

Revision of the taxonomic position of Pseudocypretta Klie, 1932 (Ostracoda: Cyprididae), with a redescription of P. maculata Klie, 1932

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ABSTRACT

Pseudocypretta maculata Klie, 1932, type species of the genus, is redescribed based on new material from Thailand. The main diagnostic features of the species are the presence of marginal septa, presence of Wouters organ on the first antenna, strongly serrated claw G2 of the second antenna (A2), small β seta on the mandibular palp, elongated terminal segment of the maxillular palp, smooth and large bristles on the third endite of the maxillula, undivided penultimate segment of the second thoracopod (T2), absence of d1 seta on the T2, completely separated terminal segment of the third thoracopod, absence of a pincer organ, and reduced caudal ramus with a triangular base. The taxonomic position of Pseudocypretta Klie, 1932 is also revised. Based on molecular analysis using the cytochrome c oxidase subunit I (COI), Pseudocypretta appears closer to Cypridopsinae Kaufmann, 1900 than to Cyprettinae Hartmann, 1971. This result is congruent with morphological evidence and, among other cypridopsine genera, Pseudocypretta shows highest similarity with Cyprettadopsis Savatenalinton, 2020 given its reduced caudal ramus, the strongly serrated claw G2 of the A2, absence of pincer organ, and presence of marginal septa. Pseudocypretta is therefore allocated to the tribe Cyprettadopsini Savatenalinton, 2020.

KEY WORDS: Crustacea, Cyprettinae, Cypridopsinae, genomic DNA analysis, integrative taxonomy, Thailand

INTRODUCTION

Pseudocypretta Klie, 1932 was erected based on specimens from Java and Sumatra (Klie, 1932) and subsequently recorded from India (Battish, 1978, 1982; Victor & Fernando, 1979), Malaysia (Victor & Fernando, 1981a), and Thailand (e.g., Savatenalinton & Suttajit, 2016). This genus has Pseudocypretta maculata Klie, 1932 as its type species, which is peculiar because it shares characters with several taxa. The taxonomic position of Pseudocypretta has been discussed for a long time and remains unclear. Victor & Fernando (1979, 1981b) placed the genus in the subfamily Cypridopsinae Kaufmann, 1900, but it was later assigned to Cyprettinae Hartmann, 1971 by Battish (1982) due to the presence of marginal septa. The latter viewpoint was followed by Martens & Savatenalinton (2011) and Meisch et al. (2019) in their world checklists of Recent non-marine ostracods. Pseudocypretta is nonetheless excluded from Cyprettinae and not assigned to any taxonomic categories by other researchers (e.g., Karanovic, 2012). A recently described species from

Hainan Island (southern China), Pseudocypretta lineata Ma & Yu, 2020, was initially placed in Cyprettinae (see Ma & Yu, 2020). Pseudocypretta maculata is herein redescribed based on specimens from Thailand and a molecular analysis undertaken together with representatives of Cypridopsinae and Cyprettinae in order to reassess the taxonomic status of Pseudocypretta.

MATERIALS AND METHODS

A survey of 318 localities in freshwater ecosystems in northern and northeastern Thailand was undertaken in 2005-2017. Specimens were collected using a hand net (mesh size 200 μ m), preserved in 70% ethanol, and sorted using an Olympus SZ-PT stereomicroscope (Olympus, Tokyo, Japan). Specimens of Pseudocypretta maculata were found in 148 localities and many specimens were examined in detail for soft parts and valve morphology. Soft parts were dissected in glycerine and sealed on glass slides. Valves were stored dry on micropaleontological

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slides. Drawings of soft parts were made with the aid of a camera lucida. Carapaces and valves were observed and illustrated using a scanning electron microscope (JSM6460LV; JEOL, Tokyo, Japan) at the Faculty of Science, Mahasarakham University, Thailand, and an XL30 scanning electron microscope (Philips, Eindhoven, The Netherlands) at the Royal Belgian Institute of Natural Sciences, Brussels). The chaetotaxy of the limbs follows the model proposed by Broodbakker & Danielopol (1982), revised for the second antenna by Martens (1987), and for the thoracopods by Meisch (2000). All specimens studied are deposited in the Ostracod Collection, Faculty of Science, Mahasarakham University, Maha Sarakham, Thailand.

