki Pref.
Hemizaptyx tantilla (Pilsbry, 1902) 2		*Nakadori Is., Shin-Kami, Goto, Nagasaki Pref.
Hemizaptyx yukitai Uozumi & Yamamoto, 1993		*Osato, Kuro-shima Is., Kagoshima Pref.
Heterozaptyx oxypomatica (Pilsbry, 1908)		*Tatsugo, Amami-Oshima Is., Kagoshima Pref.
Luchuphaedusa azumai (Pilsbry, 1905)		*Sebi, Shimo-Koshiki Is., Kagoshima Pref.
Luchuphaedusa callistochila (Pilsbry, 1901)		Nago, Okinawa Island, Okinawa Pref.
Luchuphaedusa inclyta (Pilsbry, 1908)		Nakijin, Okinawa Island, Okinawa Pref.
Luchuphaedusa mima (Pilsbry, 1901) 1		*Amami-Oshima Is., Kagoshima Pref.
Luchuphaedusa mima (Pilsbry, 1901) 2	*tokunoshimana* Pilsbry, 1905	Mt. Amagidake, Tokuno-shima Is., Kagoshima Pref.
Luchuphaedusa ophidoon (Pilsbry, 1905) 1		*Sebi, Shimo-Koshiki Is., Kagoshima Pref.
Luchuphaedusa ophidoon (Pilsbry, 1905) 2		*Kashima, Shimo-Koshiki Is., Kagoshima Pref.
Luchuphaedusa oshimae degenerata (Pilsbry, 1905)		*Mt. Amagidake, Tokuno-shima Is., Kagoshima Pref.
Luchuphaedusa oshimae oshimae (Pilsbry, 1901)		*Amami-Oshima Is., Kagoshima Pref.
Luchuphaedusa una (Pilsbry, 1902)		*Fukue Is., Goto, Nagasaki Pref.
Margaritiphaedusa sp. aff. *amoena*		Youyicun, Qingchengshan, Dujiangyan, Sichuan Province, China
Margaritiphaedusa ziyuanensis (Chen & Zhang, 1999)		Longsheng Hot Springs National Forest Park, Multinational Autonomous County of Longsheng, Guangxi Zhuang Autonomous Region, China
Megalophaedusa martensi (Martens, 1860) 1		Suruga, Shizuoka, Shizuoka Pref.
Megalophaedusa martensi (Martens, 1860) 2		Yugashima, Izu, Shizuoka Pref.
Mesophaedusa aethiops (Moellendorff, 1882)		Amakusa, Kumamoto Pref.
Mesophaedusa cymatodes (Pilsbry, 1905) 1		Mt. Inaodake, Kinko, Kagoshima Pref.
Mesophaedusa cymatodes (Pilsbry, 1905) 2		Sukishimoda, Kobayashi, Miyazaki Pref.
Mesophaedusa elongata Minato & Tada, 1979		*Mitai, Takachiho, Miyazaki Pref.
Mesophaedusa hickonis fultoni (Sykes, 1895) 1		Tsuno, Takaoka, Kochi Pref.
Mesophaedusa hickonis fultoni (Sykes, 1895) 2	*sausia* Pilsbry, 1904	*Mt. Sodayama, Susaki, Kochi Pref.
Mesophaedusa hickonis hickonis (Boettger, 1877)		Mt. Kongo, Minamikawachi, Osaka Pref.
Mesophaedusa hiraseana (Pilsbry, 1901)		*Okino-shima Is., Sukumo, Kochi Pref.
Mesophaedusa hooyoensis Minato & Tada, 1987		Mt. Yokokura, Ochi, Kochi Pref.
Mesophaedusa ijimae (Ehrmann, 1900)		*Ryugado Cave, Kami, Kochi Pref.
Mesophaedusa ikenoi Minato, 1980 1		Komatsuzaki, Hamamatsu, Shizuoka Pref.
Mesophaedusa ikenoi Minato, 1980 2		Tenryu, Hamamatsu, Shizuoka Pref.
Mesophaedusa interlamellaris (Martens, 1876)		Itsuki, Kuma, Kumamoto Pref.
Mesophaedusa mikawa (Pilsbry, 1905)		Arai, Kosai, Shizuoka Pref.
Mesophaedusa moriyai (Kuroda & Taki, 1944)		Fukagawayumoto, Nagato, Yamaguchi Pref.
Mesophaedusa okimodoki Minato & Tada, 1990 1		Sakataniko, Nichinan, Miyazaki Pref.
Mesophaedusa okimodoki Minato & Tada, 1990 2		Sakataniko, Nichinan, Miyazaki Pref.
Mesophaedusa tabukii Kuroda & Minato, 1985		Mt. Konogaratake, Tarumizu, Kagoshima Pref.
Mesophaedusa ujiguntoensis Minato, 1982		Hachijo Is., Tokyo Pref.
Mesophaedusa vasta (Boettger, 1877) 1		Amakusa, Kumamoto Pref.

Table 2.2. *Continued*

Mesophaedusa vasta (Boettger, 1877) 2		Takaki, Isahaya, Nagasaki Pref.
Mesophaedusa viridiflava (Boettger, 1877)		*Mitai, Takachiho, Miyazaki Pref.
Mesozaptyx ishikawai (Kuroda & Minato, 1975)		*Chuo, Shimomaki, Kumamoto Pref.
Metazaptyx daemonorum (Pilsbry, 1902) 1	*viva* Pilsbry, 1905	*Mt. Nagoro, Tokuno-shima Is., Kagoshima Pref.
Metazaptyx daemonorum (Pilsbry, 1902) 2		Akune, Kagoshima Pref.
Metazaptyx daemonorum (Pilsbry, 1902) 3	*tokarana* Pilsbry, 1909	Mt. Megami-yama, Takara Is., Kagoshima Pref.
Metazaptyx daemonorum (Pilsbry, 1902) 4	*saccatibasis* Pilsbry, 1909	*Mt. Ontake, Nakano-shima Is., Kagoshima Pref.
Metazaptyx hachijoensis (Pilsbry, 1901)		*Hachijo-kojima Is., Tokyo Pref.
Metazaptyx pattalus (Pilsbry, 1905)		Miyako, Miyako Is., Okinawa Pref.
Mundiphaedusa akiratadai (Minato, 1978) 1		Mt. kanpu, Saijo, Ehime Pref.
Mundiphaedusa akiratadai (Minato, 1978) 2		Mt. kanpu, Saijo, Ehime Pref.
Mundiphaedusa albela (Minato, 1976)		Shiiba, Higashiusuki, Miyazaki Pref.
Mundiphaedusa aratorum (Pilsbry, 1903)		Yaiga, Takaoka, Kochi Pref.
Mundiphaedusa decapitata (Pilsbry, 1902)		Yamada, Kobe, Hyogo Pref.
Mundiphaedusa decussata (Martens, 1877)		*Mt. Tsukuba, Tsukuba, Ibaraki Pref.
Mundiphaedusa dorcas (Pilsbry, 1902) 1		Numazu, Shizuoka Pref.
Mundiphaedusa dorcas (Pilsbry, 1902) 2		Mt. Amari, Nirasaki, Yamanashi Pref.
Mundiphaedusa ducalis (Kobelt, 1876)		Mt. Hakusan, Hakusan, Ishikawa Pref.
Mundiphaedusa hosayaka (Pilsbry, 1905)		*Mt. Aomine, Toba, Mie Pref.
Mundiphaedusa iijimakuniakii Minato & Habe, 1983		Aoi, Shizuoka, Shizuoka Pref.
Mundiphaedusa kawasakii (Kuroda, 1936)		Shitara, Kitashitara, Aichi Pref.
Mundiphaedusa kuninoae (Pilsbry, 1936) 1	*matushimai* Habe, 1940	*Shirabu-Onsen, Yonezawa, Yamagata Pref.
Mundiphaedusa kuninoae (Pilsbry, 1936) 2	*discrepans* Azuma, 1982	Misaka, Fuefuki, Yamanashi Pref.
Mundiphaedusa kurozuensis (Pilsbry, 1902)		*Kozagawa, Higashimuro, Wakayama Pref.
Mundiphaedusa kyotoensis (Kuroda, 1936) 1		Mt. Kanmuri-yama, Imadate, Fukui Pref.
Mundiphaedusa kyotoensis (Kuroda, 1936) 2		Mt. Ibuki, Maibara, Shiga Pref.
Mundiphaedusa masatokandai masatokandai (Minato, 1978)		Mt. Goyodake, Hinokage, Miyazaki Pref.
Mundiphaedusa micropeas (Moellendorff, 1882) 1		Mt. Tsukuba, Tsukuba, Ibaraki Pref.
Mundiphaedusa micropeas (Moellendorff, 1882) 2		Mt. Mitsumine, Chichibu, Saitama Pref.
Mundiphaedusa micropeas (Moellendorff, 1882) 3	*hokkaidoensis* Pilsbry, 1901	*Assabu, Hiyama, Hokkaido Pref.
Mundiphaedusa miyoshii Kuroda & Minato, 1979 1		*Kunimi-Onsen, Shizukuishi, Iwate, Iwate Pref.
Mundiphaedusa miyoshii Kuroda & Minato, 1979 2		*Kunimi-Onsen, Shizukuishi, Iwate, Iwate Pref.
Mundiphaedusa miyoshii Kuroda & Minato, 1979 3		*Kunimi-Onsen, Shizukuishi, Iwate, Iwate Pref.
Mundiphaedusa pachyspira (Pilsbry, 1902)		*Miyai, Kumanogawa, Shingu, Wakayama Pref.
Mundiphaedusa pilsbryi (Nordsieck, 1997)		Misugi, Tsu, Mie Pref.
Mundiphaedusa rex (Pilsbry, 1905) 1		*Nashimoto, Kawazu, Shizuoka Pref.
Mundiphaedusa rex (Pilsbry, 1905) 2		*Nashimoto, Kawazu, Shizuoka Pref.
Mundiphaedusa rhopalia (Pilsbry, 1902) 1		Aoi, Shizuoka, Shizuoka Pref.
Mundiphaedusa rhopalia (Pilsbry, 1902) 2		Mt. Takao, Hachioji, Tokyo Pref.
Mundiphaedusa stenospira (A. Adams, 1868)		Fukatani, Tanabe, Wakayama Pref.
Mundiphaedusa sublunellata (Moellendorff, 1885)		Kamoi, Yokosuka, Kanagawa Pref.
Mundiphaedusa subulina (Moellendorff, 1882) 1		Kamoi, Yokosuka, Kanagawa Pref.
Mundiphaedusa subulina (Moellendorff, 1882) 2		*Nikko, Tochigi Pref.
Mundiphaedusa toshiyukii (Minato & Habe, 1983)		Mt. Omoridake, Miyazaki Pref.
Mundiphaedusa yagurai (Kuroda, 1936)		Otaki, Saitama Pref.

