

Systematics and Phylogeny of the Arboreal Snail *Satsuma albida* (Pulmonata: Camaenidae) Species Complex from Taiwan: Species and Speciation

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Abstract

Traditional taxonomy methods and molecular survey were used to probe into the phylogeny of an arboreal *Satsuma* snail species complex from Taiwan, called *Satsuma albida* species complex. In this study, fifteen species were identified and described as new species from the group. Two subspecies of *S. albida*, *S. a. insignis* and *S. a. mollucula* were promoted to an independent species based on the characters of their reproductive system and the molecular phylogenetic relationships from other taxa. An explicit phylogenetic relationship of all Camaenidae land snails from Taiwan are shown *ad int.*, which is based on the molecular markers of mtDNA and nucleus genes reflecting their evolutionary history. Species formation can be promoted via ecological reasons, such as spatial allocation in the group of arboreal species; or via single-gene mutation such as chiral reverse from sinistral to dextral shells. Such can cause mismatch mating and procure incipient species formation. Speciation can also be happened with a long term evolutionary process, through the vicariance or dispersal events and cause a monophyletic clade within high diversity taxa on the species level within a genus, even though confined through an island.

Introduction

Concerning the Camaenidae
Mollusca More than 90 genera, 3000 species of the world.
Gastropoda Four genera of Taiwan:
Stylommatophora *Satsuma* H. Adams, 1868 *Pancala* Kuroda & Habe, 1949
Helicid-Sigmurethra
Camaenoidea *Yakuchloritis* Habe, 1955 *Moellendorffia* Ancey, 1887
Camaenidae

Concerning the *Satsuma albida*

- R. Swinhoe's collections and the unfinished itinerary
- Missing information of original type specimen and locality
- Similar neighbors from Ryukyu Isl.: *Luchuhadra* spp.

Aftermath: Pilsbry & Hirase's tour, two subspecies of *S. albida*
Satsuma albida insignis (Pilsbry & Hirase, 1905)
Satsuma albida mollucula (Pilsbry & Hirase, 1909)

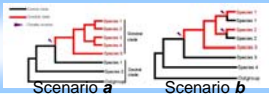
And others... **unsolved enigma, WHO ARE THEY?**



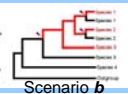
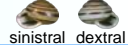
How about the **phylogenetic relationships** and **species formation** of them?
Thinking about species, speciation and the relevance.

Single-gene speciation of pulmonata snails: chiral speciation

An ideal phylogenetic relationship concerning the chirality of *Satsuma* species from Taiwan inferred in scenario **a** (left) or **A** more perplex phylogenetic relationship concerning the chirality of *Satsuma* species from Taiwan inferred in scenario **b** (right)



The topology shows the 50% major rule consensus of 4 phylogenetic trees using Bayesian analysis (BA), maximum parsimony (MP), maximum likelihood (ML) and neighbor-joining (NJ) method performed by the program MrBayes 3.1.2 and the parameters for the combined sequences were tested using the program MrModeltest 2.2. Bayesian posterior probabilities were estimated using Markov chain Monte Carlo analysis for 1000000 generations and sampled every 50 generations. The support for branches was evaluated by 1000 bootstrap re-sampling for MP, ML and NJ trees. The probabilities > 50% are shown.



Materials and Methods

To track back evidences of types, *S. albida* and others:

"One Long Argument"

45 sampling localities around the Taiwan Isl., sample size = 625 of these arboreal snails.

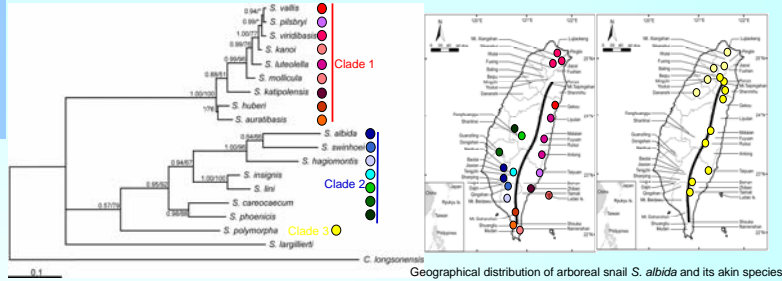
Taxa were distinguished via traditional taxonomy method and molecular survey.