The following abbreviations are used in the text and figures: MSU-ZOC, Ostracod Collection, Science Faculty Museum, Mahasarakham University, Maha Sarakham, Thailand; Cp, carapace; H, height of valves; L, length of valves; LV, left valve; RV, right valve; W, width of carapace; A1, first antenna; A2, second antenna; Md, mandibula; Mx1, maxillula; T1, first thoracopod (maxilliped); T2, second thoracopod (walking leg); T3, third thoracopod (cleaning leg); CR, caudal ramus; il, inner list; im, inner margin; st, septum/septa.

Molecular analyses

Total genomic DNA extraction was performed using the Chelexresin method (Palero et al., 2010) after the morphological examination of specimens. In order to amplify the standard COI gene region, we used the pair of primers proposed by Krehenwinkel et al. (2018) specifically for arthropod studies (ArF1: GCNCCWGAYATRGCNTTYCCNCG and Fol-degen-rev: TANACYTCNGGRTGNCCRAARAAYCA). Amplifications were performed using ~10 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham Biosciences, Amersham, UK), 1 × buffer (Amersham Biosciences), 0.2 mM of each primer, and 0.12 mM dNTPs. The polymerase chain reaction (PCR) thermal profile was 94 °C for 4 min for initial denaturation, followed by 38 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s, and a final extension at 72 °C for 4 min. Amplified PCR products were cleaned with Exo-SAP enzyme and sequenced using the Big-Dye Ready-Reaction kit ver. 3.1 (Applied Biosystems, Foster City, CA, USA) on an ABI Prism 3770 automated sequencer (Macrogen, Seoul, South Korea). Chromatograms for each DNA sequence were checked with BioEdit v.7.2.5 (Hall, 1999) and all sequences were translated into amino acids to detect possible insertions and/or stop codons to rule out the presence of pseudogenes. Sequence alignment was conducted using Muscle v3.6 (Edgar, 2004) with default parameters. The model selection was carried out according to the Bayesian information criterion (BIC), as implemented in MEGA X (Kumar et al., 2018). Phylogenetic relationships were then inferred using maximum-likelihood analysis (ML) and the bootstrap test (500 replicates) as implemented in MEGA X (Kumar et al., 2018).

TAXONOMY

Class Ostracoda Latreille, 1802 Subclass Podocopa G.O. Sars, 1866 Order Podocopida G.O. Sars, 1866 Suborder Cypridocopina Baird, 1845 Superfamily Cypridoidea Baird, 1845 Family Cyprididae Baird, 1845 Subfamily Cypridopsinae Kaufmann, 1900 Tribe Cyprettadopsini Savatenalinton, 2020

Genera included: *Cyprettadopsis* Savatenalinton, 2020, *Pseudocypretta* Klie, 1932

Genus Pseudocypretta Klie, 1932

Diagnosis: Cp in lateral and dorsal views subovate, marginal septa complete, stable on RV anterior and posterior margins; A1 with 7 segments; A2 with strongly serrated claw G2, natatory setae long; terminal segment of Mx1 palp elongated, dorsal subapical seta on basal segment present; d seta on T1 absent; T2 without d1 seta, penultimate segment undivided; T3 with completely separated terminal segment, pincer organ absent, h2 seta claw-like, long; CR reduced, triangular base.

Remarks: Cyprettadopsis is a close relative of *Pseudocypretta,* from which it can be distinguished by the presence of stable complete septa only on the RV anteriorly and posteriorly (on posterior part of both valves in *Cyprettadopsis*), the absence of minute needlepoint-like pores along anterior and ventral margins of both valves (present in *Cyprettadopsis*), the presence of A1 Wouters organ, the small β seta and S setae on the Md-palp, the long and slim d2 seta on the T2 (remarkably short in *Cyprettadopsis*), and the reduced CR with triangular base (cylindrical base in *Cyprettadopsis*).