Table 2.2. *Continued*

Nesiophaedusa bernardii (Pfeiffer, 1861) 1		*Kume Is., Okinawa Pref.
Nesiophaedusa bernardii (Pfeiffer, 1861) 2	*okinoerabuensis* Pilsbry, 1905	*Okinoerabu Is., Kagoshima Pref.
Nesiophaedusa nesiothauma (Pilsbry, 1901) 1		*Tatsugo, Amami-Oshima Is., Kagoshima Pref.
Nesiophaedusa nesiothauma (Pilsbry, 1901) 2		*Mt. Amagidake, Tokuno-shima Is., Kagoshima Pref.
Oligozaptyx hedleyi (Pilsbry, 1905) 1		*Mt. Inokawadake, Tokuno-shima Is., Kagoshima Pref.
Oligozaptyx hedleyi (Pilsbry, 1905) 2	*hyperodonta* Pilsbry, 1908	*Uken, Amami-Oshima Is., Kagoshima Pref.
Oospira ootayoshinarii Hunyadi & Szekeres, 2016		Youyicun, Qingchengshan, Dujiangyan, Sichuan Province, China
Papilliphaedusa kunmingensis Chen & Zhang, 1999		West Hill forest Park, Xishan, Kunming, Yunnan Province, China
Papilliphaedusa porphyrea (Moellendorff, 1882)		Xinzhai, Yangshuo, Guangxi Zhuang Autonomous Region, China
Parareinia euholostoma (Pilsbry, 1901) 1		*Yugawara, Ashigarashimo, Kanagawa Pref.
Parareinia euholostoma (Pilsbry, 1901) 2		Mt. Amagi, Izu, Shizuoka Pref.
Parazaptyx thaumatopoma (Pilsbry, 1905)		*Kadekaru, Kume Is., Okinawa Pref.
Phaedusa dichroa (Bavay & Dautzenberg, 1899)		Dong Troi Cave, BaBe National Park, Vietnam
Phaedusa filicostata (Stoliczka, 1873)		Gua Bama, Kuala Lipis, Pahang, Malaysia
Phaedusa kelantanensis (Sykes, 1902)		Taman Negara, Merapoh, Pahang, Malaysia
Phaedusa sorella Nordsieck 2003		Na Phoong Cave, BaBe National Park, Vietnam
Pictophaedusa holotrema (Pilsbry, 1902)		Mt. Tamaki, Totsukawa, Nara Pref.
Pictophaedusa hungerfordiana hungerfordiana (Moellendorff, 1882) 1		Misugi, Tsu, Mie Pref.
Pictophaedusa hungerfordiana hungerfordiana (Moellendorff, 1882) 2		Kimino, Kaiso, Wakayama Pref.
Pictophaedusa hungerfordiana hungerfordiana (Moellendorff, 1882) 3		*Mt. Kasuga, Nara, Nara Pref.
Pictophaedusa hungerfordiana tokushimensis Kuroda & Abe, 1980		*Takarada, Anan, Tokushima Pref.
Pictophaedusa masaoi (Habe, 1940)		*Mt. Yokokura, Ochi, Kochi Pref.
Pictophaedusa monelasmus (Pilsbry, 1900) 1		Oshu, Iwate Pref.
Pictophaedusa monelasmus (PIlsbry, 1900) 2		*Assabu, Hiyama, Hokkaido Pref.
Pinguiphaedusa attrita attrita (Boettger, 1877) 1		Mt. Fujiwaradake, Inabe, Mie Pref.
Pinguiphaedusa attrita attrita (Boettger, 1877) 2		Mt. Hiei, Otsu, Shiga Pref.
Pinguiphaedusa attrita infausta (Pilsbry, 1902)		Aridagawa, Arida, Wakayama Pref.
Pinguiphaedusa hakonensis (Pilsbry, 1900) 1		Saru-shima Is., Yokosuka, Kanagawa Pref.
Pinguiphaedusa hakonensis (Pilsbry, 1900) 2		Mt. Kiyosumiyama, Kamogawa, Chiba Pref.
Pinguiphaedusa kawamotoi (Kuroda & Taki, 1944)		Fukagawayumoto, Nagato, Yamaguchi Pref.
Pinguiphaedusa kubinaga (Kuroda, 1936)		*Mt. Ishimaki, Toyohashi, Aichi Pref.
Pinguiphaedusa miyazakii (Minato & Tada 1977)		*Nanaore limestone cave, Nishi-usuki, Miyazaki Pref.
Pinguiphaedusa pinguis (A.Adams, 1868)		*Hiramatsu, Kushimoto, Wakayama Pref.
Pinguiphaedusa platyauchen (Martens, 1877) 1		Mt. Arafuneyama, Kanra, Gunma Pref.
Pinguiphaedusa platyauchen (Martens, 1877) 2		Kurikaeshifudo, Yonezawa, Yamagata Pref.
Pinguiphaedusa platyauchen (Martens, 1877) 3		Mt. Yamizo, Kuji, Ibaraki Pref.
Pinguiphaedusa platydera (Martens, 1876) 1		Mt. Horaiji, Shinshiro, Aichi Pref.
Pinguiphaedusa platydera (Martens, 1876) 2		Tanabe, Kashiwara, Osaka Pref.
Pinguiphaedusa platydera (Martens, 1876) 3		Mt. Hiei, Otsu, Shiga Pref.
Pinguiphaedusa puellaris (Minato & Tada 1978)		*Yakata Is., Saiki, Oita Pref.

Table 2.2. *Continued*

Pinguiphaedusa schmackeri (Sykes, 1895)		Ino, Agawa, Kochi Pref.
Pinguiphaedusa sugimotonis misaki (Minato & Tada, 1978)		*Misaki, Nishiuwa, Ehime Pref.
Pinguiphaedusa sugimotonis sugimotonis (Minato & Tada, 1978)		Oura, Saiki, Oita Pref.
Placeophaedusa awajiensis (Pilsbry, 1900) 1	*shikokuensis* Moellendorff, 1901	Mt. Yokokura, Ochi, Kochi Pref.
Placeophaedusa awajiensis (Pilsbry, 1900) 2		Shodo-shima Is., Kagawa Pref.
Placeophaedusa expansilabris (Boettger, 1878) 1		Mt. Shiratori, Yatsushiro, Kumamoto Pref.
Placeophaedusa expansilabris (Boettger, 1878) 2	*pigra* Pilsbry, 1902	Shingu, Tatsuno, Hyogo Pref.
Placeophaedusa expansilabris (Boettger, 1878) 3		Fukaura, Nishitsugaru Dist. Aomori Pref.
Pliciphaedusa aenea (Pilsbry, 1903)		Mt. Yokokura, Ochi, Kochi Pref.
Pliciphaedusa hemileuca hemileuca (Pilsbry, 1909)		*Mt. Oe-takayama, Oda, Shimane Pref.
Pliciphaedusa hemileuca takii (Kuroda, 1936)		Niyodogawa, Agawa, Kochi Pref.
Pliciphaedusa koshikijimana (Pilsbry, 1905)		*Sebi, Shimo-Koshiki Is., Kagoshima Pref.
Pliciphaedusa sp. aff. *tosana* 1		Tsuno, Kochi Pref.
Pliciphaedusa sp. aff. *tosana* 2		Tsuno, Takaoka, Kochi Pref.
Pliciphaedusa tosana (Pilsbry, 1901) 1		Niyodogawa, Agawa, Kochi Pref.
Pliciphaedusa tosana (Pilsbry, 1901) 2		Mt. Yokokura, Ochi, Kochi Pref.
Pseudonenia aenigmatica (Sykes, 1893)		Pagar Alam, South Sumatra, Indonesia
Pseudophaedusa arborea (Tomiyama, 1984)		*Uji-muko Is., Kagoshoma Pref.
Pseudophaedusa horikawai (Kuroda, 1941) 1		Taiwan
Pseudophaedusa horikawai (Kuroda, 1941) 2		Feng Mei, Miaoli, Taiwan
Pseudophaedusa neniopsis (Pilsbry 1902) 1		*Amami-Oshima Is., Kagoshima Pref.
Pseudophaedusa neniopsis (Pilsbry 1902) 2		*Amami-Oshima Is., Kagoshima Pref.
Pseudophaedusa sieboldtii (Pfeiffer, 1848) 1		Shiroyama, Kagoshima, Kagoshima Pref.
Pseudophaedusa sieboldtii (Pfeiffer, 1848) 2		Tsushima Is., Nagasaki Pref.
Pseudophaedusa tokunoshimaensis (Minato, 1997) 1		*Mt. Inokawadake, Tokuno-shima Is., Kagoshima Pref.
Pseudophaedusa tokunoshimaensis (Minato, 1997) 2		*Mt. Amagidake, Tokuno-shima Is., Kagoshima Pref.
Pulchraptyx longiplicata (Pilsbry, 1908)		*Mt. Nakadake, Akajima Is., Okinawa Pref.
Reinia ashizuriensis (Azuma, 1968) 1	*vaga* Pilsbry, 1909	Amami-Oshima Is., Kagoshima Pref.
Reinia ashizuriensis (Azuma, 1968) 2	*vaga* Pilsbry, 1909	Akuseki Is., Kagoshima Pref.
Reinia eastlakeana tayalis (Kuroda, 1941) 1		Xiulin, Hualien, Taiwan
Reinia eastlakeana tayalis (Kuroda, 1941) 2		Xiulin, Hualien, Taiwan
Reinia echo (Pilsbry, 1909)		*Akuseki Is., Kagoshima Pref.
Reinia elegans (Habe, 1962)		*Komi, Iriomotejima Is., Okinawa Pref.
Reinia nakadai (Pilsbry, 1902)		*Hachijo Is., Tokyo Pref.
Reinia variegata (A. Adams, 1868) 1		Tokyo Imperial Palace, Chiyoda, Tokyo Pref.
Reinia variegata (A. Adams, 1868) 2	*nesiotica* Pilsbry, 1901	*Hachijo Is., Tokyo Pref.
Reinia variegata (A. Adams, 1868) 3	*nesiotica* Pilsbry, 1901	*Hachijo-kojima Is., Tokyo Pref.
Reinia variegata (A. Adams, 1868) 4		Mt. Kasayama, Hagi, Yamaguchi Pref.
Selenophaedusa bavayi (Nordsieck, 2002)		Longsheng Hot Springs National Forest Park, Multinational Autonomous County of Longsheng, Guangxi Zhuang Autonomous Region, China
Selenoptyx inversiluna (Pilsbry, 1908)		Mt. Nekumachidji, Okinawa Island, Okinawa Pref.