Molecular markers: partial sequence of mtDNA CO1 and 16S genes, 5.8S rRNA, ITS2, 28S rRNA.

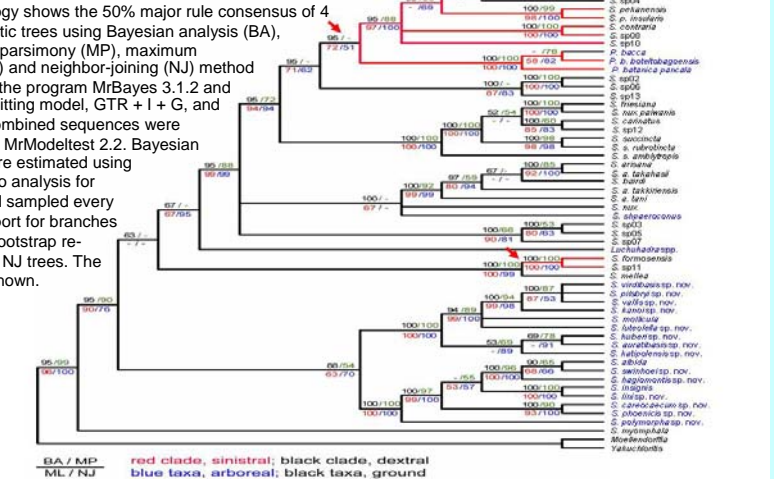
Comparative evidences of BSC and PSC

The explicit phylogenetic relationship of all Camaenidae land snails from Taiwan Isl., 52 taxa were distinguished. $n > 10$ / each taxon.

- The phylogenetic relationships of the species complex *Satsuma albida* from Taiwan based on the tree reconstructed by Bayesian method. Numbers beside the nodes refer to the posterior probabilities of Bayesian analysis (left) and the percentage of the bootstrap values of 1000 replicates of neighbor-joining tree (right). Asterisk indicates the probability < 0.5 or the bootstrap value less than 50%.
- Asymmetric divergence of morphological and genetic variation of these arboreal land snail species from the east and the west clades.



The actual phylogenetic relationships of all camaenids snails from Taiwan.



BA / MP / ML / NJ red clade, sinistral; black clade, dextral blue taxa, arboreal; black taxa, ground

→ : Chiral speciation from dextral to sinistral

Most taxa: Limited geographical distribution

Stories from the ground: Left or Right, and others

Stories out of ground: A New World

Numerous "Cryptic Species" were distinguished

Discussion

Evolutionary history of these *Satsuma* snails from Taiwan concerning species formation can be promoted via several different pathways.

First, species formation can be promoted via ecological reasons, the so called "**spatial allocation**" in the group of arboreal species *S. albida* and its akins. Ancestors of this clade of arboreal snails moved upon trees to a new environment, the allocated space and invasion into a whole empty niche for snails. Then the species formation events happened through the new world and caused the high diversity of these arboreal species.

The **second** species formation pathway of these *Satsuma* snails is due to chirality reverse of the so known "single-gene speciation", this kind of species formation happened for at least three times from dextral ancestors to the sinistral descents, and twice from sinistral ancestors to dextral descents. Due to the shell chirality from dextral to sinistral is more difficult as to sinistral to dextral is more facile, this only appeared once in the Japanese land snail *Euhadra* spp. group. The Taiwanese *Satsuma* revealed three times of chirality reverse from dextral to sinistral, a special evolutionary pattern. Furthermore, through this study the author discovered a species underwent a peculiar species formation, from dextral to sinistral, then from sinistral back to dextral followed by from dextral to sinistral again.

This may be the unique chirality reverse speciation model of all known hermaphroditic snails.

The **third** speciation of these *Satsuma* snails can also happen within a long term evolutionary process, through the vicariance or dispersal events along with the geographical distribution, the well known speciation mechanism.

Acknowledgements

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Results

To affirm types from BMNH, London and ANSP, Philadelphia. **Otherwise, un-described species.**