Pseudocypretta maculata Klie, 1932

(Figs. 1–4, 6)

Six dissected females (soft parts Material examined: dissected in glycerin on a sealed glass slide, and valves stored dry in a micropalaeontological slide) (MSU-ZOC.338-MSU-ZOC.343), four undissected females (stored dry in slides) micropalaeontological (MSU-ZOC.344-MSU-ZOC.347), and many females in 70% EtOH. All studied specimens from six localities: 1) Mae Peum Reservoir, Mae Jai District, Phayao Province, 19°21' 29"N, 99°51'45"E, 24 September 2005; 2) rice field, Chomthong District, Chiang Mai Province, 18°31′30″N, 98°37′4″E, 23 September 2005; 3) Huai Chiang Kham Reservoir, Borabue District, Maha Sarakham Province, 15°58′24″N, 103°6′9″E, 13 February 2010; 4) Kaeng Sapue River, Phibunmangsahan District, Ubon Ratchathani Province, 15°14′37″N, 105°14′37″E, 24 October 2010; 5) rice field, Muang Sam Sip District, Ubon Ratchathani Province, 15°23'36"N, 104°48'54"E, 25 October 2010; 6) Huai Ta Mai Reservoir, Kantharalak District, Si Sa Ket Province, 9 February 2011.

Diagnosis: Cp in lateral view subovate (L/H ~1.45), Cp in dorsal view subovate (L/W ~1.33), LV slightly larger than RV, LV overlapping RV anteriorly and ventrally, RV slightly overlapping LV posteriorly, LV with double posterior inner list well-developed but not parallel to valve margin at posteroventral part, consequently with space between inner list and valve margin, RV with marginal septa on anterior (12–13 septa) and posteroventral (7–9 septa) parts, valve surface with very shallow pits and scattered, thin setules; A1 7-segmented, Wouters organ present; A2 with strongly serrated claw G2, terminal claws long (length ~2.4× that of penultimate segment), natatory setae long; β and S setae on Md palp small, terminal claws long (length ~1.3× that of last 2 segments); terminal segment of Mx1 palp elongated (length ~2× width), dorsal subapical seta on basal segment present, 2 large bristles on third endite smooth; a setae on T1 present (b, c, d setae on T1 absent), subapical setae on protopodite absent; T2 without d1 seta, d2 seta long, slim, penultimate segment undivided; T3 with completely separated terminal segment, h2 seta claw like, markedly long (length ~3/4 of penultimate segment), h3 seta remarkably short (~4/5 length of h2 seta); CR reduced with triangular base, length of flagellumlike seta ~2× that of ramus.

Measurements (in µm): Cp (*N* = 5), L 369–400, H 253–280, W 277–300; LV (*N* = 5), L 377–412, H 262–294; RV (*N* = 5), L 369–408, H 262–287.

Remarks: Pseudocypretta has so far comprised two species, *P. maculata* and *P. lineata*. They can be distinguished from each other mainly by the Cp shape in dorsal view (more ovate in *P. maculata*), the longitudinal lines in central-ventral area (present in *P. lineata*, absent in *P. maculata*), the G2 claw on A2 (less serrated in *P. maculata*), and the shape of CR (longer flagellum-like seta in *P. maculata*).

Description of female: Cp in lateral view (Fig. 1C) subovate (L/H \sim 1.45), anterior and posterior ends widely, subequally rounded, dorsal margin strongly arched, maximum height slightly before mid-length, ventral margin slightly sinuous at mid length, LV slightly larger than RV, LV overlapping RV anteriorly and ventrally, RV slightly overlapping LV posteriorly, valve surface with very shallow pits and very thin scattered setae.

Cp in dorsal and ventral views (Fig. 1A, B) subovate (L/W \sim 1.33) with evenly curved lateral margins, maximum width situated about mid-length, posterior end rounded, anterior end more pointed.

LV in internal view (Fig. 1D, F) with anterior valve margin more broadly rounded than posterior one, ventral margin slightly sinuous at mid length. Anterior margin with submarginal selvage, anterior calcified inner lamella wide with one inner list, posterior calcified inner lamella very narrow with double posterior inner list. Double inner list well developed and oblique, straight, not curved nor parallel to valve margin, consequently wide space between inner list and valve margin at posteroventral part. Marginal septa variable (see Fig. 6), leading to 3 morphotypes: 1) no septa on anterior and posterior parts, 2) incomplete septa (\sim 11 or 12) on anterior part and complete septa (\sim 4–6) on posteroventral parts, and 3) complete septa on anterior and posterior parts.