Table 2.2. *Continued*

Selenoptyx noviluna (Pilsbry, 1908)		*Mt. Koshidake, Iheya Is., Okinawa Pref.
Serriphaedusa violacea Grego & Szekeres, 2011		Shangqing Palace, Qingchengshan, Dujiangyan, Sichuan Province, China
Stereophaedusa addisoni (Pilsbry, 1901) 1		Kushima, Miyazaki Pref.
Stereophaedusa addisoni (Pilsbry, 1901) 2		Hakotsukuri, Hannan, Osaka Pref.
Stereophaedusa costifera Kuroda & Taki, 1944		Yoshii, Ibara, Okayama Pref.
Stereophaedusa goniopoma (Pilsbry, 1902) 1		*Shirasaki, Wakayama, Wakayama Pref.
Stereophaedusa goniopoma (Pilsbry, 1902) 2		*Wakayama Castle, Wakayama, Wakayama Pref.
Stereophaedusa gouldi (A. Adams, 1868) 1		Shimoda, Shizuoka Pref.
Stereophaedusa gouldi (A. Adams, 1868) 2		Kamoi, Yokosuka, Kanagawa Pref.
Stereophaedusa gouldi (A. Adams, 1868) 3		Saru-shima Is., Yokosuka, Kanagawa Pref.
Stereophaedusa gouldi (A. Adams, 1868) 4	*hondana* Pilsbry, 1901	*Amatsu, Kamogawa, Chiba Pref.
Stereophaedusa jacobiana (Pilsbry, 1902) 1		*Nishinoomote, Tanegashima Is., Kagoshima Pref.
Stereophaedusa jacobiana (Pilsbry, 1902) 2		*Nishinoomote, Tanegashima Is., Kagoshima Pref.
Stereophaedusa jacobiella (Pilsbry, 1909)		*Akuseki Is., Kagoshima Pref.
Stereophaedusa japonica (Crosse, 1871) 1	*echigoensis* Pilsbry, 1903	Agewa, Kashiwazaki, Niigata Pref.
Stereophaedusa japonica (Crosse, 1871) 2		Kitaura, Nobeoka, Miyazaki Pref.
Stereophaedusa japonica (Crosse, 1871) 3	*okinoshimana* Pilsbry, 1902	*Okino-shima Is., Sukumo, Kochi Pref.
Stereophaedusa japonica (Crosse, 1871) 4	*eurystoma* Martens, 1877	Mt. Yamizo, Kuji, Ibaraki Pref.
Stereophaedusa japonica (Crosse, 1871) 5	*vespertina* Pilsbry, 1908	*Nishino-shima Is., Oki, Shimane Pref.
Stereophaedusa japonica (Crosse, 1871) 6	*kobensis* Smith, 1876	*Yamada, Kobe, Hyogo Pref.
Stereophaedusa nishinoshimana (Pilsbry, 1909)		*Nishino-shima Is., Oki, Shimane Pref.
Stereophaedusa nugax (Pilsbry 1901) 1		*Funayuki, Yakushima Is., Kagoshima Pref.
Stereophaedusa nugax (Pilsbry 1901) 2		*Nagakubo, Yakushima Is., Kagoshima Pref.
Stereophaedusa oostoma chichibuensis Sorita & Azuma, 1982		*Mt. Mitsumine, Chichibu, Saitama Pref.
Stereophaedusa oostoma oostoma (Moellendorff, 1882)		Kamisone, Kofu, Yamanashi Pref.
Stereophaedusa pallens (Moellendorff, 1882)		*Ikawadani, Kobe, Hyogo Pref.
Stereophaedusa stereoma (Pilsbry, 1901) 1		*Onoaida, Yakushima Is., Kagoshima Pref.
Stereophaedusa stereoma (Pilsbry, 1901) 2		*Funayuki, Yakushima Is., Kagoshima Pref.
Stereophaedusa stereoma (Pilsbry, 1901) 3	*cognata* Pilsbry, 1901	*Nishinoomote, Tanegashima Is., Kagoshima Pref.
Stereophaedusa striatella (Pilsbry, 1901)		*Miyako, Miyako Is., Okinawa Pref.
Stereophaedusa tripleuroptyx (Pilsbry, 1909)		*Kuro-shima Is., Kagoshima Pref.
Stereophaedusa tryoni miyakejimana (Pilsbry, 1905)		*Tsubota, Miyake Is., Tokyo Pref.
Stereophaedusa tryoni tryoni (Pilsbry, 1901)		*Hachijo-kojima Is., Tokyo Pref.
Stereophaedusa ultima (Pilsbry, 1909)		*Nakatani, Okino-shima Is., Oki, Shimane Pref.
Stereophaedusa valida fasciata Sykes, 1893		*Camp Gonsalves, Higashi, Okinawa Is., Okinawa Pref.
Stereophaedusa valida valida (Pfeiffer, 1850)		*Chinen, Nanjo, Okinawa Is., Okinawa Pref.
Stereozaptyx entospira (Pilsbry, 1901)		*Nishinoomote, Tanegashima Is., Kagoshima Pref.
Stereozaptyx exodonta (Pilsbry, 1909)		*Tatsugo, Amami-Oshima Is., Kagoshima Pref.

Table 2.2. *Continued*

Stereozaptyx exulans (Pilsbry, 1908)	*Tatsugo, Amami-Oshima Is., Kagoshima Pref.
Synprosphyma babeensis (Bavay & Dautzenberg, 1899)	Dong Troi Cave, BaBe National Park, Vietnam
Synprosphyma basillissa planicollis Nordsieck, 2007	Tai'an, Dujiangyan, Sichuan Province, China
Synprosphyma sp.	Tai'an, Dujiangyan, Sichuan Province, China
Tauphaedusa comes (Pilsbry, 1900)	Ikawadani, Kobe, Hyogo Pref.
Tauphaedusa digonoptyx (Boettger, 1877)	Oshimizu, Kashiwazaki, Niigata Pref.
Tauphaedusa sp.	Assabu, Hiyama, Hokkaido Pref.
Tauphaedusa stearnsii iriomotensis (Kuroda, 1960) 1	*Ohara, Iriomotejima Is., Okinawa Pref.
Tauphaedusa stearnsii iriomotensis (Kuroda, 1960) 2	*Mt. Komidake, Iriomotejima Is., Okinawa Pref.
Tauphaedusa stearnsii stearnsii (Pilsbry,1894) 1	*Miyara, Ishigaki Is., Okinawa Pref.
Tauphaedusa stearnsii stearnsii (Pilsbry,1894) 2	Mt. Omange, Ishigaki Is., Okinawa Pref.
Tauphaedusa subaculus (Pilsbry, 1902) 1	Konan, Miyazaki, Miyazaki Pref.
Tauphaedusa subaculus (Pilsbry, 1902) 2	Hirano, Kagoshima, Kagoshima Pref.
Tauphaedusa tau (Boettger, 1877) 1	Matsusaka, Mie Pref.
Tauphaedusa tau (Boettger, 1877) 2	The University of Tokyo, Bunkyo, Tokyo Pref.
Thaumatoptyx crassilamellata (Kuroda, 1941)	Fengtian, Hualien, Taiwan
Thaumatoptyx sp.	Taroko National Park, Xiulin, Hualien, Taiwan
Thaumatoptyx sp. cf. *aptyx*	Jianshi, Hsinchu, Taiwan
Thaumatoptyx sp. cf. *diacoptyx* 1	Sungkang, Nantou, Taiwan
Thaumatoptyx sp. cf. *diacoptyx* 2	Tsuifeng, Nantou, Taiwan
Thaumatoptyx sp. cf. *gonyptyx*	Cingjing Farm, Ren'ai, Nantou, Taiwan
Tosaphaedusa cincticollis (Ehrmann, 1900) 1	*Tosayamakuwao, Kochi, Kochi Pref.
Tosaphaedusa cincticollis (Ehrmann, 1900) 2	*Tosayamakuwao, Kochi, Kochi Pref.
Tyrannophaedusa aurantiaca (Boettger, 1877) 1	Yamada, Kobe, Hyogo Pref.
Tyrannophaedusa aurantiaca (Boettger, 1877) 2	Yura, Hidaka, Wakayama Pref.
Tyrannophaedusa bilabrata (Smith, 1876) 1	Kushima, Omura, Nagasaki Pref.
Tyrannophaedusa bilabrata (Smith, 1876) 2	Fukue Is., Goto, Nagasaki Pref.
Tyrannophaedusa bilabrata (Smith, 1876) 3	Shingu, Tatsuno, Hyogo Pref.
Tyrannophaedusa caryostoma (Moellendorff, 1882) 1	Mt. Otaki, Shionoe, Kagawa Pref.
Tyrannophaedusa caryostoma (Moellendorff, 1882) 2	Mihama, Hidaka, Wakayama Pref.
Tyrannophaedusa dalli (Pilsbry, 1902)	*Sui-i, Anan, Tokushima Pref.
Tyrannophaedusa fukudainadai Minato, 2014	*Oge-jima Is., Naruto, Tokushima Pref.
Tyrannophaedusa iotaptyx (Pilsbry, 1900)	*Mt. Ibuki, Maibara, Shiga Pref.
Tyrannophaedusa kanjiookuboi Minato, 1980	*Okushiri Is., Hokkaido Pref.
Tyrannophaedusa mikado (Pilsbry,1900) 1	*Mt. Ibuki, Maibara, Shiga Pref.
Tyrannophaedusa mikado (Pilsbry,1900) 2	*Mt. Ibuki, Maibara, Shiga Pref.
Tyrannophaedusa moellendorffi Nordsieck, 2003	Shingu, Tatsuno, Hyogo Pref.
Tyrannophaedusa nankaidoensis (Kuroda, 1955)	Hukatani, Tanabe, Wakayama Pref.
Tyrannophaedusa oxycyma (Pilsbry, 1902)	*Mt. Takakuma, Kanoya, Kagoshima Pref.
Tyrannophaedusa pilsbryana (Ancey, 1904) 1	Saigawa, Miyako, Fukuoka Pref.
Tyrannophaedusa pilsbryana (Ancey, 1904) 2	*Amakusa, Kumamoto Pref.
Tyrannophaedusa plicilabris (A. Adams, 1868)	*Shirahama, Nishimuro, Wakayama Pref.
Tyrannophaedusa proba (A. Adams, 1868)	*Kushimoto, Higashimuro, Wakayama Pref.
Tyrannophaedusa sp.	Koizumi, Maibara, Shiga Pref.
Tyrannophaedusa surugensis (Pilsbry, 1902)	Shimoda, Shizuoka Pref.
Tyrannophaedusa tanegashimae (Pilsbry, 1901) 1	*Nishinoomote, Tanegashima Is., Kagoshima Pref.
Tyrannophaedusa tanegashimae (Pilsbry, 1901) 2	Yakushima Is., Kagoshima Pref.
Tyrannophaedusa tosaensis (Pilsbry, 1903)	*Hidaka, Takaoka, Kochi Pref.

Table 2.2. *Continued*

Tyrannophaedusa ventriluna (Pilsbry, 1905)	Muroto, Kochi Pref.
Tyrannozaptyx adulta Käufel, 1930 1	*Ishigaki Is., Okinawa Pref.
Tyrannozaptyx adulta Käufel, 1930 2	Taketomi, Iriomote Is., Okinawa Pref.
Tyrannozaptyx deminuta (Käufel, 1930) 1	*Mt. Omotodake, Ishigaki Is., Okinawa Pref.
Tyrannozaptyx deminuta (Käufel, 1930) 2	*Mt. Maesedake, Ishigaki Is., Okinawa Pref.
Zaptychopsis buschii (Küster, 1844) 1	The University of Tokyo, Bunkyo, Tokyo Pref.
Zaptychopsis buschii (Küster, 1844) 2	Kurikaeshifudo, Yonezawa, Yamagata Pref.
Zaptyx dolichoptyx (Pilsbry, 1908)	*Kunigami, Okinawa Is., Okinawa Pref.
Zaptyx hirasei (Pilsbry, 1900)	Ao-shima Is., Miyazaki, Miyazaki Pref.
Zaptyx hyperoptyx (Pilsbry,1900)	*Motobu, Okinawa Island, Okinawa Pref.
Zaptyx kikaiensis (Pilsbry, 1905)	Kamiya, Amami-Oshima Is., Kagoshima Pref.
Zaptyx kotoshoensis Kuroda, 1932	Lanyu Is., Taitung, Taiwan
Zaptyx nakanoshimana (Pilsbry, 1909)	*Nakano-shima Is., Kagoshima Pref.
Zaptyx sarissa (Pilsbry, 1905)	*China, Okinoerabu Is., Kagoshima Pref.
Zaptyx yaeyamensis (Pilsbry, 1905)	*Yonehara, Ishigaki Is., Okinawa Pref.

Table 2.3. Primers used for PCR amplification and sequencing. PCR primers were highlighted in bold italic.

Primer	Sequence (5' –3')	Direction	Target	Reference
18S-1666	TTTGYACACACCGCCCGTCG	Forward	*ITS1*-5.8S-*ITS2*	Winnepenninckx et al., 1994
18S-1676	CCTCGGATTGGTCTCGGTCT	Forward	*ITS1*	This study
ls5.8f	CATTGAACATCGACATCTTGAACGC	Forward	*ITS2*	Kameda et al., 2007
ls5.8r	GCGTTCAAGATGTCGATGTTCAATG	Reverse	*ITS1*	Kameda et al., 2007
28S-700R	GGTACTTGTCCGCTATCGGA	Reverse	*ITS1*-5.8S-*ITS2*	This study
ND1-2N	GCNGARACNAAYCGNGCNCCNTTYGA	Forward	*ND1-ND4L-Cytb*	Ueshima & Asami, 2003
ND1-3N	CCNTTYGAYTTYGCNGARGGNGA	Forward	*ND1-ND4L-Cytb*	Ueshima & Asami, 2003
Cb268R	ATNGCRTANGCRAANARRAARTAYCAYTC	Reverse	*ND1-ND4L-Cytb*	Ueshima & Asami, 2003
Cb264R	RAARTAYCAYTCNGGYTGRATRTG	Reverse	*ND4L-Cytb*	This study
Cb366F	GGNTAYGTNYTNCCNTGRGGNCA	Forward	*Cytb*	This study

Table 2.4. Historical changes of supra-generic classifications of Japanese clausiliids.

Zilch, 1959	Nordsieck, 1998	Schileyko, 2000	Nordsieck, 2007
Megalophaeduseae	**Megalophaedusini**	**Megalophaedusini**	**Phaedusini**
Megalophaedusa	*Megalophaedusa*	*Hemiphaedusa*	*Megalophaedusa*
(*Megalophaesusa*)	(*Mesophaedusa*)	(*Hemizaptyx*)	(*Mesophaedusa*)
(*Vastina*)	(*Mesozaptyx*)	(*Pinguiphaedusa*)	(*Mesozaptyx*)
Mesophaedusa	(*Megalophaedusa*)	(*Placeophaedusa*)	(*Megalophaedusa*)
Hemiphaedusa	(*Mundiphaedusa*)	*Megalophaedusa*	(*Mundiphaedusa*)
(*Tyrannophaedusa*)	(*Pauciphaedusa*)	(*Megalophaedusa*)	*Pliciphaedusa*
(*Tosaphaedusa*)	*Pliciphaedusa*	(*Mesophaedusa*)	*Hemiphaedusa*
Luchuphaedusa	*Hemiphaedusa*	(*Mundiphaedusa*)	(*Hemizaptyx*)
(*Luchuphaedusa*)	(*Hemizaptyx*)	(*Pauciphaedusa*)	(*Pinguiphaedusa*)
(*Oophaedusa*)	(*Pinguiphaedusa*)	*Zaptychopsis*	(*Placeophaedusa*)
Nesiophaedusa	(*Placeophaedusa*)	*Zaptyx*	*Zaptychopsis*
	Zaptychopsis	*Tyrannophaedusa*	*Zaptyx*
Phaeduseae	*Zaptyx*	(*Tyrannophaedusa*)	(*Zaptyx*)
Stereophaedusa	*Tyrannophaedusa*	(*Aulacophaedusa*)	*Tyrannophaedusa*
Phaedusa	(*Aulacophaedusa*)	*Pliciphaedusa*	(*Tyrannophaedusa*)
(*Euphaedusa*)	(*Tyrannophaedusa*)	*Euphaedusa*	(*Tosaphaedusa*)
Reinia	(*Tosaphaedusa*)		*Tyrannozaptyx*
(*Proreinia*)	*Heterozaptyx*	**Phaedusini**	*Heterozaptyx*
(*Reinia*)	*Pulchraptyx*	*Neophaedusa*	*Pulchraptyx*
	Tyrannozaptyx	*Tyrannozaptyx*	*Selenoptyx*
Zaptycheae	*Selenoptyx*	*Heterozaptyx*	*Stereozaptyx*
Zaptychopsis	*Stereozaptyx*	*Pulchraptyx*	*Diceratoptyx*
Zaptyx	*Diceratoptyx*	*Selenoptyx*	*Luchuphaedusa*
(*Hemizaptyx*)	*Luchuphaedusa*	*Stereozaptyx*	(*Luchuphaedusa*)
(*Heterozaptyx*)	(*Luchuphaedusa*)	*Diceratoptyx*	(*Nesiophaedusa*)
(*Zaptyx*)	(*Nesiophaedusa*)	*Luchuphaedusa*	*Oligozaptyx*
Metazaptyx	*Oligozaptyx*	(*Luchuphaedusa*)	*Phaedusa*
(*Metazaptyx*)		(*Nesiophaedusa*)	(*Pseudophaedusa*)
(*Parazaptyx*)	**Phaedusini**	*Oligozaptyx*	(*Stereophaedusa*)
(*Stereozaptyx*)	*Phaedusa*	*Tosaphaedusa*	*Reinia*
Selenoptyx	(*Pseudophaedusa*)	*Metazaptyx*	(*Pictophaedusa*)
(*Selenoptyx*)	(*Stereophaedusa*)	*Phaedusa*	(*Parareinia*)
(*Thaumatoptyx*)	*Parazaptyx*	(*Pseudophaedusa*)	(*Reinia*)
(*Tyrannozaptyx*)	*Metazaptyx*	(*Stereophaedusa*)	*Euphaedusa*
Oligozaptyx	*Reinia*	*Parazaptyx*	(*Tauphaedusa*)
(*Oligozaptyx*)	(*Pictophaedusa*)	*Thaumatoptyx*	*Metazaptyx*
(*Diceratoptyx*)	(*Parareinia*)	*Reinia*	
(*Idiozaptyx*)	(*Proreinia*)	(*Parareinia*)	
	(*Reinia*)	(*Proreinia*)	
	Euphaedusa	(*Reinia*)	
		(*Pictophaedusa*)	

Figures

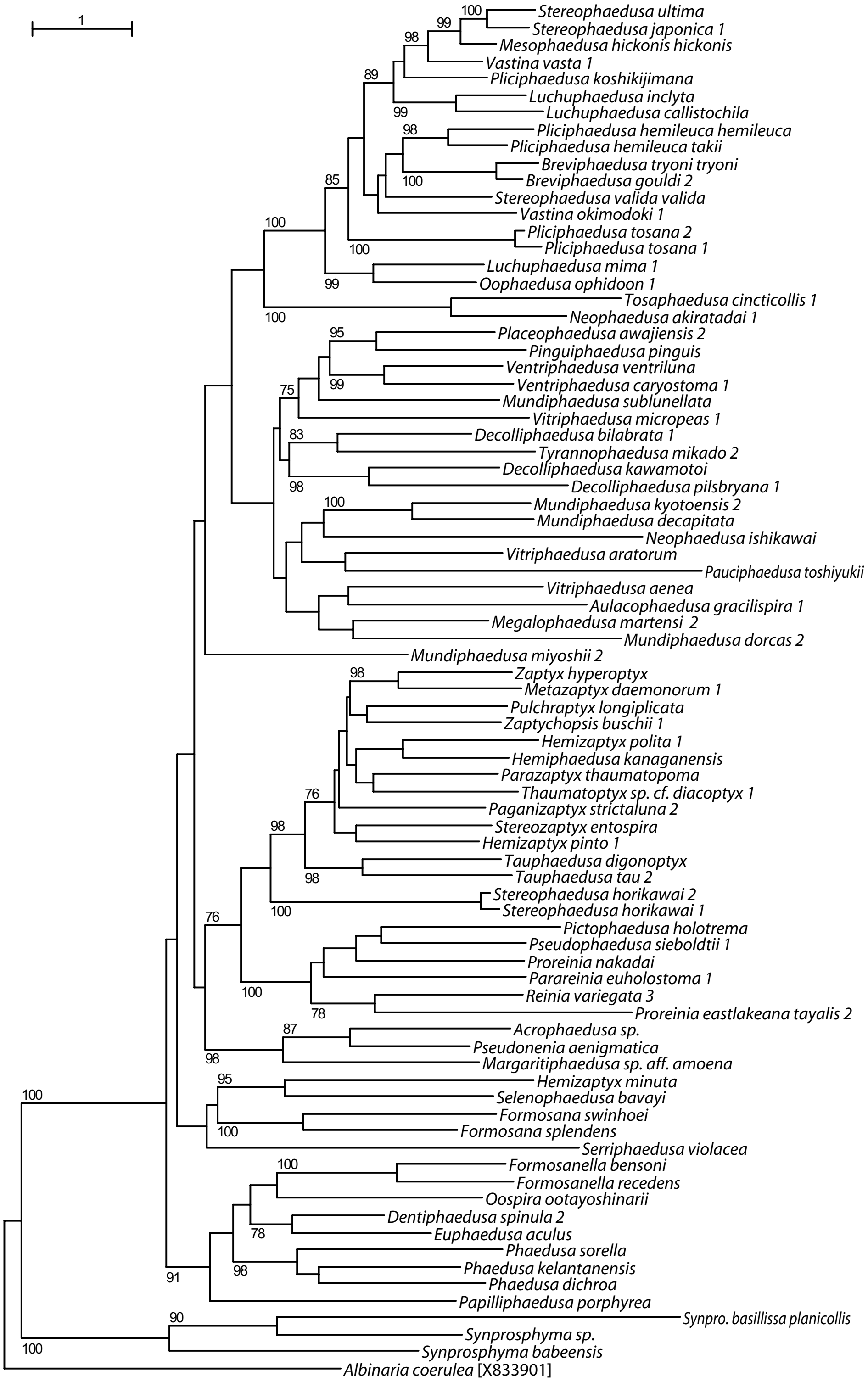

Figure 2.1. A preliminary maximum likelihood (ML) tree for 80 phaedusine clausiliid species based on mtDNA genes. An European cluasiliiid *Albinaria coerulea*, which belongs to a different subfamily Alopiinae, was used as the outgroup. Numbers at each branch indicate ML bootstraps (100 replicates) (when ≧70).