RV in internal view (Fig. 1E) with both valve margins subequally rounded, ventral margin sinuous at mid length, anterior margin with submarginal selvage, anterior calcified inner lamella wide with 2 inner lists, posterior calcified inner lamella very narrow with well-developed, double inner list, posterior selvage not submarginal at posteroventral part. Complete marginal septa on anterior (\sim 12 or 13 septa) and posteroventral (\sim 7–9 septa) parts (see Fig. 6B, D).

A1 (Fig. 2A): seven segmented, first segment with short dorso-subapical (reaching tip of next segment) and 2 long ventro-apical setae, Wouters organ present. Second segment ~2× wider than long, with short dorso-apical seta (reaching 1/4 of next segment) and small Rome organ. Third segment bearing 2 setae: one long dorso-apical (reaching beyond tip of penultimate segment) and very short ventro-apical setae (reaching half of next segment). Fourth segment with 2 long dorsal setae and 2 short ventral setae (longer seta reaching beyond tip of next segment, length of shortest seta about half of longer one). Fifth segment dorsally with 2 long setae, ventrally with 2 (one long, one short) setae, short one reaching half of terminal segment. Penultimate segment with 4 long apical setae. Terminal segment with 3 (2 long, one short) apical setae and markedly long aesthetasc ya, its length about length of last 5 segments, length of short seta $\sim 2/5$ that of aesthetasc ya.

A2 (Fig. 2B): basal segment with 2 proximal setae and long ventro-apical seta. Exopodite with 3 (one long, 2 short) setae, long one reaching tip of penultimate segment. First endopodal segment with 5 very long natatory setae (reaching beyond tips of terminal claws) and short accompanying seta (reaching tip of penultimate segment), aesthetasc Y thin, long, ventro-apical seta long, extending far beyond tip of terminal segment. Penultimate segment short, undivided, distally with 3 large, serrated claws (G1–G3), G2 strongly serrated apically, serration appearing $\sim 2/5$ length with large teeth gradually reduced in size, aesthetasc y2 very short (reaching mid-length of terminal segment), z1-z3 setae long, z1 clearly thicker than other z setae, z2 longest, z2, z3 reaching tip of claws G1-G3; segment medially with 2 subequally long dorsal setae, and 4 ventral setae of unequal length (t1-t4). Terminal segment distally with 2 serrated claws (GM, Gm), length of Gm slightly longer than half length of GM; medially with very short g seta and ventral aesthetasc y3, length of aesthetasc y3 slightly shorter than accompanying seta.

Md palp (Fig. 3A): first segment with 2 setae (S1, S2), one long and slender seta and thin, smooth α seta. Second segment dorsally with 3 unequal long apical setae, shortest almost reaching tip of next segment; ventrally with group of 3 long hirsute setae, one short hirsute seta and small, plumose, cone-shaped β seta with pointed tip. Penultimate segment bearing 3 groups of setae: dorsally with group of 4 unequal, long, subapical setae; laterally with apical γ seta and 3 further apical setae, the former slightly plumose (length ~3.2× terminal segment); ventrally with 2 subapical setae, one long (reaching tip of terminal claws), one short (almost reaching tip of terminal segment). Terminal segment bearing 3 large claws and 3 shorter setae, length of large claws ~4.2× that of terminal segment.

Mx1 (Fig. 3C) with 2-segmented palp, basal segment of palp dorsally with group of 5 long, unequal apical setae and long subapical seta; laterally with short subapical seta (reaching \sim 1/4 length of terminal segment), terminal segment elongated (length \sim 2× width), apically with 3 claws and 2 setae. Two large bristles on third endite smooth, with pointed-tip (without spatula-shaped apex).

T1 (Fig. 3D): protopodite with 2 a setae, length of short one $\sim 2/3$ that of long one, b, c and d setae absent, distally with ~ 9 hirsute apical setae of unequal length, subapical setae absent. Endopodite weakly built palp with one very long, hirsute seta and 2 unequally shorter apical setae.



Figure 1. Pseudocypretta maculata Klie, 1932, female. Carapace, dorsal view (A); carapace, ventral view (B); carapace, right lateral view (C); left valve, internal view (D); right valve, internal view (E); left valve, internal view (F); right valve, internal view (G) (F, G from Savatenalinton, 2015). Scale bar: 100 μ m.

T2 (Fig. 4A) with very thin, long d2 seta, d1 absent. Second segment with long e seta (length $\sim 3/4$ of penultimate segment). Penultimate segment undivided, medially with long f seta (reaching beyond tip of terminal segment), distally with short apical g seta (not reaching tip of segment). Terminal segment with 2 (one dorsal, one ventral) apical h1 and h3 setae (length of the former $\sim 1/5$ of claw, the latter very short) and serrated claw (h2). Length of h2 longer than that of last three segments.

T3 (Fig. 4B) first segment with short d1, long d2 and dp setae, length of d1 seta ~1/3 of d2 and dp setae. Second segment with short apical e seta (reaching ~1/3 of next segment). Third segment with short f seta (not reaching tip of segment). Terminal segment completely separated from previous segment, bearing markedly long claw-like seta (h2), short seta (h1) and one reflexed subapical seta (h3), length of h1 less than half length of h2, length of h2 ~2/3 of third segment, h3 shorter than h2 (~4/5 of h1). Pincer organ absent.



Figure 2. *Pseudocypretta maculata* Klie, 1932, female. First antenna (A); second antenna (B). Scale bars: $A = 50 \mu m$, $B = 56 \mu m$.

CR (Fig. 4C) reduced, flagellum-like with triangular base, medially with very short seta, length of flagellum-like seta ~2× that of ramus. Male unknown.

Molecular analyses: New sequences for *Eucypris virens* (Jurine, 1820), *Pseudocypretta maculata*, and *Cypretta triangulata* Savatenalinton, 2018 have been uploaded to Genbank with accession numbers OM791612–OM791614. There was a total of 35 sequences and 132 amino acid positions in the final dataset. The model with the lowest BIC score, which is considered to best describe the observed nucleotide substitution pattern, was the empirical amino acid substitution model mtREV24. Non-uniformity of evolutionary rates among sites was modelled by using a discrete Gamma distribution (+G) with five rate categories. ML analysis using protein-translated COI gene sequences

yielded the topology shown in Figure 5, suggesting the most likely relationships among *Pseudocypretta*, *Cypretta* Vávra, 1895 and Cypridopsinae representatives. In the tree, *Pseudocypretta maculata* and *Cypretta* species are separated, belonging to two different and well-supported clusters (Fig. 5). *Pseudocypretta maculata* clusters with *Cypridopsis* species (with bootstrap value of 75) and *Potamocypris* Brady, 1870 (bootstrap 77%), *Cypretta* species form a distinct cluster grouping with other unknown Cyprididae (bootstrap 87%) and with *Strandesia* representatives.

DISCUSSION

Taxonomic position of Pseudocypretta

Pseudocypretta is a peculiar taxon because it combines characters thought to be diagnostic of different genera, which results



Figure 3. *Pseudocypretta maculata* Klie, 1932, female. Mandibular palp (**A**); mandibular coxa (**B**); maxillula (**C**); terminal part of first thoracopod protopodite (**D**). Scale bars: $A = 32 \mu m$, $B = 50 \mu m$, C, $D = 25 \mu m$.

in conflicting arguments about its taxonomic position. Our morphological study of valves and soft parts revealed that *Pseudocypretta* shares features with both subfamilies Cyprettinae and Cypridopsinae. General carapace shape and the presence of marginal septa seem to relate it to Cyprettinae. The morphology of soft parts is nevertheless incongruent between *Pseudocypretta* and Cyprettinae, especially in the reduced CR and the existence of strongly serrated claw G2 of the A2, which obviously differ from Cyprettinae representatives. Furthermore, the morphologies of both valves and soft parts link *Pseudocypretta* to Cypridopsinae



Figure 4. *Pseudocypretta maculata* Klie, 1932, female. Second thoracopod (**A**); third thoracopod (**B**); caudal ramus (**C**). Scale bars: $A = 54 \mu m$, $B, C = 25 \mu m$.