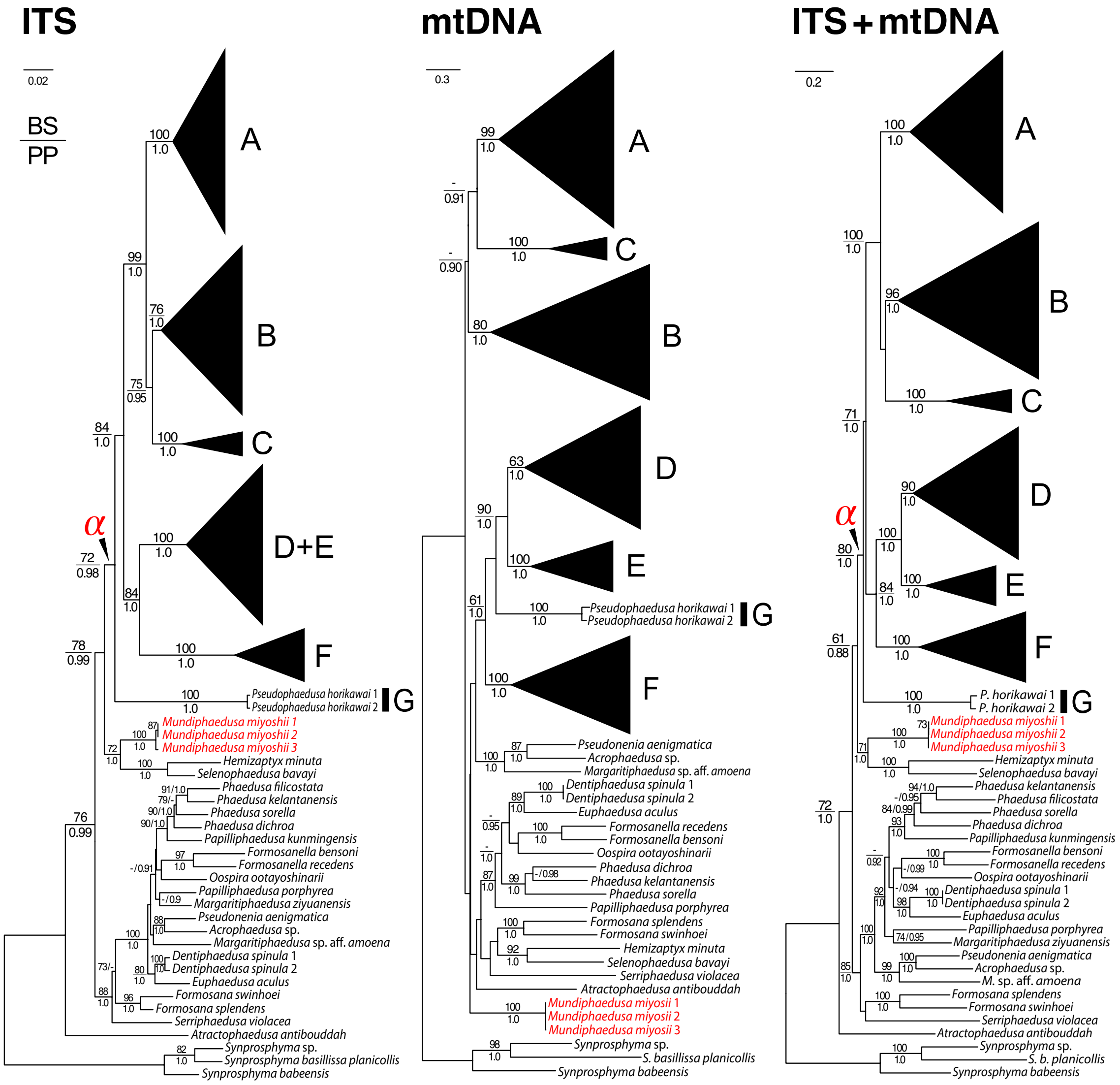

Figure 2.2. ML trees of Japanese clausiliids based on nuclear *ITS* (left), mtDNA (middle), and the combined sequences (right). All Japanese taxa except "*Mundiphaedusa*" *miyoshii* and all Taiwanese taxa except *Formosana* constitute a large clade α, which is divided into seven clades (A–G). Numbers above and below branches indicate bootstrap values in ML analysis (when ≧70) and posterior probabilities in Bayesian analysis (when ≧0.9), respectively. "*M.*" *miyoshii*, whose phylogenetic position is isolated from all other Japanese clausiliids, is highlighted by red letters. Phylogenetic relationships within clades A to F are detailed in Figs 2.3–2.5.

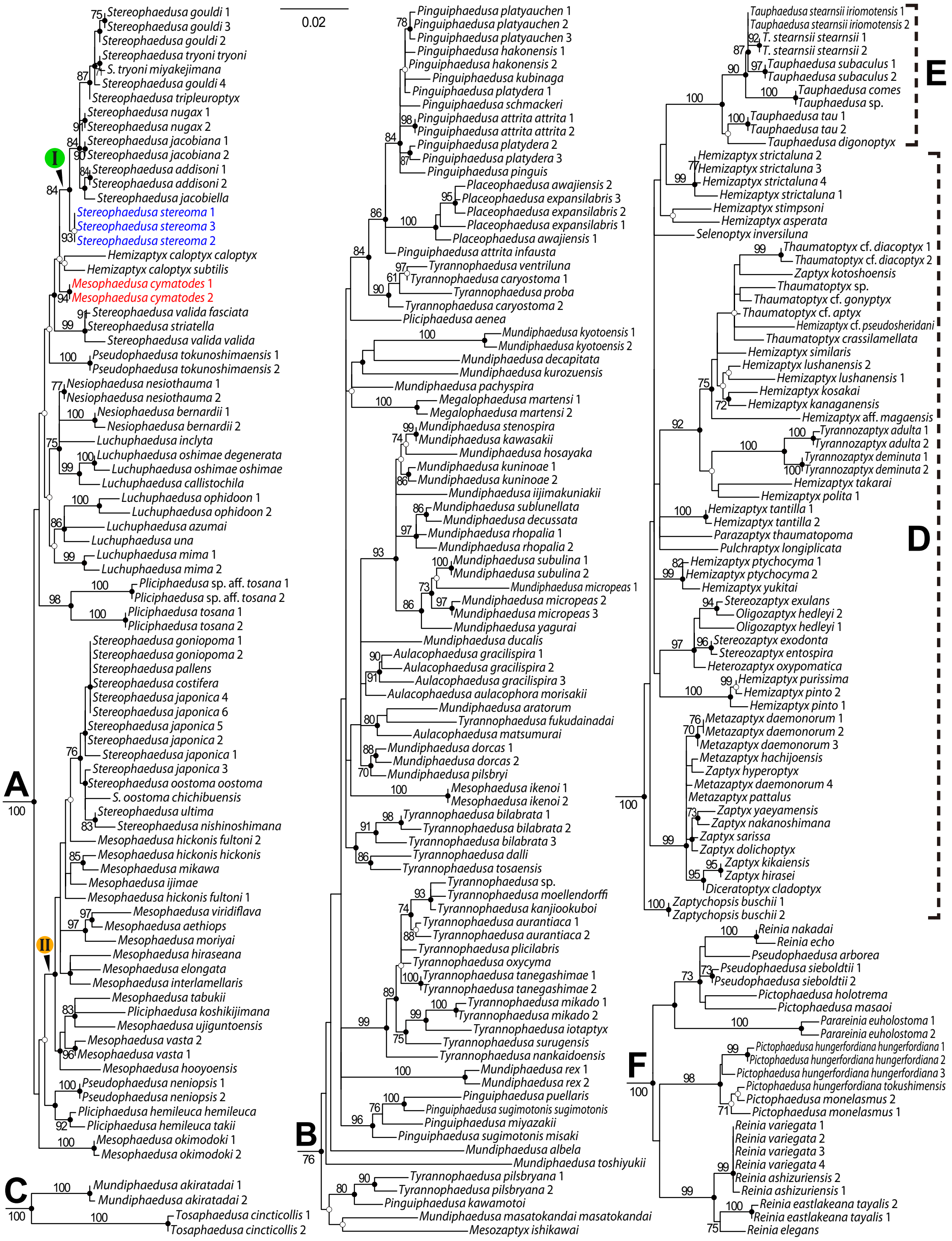

Figure 2.3. ML trees for lades A, B, C, D+E, and F based on nuclear *ITS* sequences. Numbers at the branches indicate bootstrap values in ML analysis (when ≧70). Posterior probabilities (PP) in Bayesian analysis are shown by symbols at each node (closed circle, PP ≧0.98; open circle, 0.90≦ PP <0.98). Two problematic clausiliids of probable hybrid origin are highlighted by red and blue letters. Subclades I and II in clade A correspond to the subgenera *Breviphaedusa* and *Mesophaedusa*, respectively, in the newly proposed system.