genera like *Cypridopsis* Brady, 1867 and *Cyprettadopsis*. The gap between the double inner list and posteroventral margin of the LV observed in *Pseudocypretta* can also be seen in *Cyprettadopsis sutura* Savatenalinton, 2020 (see Savatenalinton, 2020) and several *Cypridopsis* species (i.e., *C. vidua* (O.F. Müller, 1776), *C. hartwigi* G.W. Müller, 1900, *C. elongata* (Kaufmann, 1900), and *C. lusatica* Schäfer, 1943) (see Meisch, 2000; Savatenalinton, 2015). Among Cypridopsinae genera, the soft part features of *Pseudocypretta* are most similar to those of *Cyprettadopsis*, the Cyprettadopsini genus of the subfamily. Apart from the reduced CR, the species of *Pseudocypretta* also resemble *Cyprettadopsis* by their strongly serrated claw G2 of the A2, the elongated terminal segment of the Mx1 palp, the absence of d1 seta of the T2, the distinct separated terminal segment of the T3, and the presence of septa, which are indicative characters of the tribe Cyprettadopsini (see Savatenalinton, 2020). Given that valve and soft-part morphology of *Pseudocypretta* is closest to that of Cypridopsinae rather than to Cyprettinae, we suggest transferring the genus to Cypridopsinae (tribe Cyprettadopsini). Consequently, the tribe Cyprettadopsini includes now two genera: *Cyprettadopsis* (see Savatenalinton, 2020) and *Pseudocypretta* (herein).

Apart from the key characters of the tribe, *Pseudocypretta* is also similar to *Cyprettadopsis* in terms of the valves overlap and the undivided penultimate segment of the T2. This raises the question of whether these two taxa may possibly belong to the same genus. Several features, however, indicate *Pseudocypretta* should remain as a separate genus within Cyprettadopsini. First of all, *Pseudocypretta* can be clearly distinguished from *Cyprettadopsis* by the presence of complete septa on the posterior and anterior parts of the RV (present only on the posterior part of both valves in *Cyprettadopsis*; see Savatenalinton, 2020), the triangular base of the reduced CR (cylindrical in *Cyprettadopsis*), the presence of Wouters organ on the A1 (absent in *Cyprettadopsis*), the small β seta on the Md palp (remarkably large in *Cyprettadopsis*), and the presence of a dorsally subapical seta on the basal segment of the Mx1 palp (absent in *Cyprettadopsis*). Moreover, the valve also shows different features. The surface has very shallow pits with about four dark patches on each valve in *Pseudocypretta* (absent in *Cyprettadopsis*), whereas the minute needlepoint-like pores are noticed along anterior and ventral margins on both valves of *Cyprettadopsis* (absent in *Pseudocypretta*).

In addition to morphological features, the molecular data provides additional evidence that helps clarifying the taxonomic position of *Pseudocypretta* in relation to Cyprettinae and Cypridopsinae. The ML tree (Fig. 5) shows *P. maculata* clustering with *Cypridopsis* and *Potamocypris*, forming an independent lineage, well-separated from the *Cypretta* species. Only two cypridopsine genera, however, were analyzed, and *Cyprettadopsis*, the most morphologically similar genus to *Pseudocypretta* (see below) should be included in a future analysis. In any case, the new molecular results are congruent with the morphological data in showing higher similarity of *Pseudocypretta* to other Cypridopsinae rather than to Cyprettinae genera. *Pseudocypretta* is thus herein allocated to the tribe Cyprettadopsini, as supported by both morphological and molecular data.

Morphology

The morphology of the Thai Pseudocypretta maculata is congruent with that of southeast Asian and Indian specimens. Apart from the taxonomic characters of the tribe Cyprettadopsini mentioned above, Pseudocypretta maculata is characterized mainly by the subovate carapace with about four dark patches on the surface of each valve, the presence of steadily complete septa on the RV (see below), the presence of Wouters organ on A1, the small β seta on the Md palp, the presence of dorsally subapical seta on the basal segment of the Mx1 palp, the undivided penultimate segment of the T2, and the completely separated terminal segment of the T3. Several key characters indicate Zonocypridini to be the closest relatives of Cyprettadopsini, namely the reduced CR, the strongly serrated claw G2 of the A2, the elongated terminal segment of the Mx1 palp, and the absence of d1 seta on the T2. In this context, the morphology and taxonomic characters of Pseudocypretta are briefly discussed below, comparing to related taxa, especially with genera within these two tribes.

Septa: One of the indicative characters of *Pseudocypretta* is the presence of marginal septa. Klie (1932) discussed some features of the RV in the description of *P. maculata*, including the septa, but no information on the presence of septa in the LV was provided. It could thus be interpreted that the LV did not bear marginal septa. This was supported by Battish (1978) and Victor & Fernando (1981a), who mentioned that septa appeared on the RV only. Battish (1982), however, reported that very short and poorly developed septa were recognized on the anterior margin of the LV. All specimens we examined from Thailand are adults and most of them have well-developed (or complete) septa on the anterior margins of the RV only (no septa on

the LV; see Fig 1D). The LV of some specimens, however, show poorly developed septa on the anterior margin and complete septa on the posterior one (Fig 1F). No complete septa were seen on the anterior margin of the LV in our material. Complete septa on the anterior and posterior parts of both valves were nonetheless found in the Indian specimens by Victor & Fernando (1979). These observations suggest that: 1) complete RV septa have developed before those in the LV and are quite stable structures in adults, 2) the posterior LV septa have developed before the anterior ones, and 3) the LV septa can vary in adults (Fig. 6), being either absent on both anterior and posterior margins, poorly developed on the anterior margin but welldeveloped on the posterior margins, or well-developed on both anterior and posterior margins. This scenario on the LV might reflect the effects of ecophenotypic processes or the maturity state of specimens. Ecophenotypic effects may influence valve variability, such as valve ornamentation and valve shape and size, as shown, for example, in *Limnocythere inopinata* (Baird, 1843) (Yin et al., 1999) and Cyprideis torosa (Jones, 1850) (Ruiz et al., 2013). Other valve structures, such as marginal grooves, inner lists, and inner lamella and septa, however, seem not to be affected so much by environmental factors, as their appearances are quite consistent within species. This situation thus seems to weaken the possible ecophenotypic cause of septa variability in the LV of Pseudocypretta. According to septa formation in other Cyprididae taxa such as Stenocypris Sars, 1889, the septa appear after the final molt allowing individuals to become adults. The adult stage can thus also be indicated by the existence of the septa. It has been noticed, however, that the width of the septa can be influenced by the maturity of the animals, older specimens showing wider septa (see Wouters, 1999; Smith et al., 2011, Moonchaisook & Savatenalinton, 2020). If this is the case of Pseudocypretta, the septa on the anterior and posterior margins of the RV possibly appear just after the final molt and the development of septa on the LV may subsequently develop, corresponding to older specimens. Specimens without septa on the LV might thus be the youngest adults while the ones with complete septa on the anterior and posterior margins of the LV would be the oldest individuals. It cannot however be discarded the possibility that the variation in the LV results from genetic factors affecting valve structure along an evolutionary pathway. It is thus currently premature to establish the actual mechanisms behind septa variability in the LV of Pseudocypretta maculata, and it is left unsolved waiting additional studies on carapace ontogeny.

Among Cypridopsinae genera, marginal septa are only present in *Cyprettadopsis* (see Savatenalinton, 2020) and *Pseudocypretta* (herein). These two taxa, however, display differences on the distribution of septa. The stable septa of *Pseudocypretta* are present on the anterior and posterior margins of the RV only, but recognized on the posterior margins of both valves in *Cyprettadopsis*. This suggests that septa formation follows different processes in both genera. The variability in the septa is observed on the *LV* of *Pseudocypretta*, so that posterior septa may develop before the anterior ones. The latter phenomenon seems to resemble the situation in *Cyprettadopsis*. Although no morphological variation of septa has been observed on both valves of *Cyprettadopsis*, the formation of posterior septa may take place prior to that



0.01

Figure 5. Maximum likelihood phylogenetic tree (rooted phylogram) showing the position of *Pseudocypretta maculata* Klie, 1932 relative to other Cyprididae representatives. Only significant bootstrap values (> 70%) are shown.