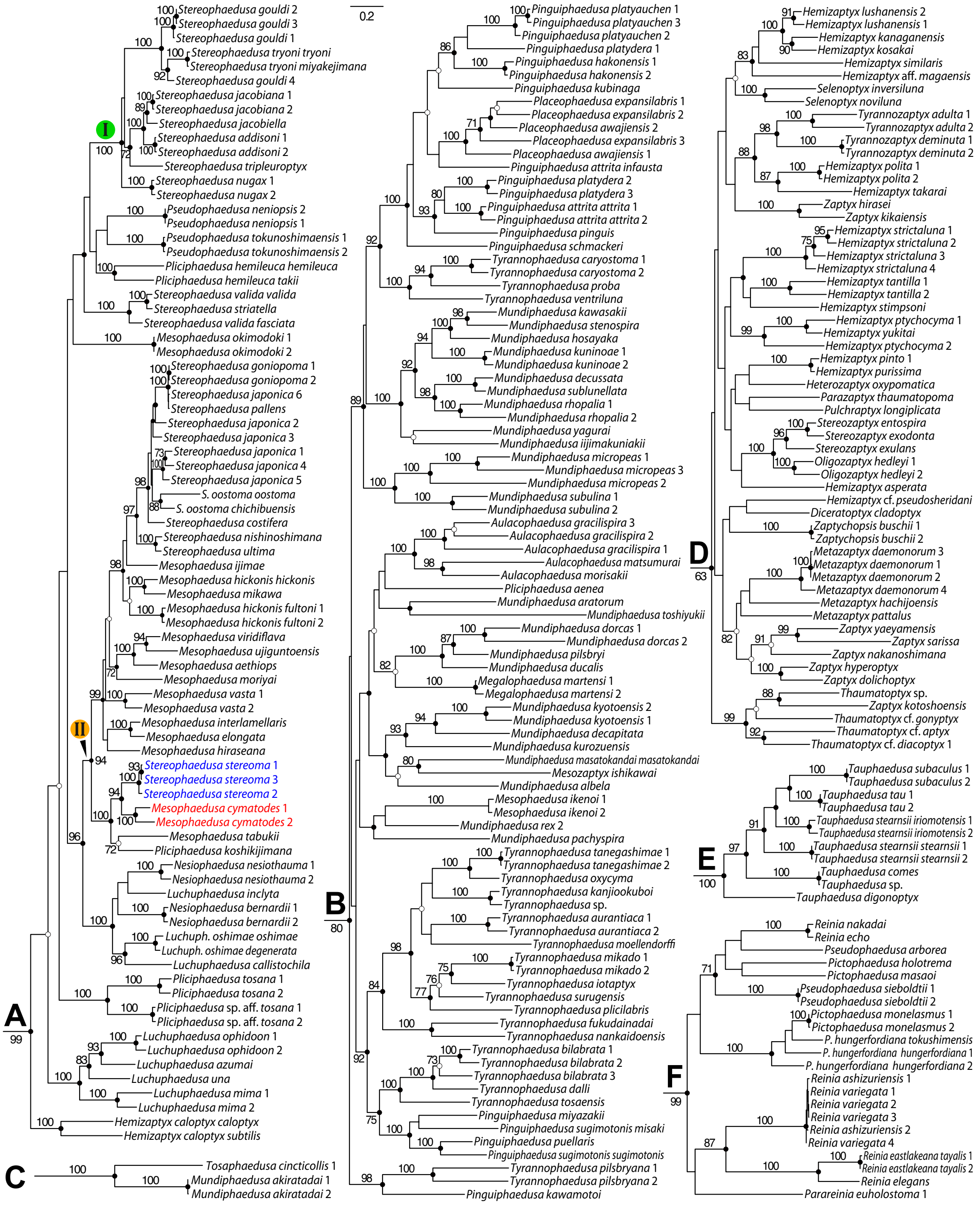

Figure 2.4. ML trees for clades A, B, C, D, E, and F based on mtDNA sequences. Bootstrap and posterior probability are shown as in Figure 2.3. Two problematic clausiliids of probable hybrid origin are highlighted by red and blue letters. Subclades I and II in clade A correspond to subgenera *Breviphaedusa* and *Mesophaedusa*, respectively, in the newly proposed system.

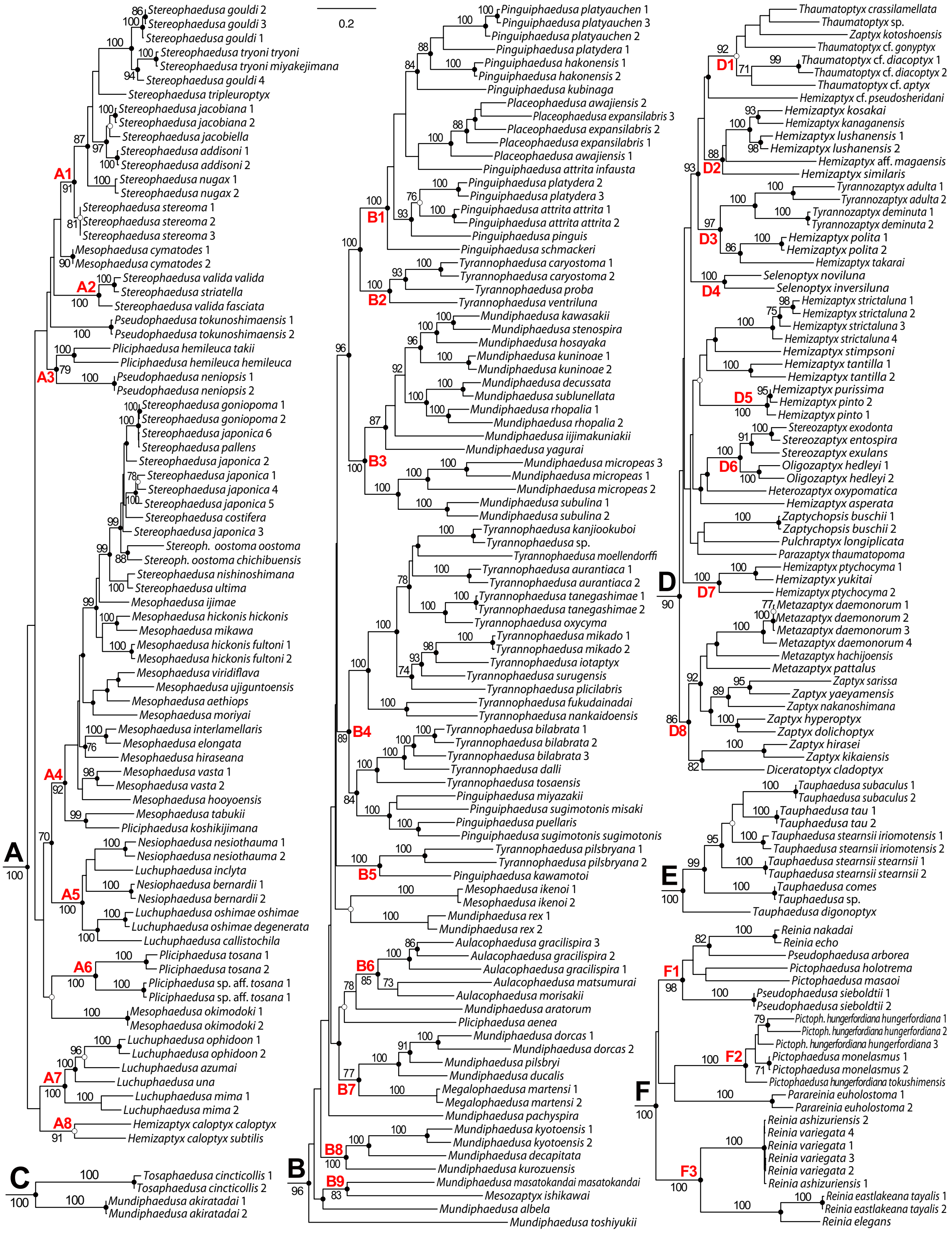

Figure 2.5. ML trees for clades A, B, C, D, E, and F based on combined (*ITS*+mtDNA) sequences. Bootstrap and posterior probabilities are shown as in Figure 2.3. Well-supported subclades within each clade are indicated by red letters.

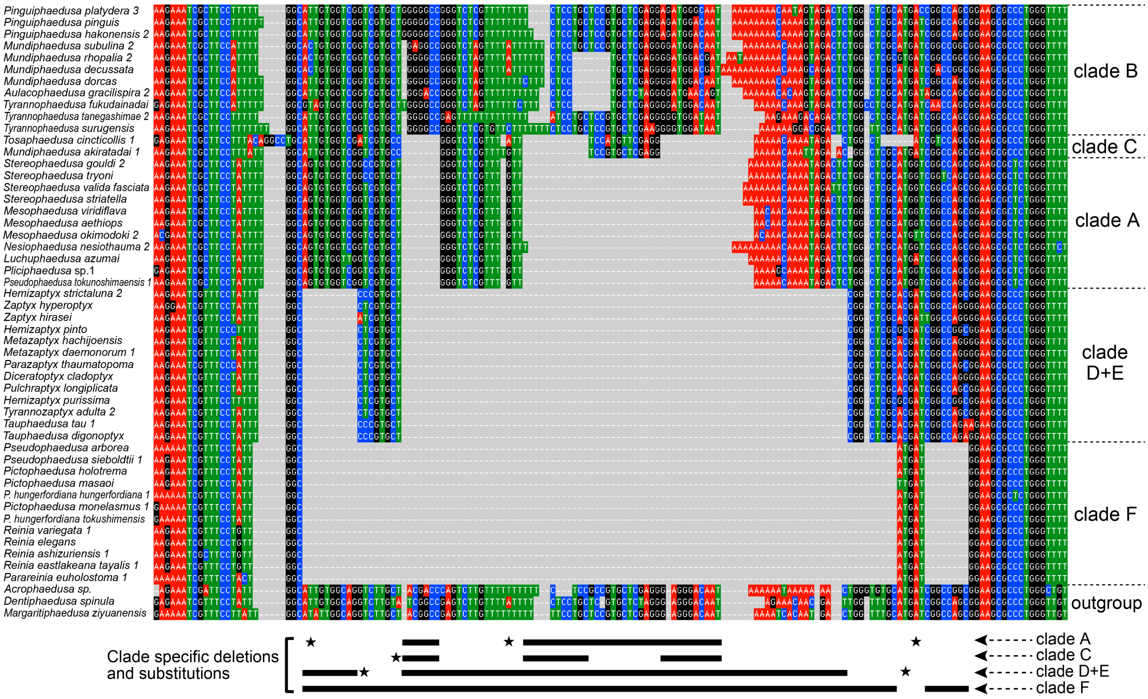

Figure 2.6. Alignment of nucleotide sequences of a hyper variable region of *ITS2* for the representatives of Japanese clausiliids and some outgroup taxa. Clade B has presumably plesiomorphic sequences that are shared with outgroups. Members of clades A, C, D+E, and F share unique patterns of deletions (shown as horizontal bars at the bottom) and fixed substitutions (shown as stars at the bottom) in this region.

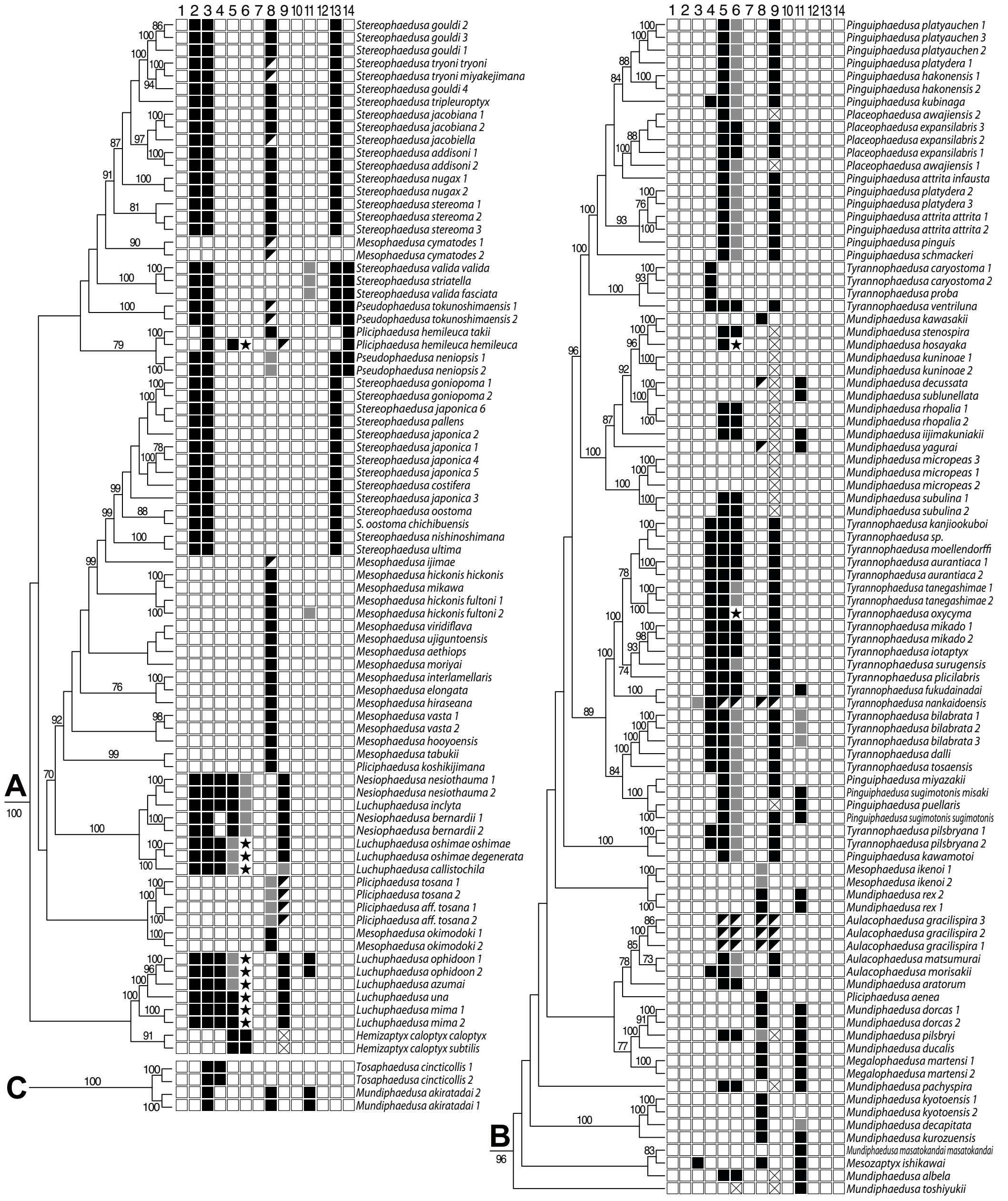

Figure 2.7. Character mapping of 14 taxonomically important characters of Japanese and Taiwanese clausiliids. Eleven shell characters, one genital character, one reproductive, and one ecological characters that have been used in traditional systems are mapped onto the ML trees based on the combined dataset (Fig. 2.5). Bootstrap values (when ≧70) are shown for each node. The characters and the character states are as follows.

Character 1, superior lamella; open square, developed; closed square, more or less reduced. Character 2, inferior lamella; open square, straightly or S-shaped ascending; closed square, spirally ascending. Character 3, clausilium plate; open square, narrow; closed square, wide; triangle, with a distinctive projection; cross, absent. Character 4, location of plicae and clausilium; open square, lateral; closed square, ventral to ventro-lateral. Character 5, lunella; open square, absent; closed square, present and axial; grey square, present and oblique; half closed square, present or absent. Character 6, upper palatal plica; open square, present and without a lunella; closed square, present and attached to the lunella; grey square, present and fused with the lunella; star, present and separated from the lunella; cross, absent. Character 7, upper palatal plica; open square, short; closed square, long or interrupted; cross, absent. Character 8, middle palatal plica; open square, absent; closed square, present; grey square, coalesced to a lunella; half closed square, present or absent. Character 9, lower palatal plica; open square, present and without a lunella; closed square, present and attached to the lunella; grey square, present and fused with the lunella; star, present and separated from the lunella; cross, absent. Character 10, sutural plica; open square, absent; closed square, present. Character 11, apex; open square, pointed; closed square, rounded; triangle, decollated. Character 12, diverticulum of bursa copulatrix; open square, developed; closed square, reduced or absent. Character 13, mode of reproduction; open square, oviparous; closed square, ovoviviparous. Character 14, type of habitat; open square, terrestrial; closed square, arboreal.

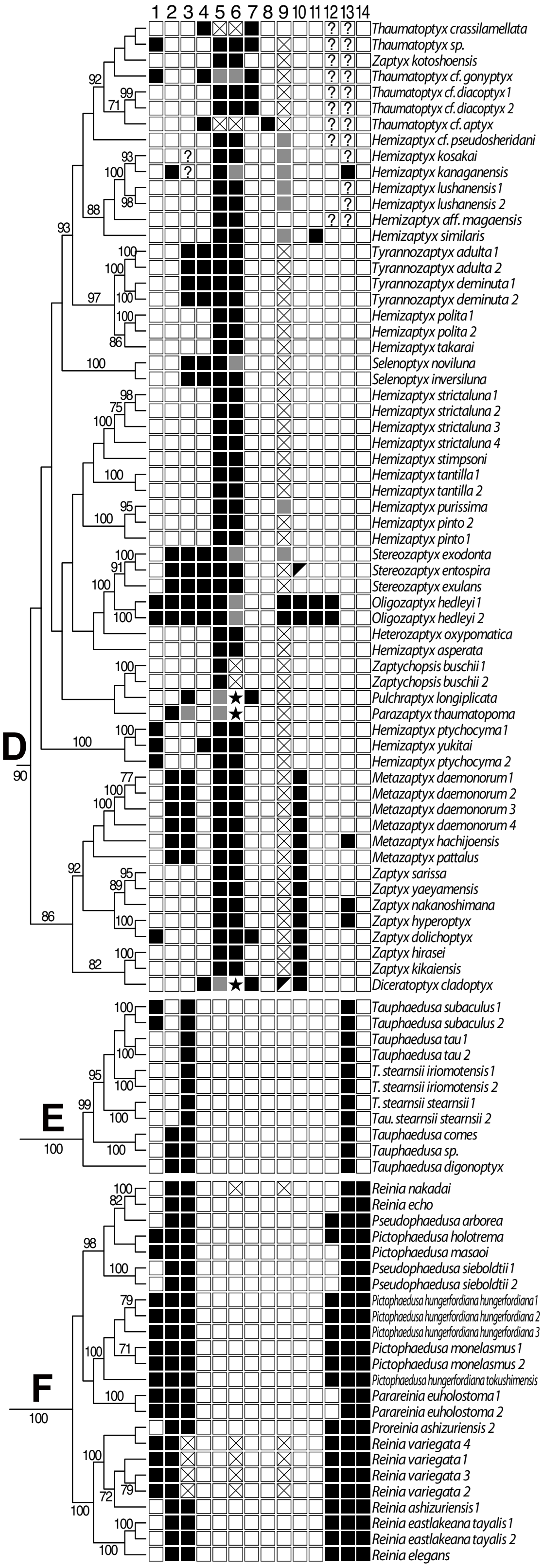

Figure 2.7. *Continued*

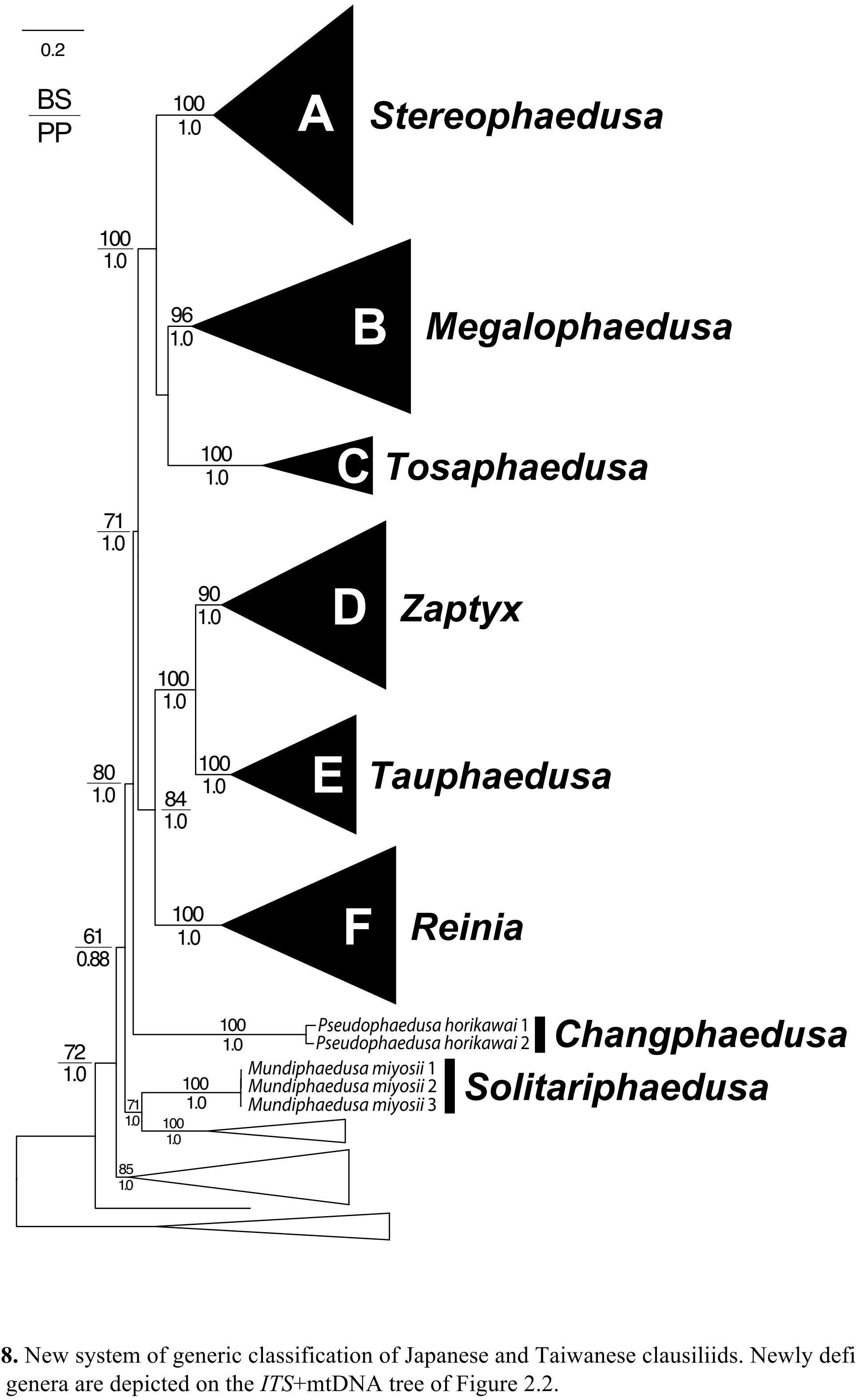

Figure 2.8. New system of generic classification of Japanese and Taiwanese clausiliids. Newly defined or described genera are depicted on the *ITS*+mtDNA tree of Figure 2.2.

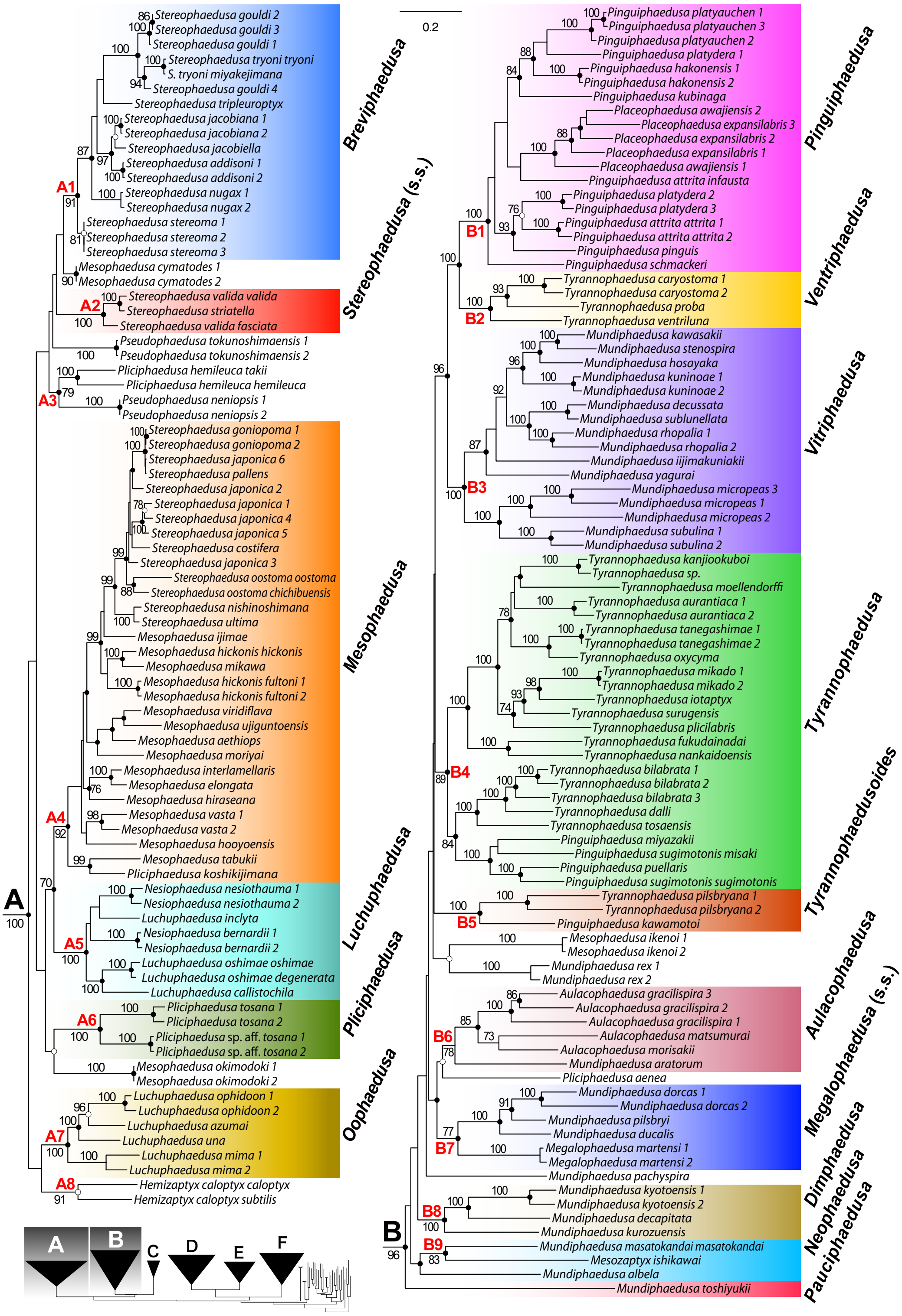

Figure 2.9. New system of subgeneric classification of Japanese and Taiwanese clausiliids. Newly defined or described subgenera are depicted on the ML trees of Fig. 2.5 for each genus. A, genus Stereophaedusa (= clade A). B, genus Megalophaedusa (= clade B). D, Zaptyx (= clade D). Subgeneric division is not proposed for genera Tosaphaedusa (= clade C), Tauphaedusa (= clade E), and Reinia (= clade F).

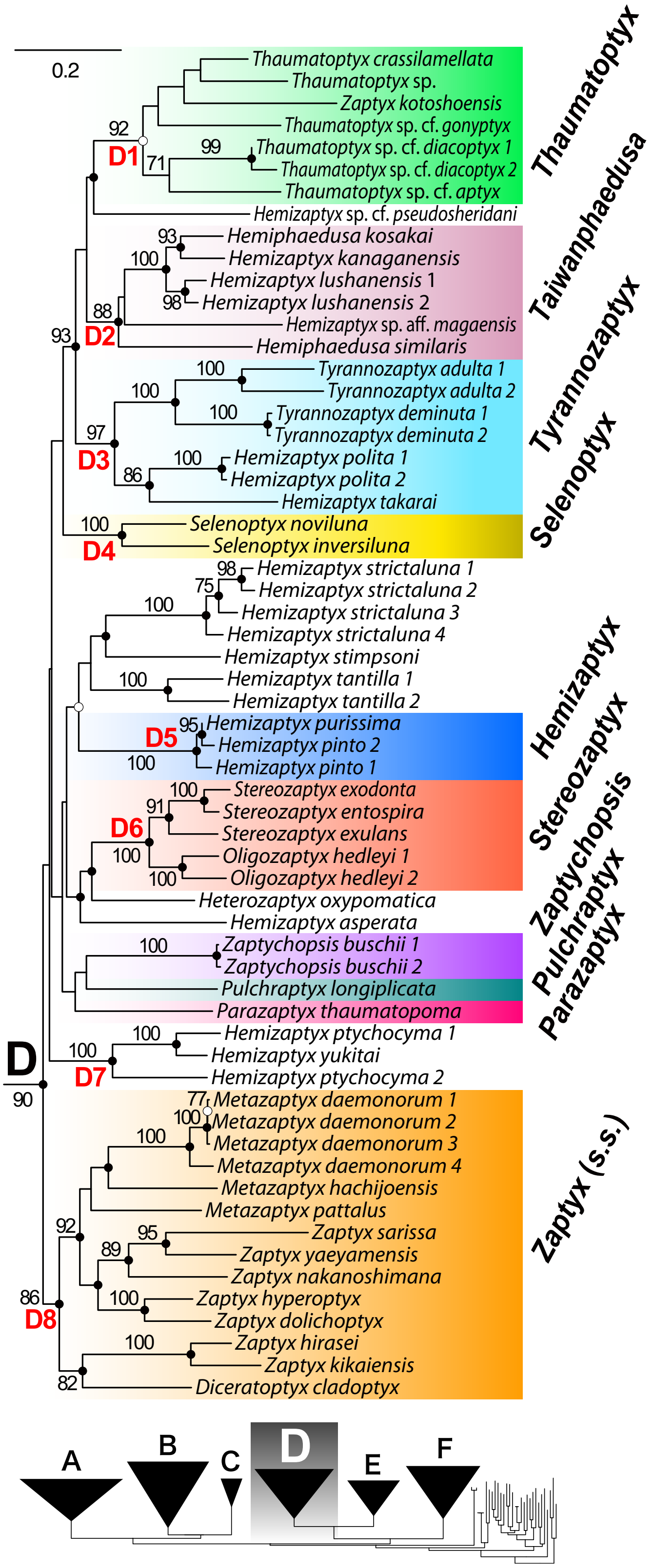

Figure 2.9. *Continued*

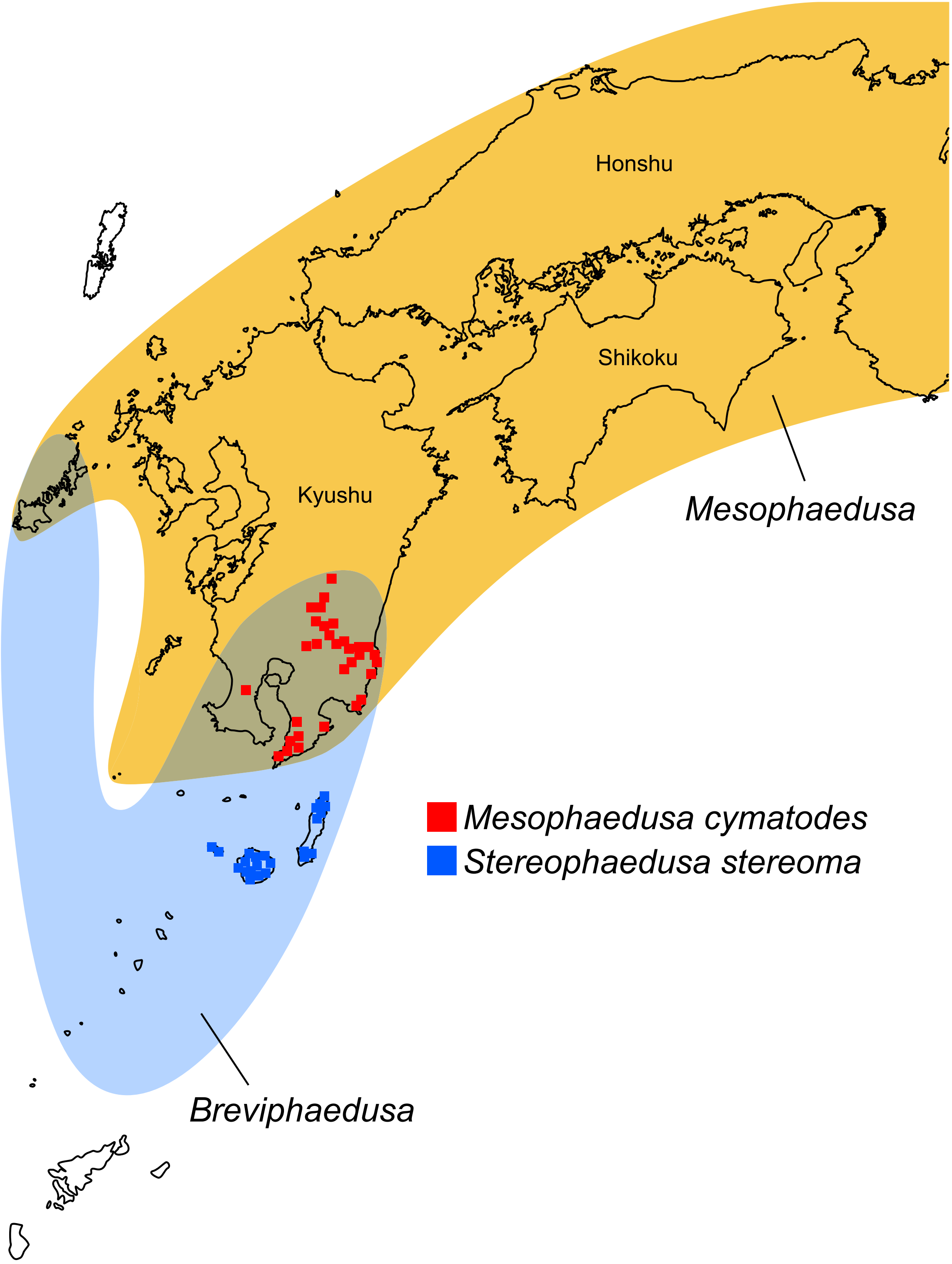

Figure 2.10. Geographical distribution of two clausiliid species of probable hybrid origin. *Stereophaedusa stereoma* and "*Mesophaedusa*" *cymatodes* are problematic species whose phylogenetic positions are discordant between nuclear and mtDNA trees (see Figs 2.3 and 2.4). The mitochondrial tree suggests their affinity to the newly defined *Mesophaedusa*, while the nuclear tree suggests their affinity to the newly defined *Breviphaedusa*. These problematic species are distributed within or near the area where the distribution ranges of *Breviphaedusa* and *Mesophaedusa* overlap. Distribution data are based on Ministry of the Environment records (2010) and unpublished data of the authors.