of the anterior ones due to the presence of complete septa on the posterior margins but incomplete septa on the anterior margins in all specimens. Such sequence of septa appearance in Pseudocypretta and Cyprettadopsis would differ from that of Cypretta in the subfamily Cyprettinae. In Cypretta species, the complete septa steadily appear only on the anterior margins of both valves, whereas the presence of postero-ventral septa differ among species. Based on the occurrence of postero-ventral septa, there are at least three groups among the species of *Cypretta*: those without septa on the postero-ventral part of both valves, those with poorly developed septa on RV postero-ventral parts (e.g., C. obfuscata Victor & Fernando, 1981, C. seurati Gauthier, 1929; see Victor & Fernando, 1981b), and those with poorly developed septa on LV postero-ventral parts (e.g., C. spinosa Cohuo-Durán et al., 2013; see Cohuo-Durán et al., 2013). Most Cypretta species belong to the first group. Complete septa have also never been recognized on the postero-ventral part of valves in this genus. This may indicate that the postero-ventral septa, if present, do not develop prior to the anterior septa in *Cypretta*. Consequently, based on the existence of stable septa and the proposed assumption on septa formation mentioned above, this may suggest that these three genera belong to different lineages. *Pseudocypretta* and *Cyprettadopsis* nevertheless show similarity in the sequence of septa formation, with posterior septa developing prior to the anterior ones. Given that posterior septa develop after the anterior septa in *Cypretta*, this character supports the taxonomic placement of *Pseudocypretta* within the Cypridopsinae rather than Cyprettinae.

Left valve: In *Pseudocypretta*, the oblique double inner list at the postero-ventral part of the LV is well-developed and not close nor parallel to the valve margin, resulting in the appearance of a space between the inner list and the valve margin. This feature also occurs in other cypridopsine genera, namely *Cabelodopsis* Higuti



Figure 6. Line drawing of values of *Pseudocypretta maculata* Klie, 1932 showing the variability of septa in the left value. Individual without septa on left value: left value (\mathbf{A}) and right value (\mathbf{B}). Individual with septa on left value: left value (\mathbf{C}) and right value (\mathbf{D}). Scale bar: 100 μ m.

& Martens, 2012 (see Higuti & Martens, 2012), *Thaicypridopsis* Savatenalinton, 2018 (see Savatenalinton, 2018), *Cyprettadopsis* (see Savatenalinton, 2020), *Zonocypris* G.W. Müller, 1898 (e.g., *Z. cordata* Sars, 1924, *Z. tuberosa* G.W. Müller, 1908; Martens *et al.*, 1996) and *Cypridopsis*, such as *C. vidua* (e.g., Meisch, 2000; Savatenalinton, 2015). This feature could be used as a taxonomic character of each tribe if re-examination is undertaken in all cypridopsine species.

A1: The presence or absence of the Wouters organ on the first segment of the A1 is informative at different taxonomic levels. For example, it has never been seen in some genera (e.g., *Stenocypris, Cypretta*), whereas it is a common feature of Cypricercinae genera. Among Cyprettadopsini and Zonocypridini, the Wouters organ is recognized only in *Pseudocypretta* (Ma & Yu, 2020; herein). This aspect should therefore be a diagnostic character at the generic level for this tribe. It should also be noted that aesthetasc ya on the A1 terminal segment is always longer than the shortest seta of the same segment in all genera of Cyprettadopsini and Zonocypridini, so it might be considered a trait shared by both tribes.

Md palp: Although the general morphology of the Md palp is similar within Cyprettadopsini and Zonocypridini, they differ in some traits. A remarkably large β seta is only observed in *Cyprettadopsis* (see Savatenalinton, 2020), whereas it is small in other genera of both tribes. The terminal claws are usually of the

same size in all genera, but *Thaicypridopsis* has one exceptionally large claw. Claws on the terminal segment are considerably long in *Pseudocypretta*, about 4.2 times the length of the terminal segment in *P. maculata*, but three times in *Cyprettadopsis*. There are five claws and setae in *P. maculata* and *Thaicypridopsis*, but all other genera of Cyprettadopsini and Zonocypridini have six.

T1: The protopodite of T1 bears several setae which are used as taxonomic characters. While the most informative setae are usually the a, b, c and d setae, some other setae like the apical and subapical setae on the distal margin have received much less attention. The number of apical setae has nevertheless been reported from many taxa and could be considered as a diagnostic character. This character should be used with caution, however, as these setae usually overlap with each other, easily leading to inaccurate accounts of the number. More attention should be paid to the occurrence of subapical setae, as they appear to be of taxonomic value. The presence of subapical setae on the T1 protopodite has been mentioned and illustrated in many Cyprididae taxa, for example, all genera of Cypricercinae (see Savatenalinton & Martens, 2009, 2010), Stenocypris or Cypretta (e.g., Sohn & Kornicker, 1973; Cohuo-Durán et al., 2013; Smith et al., 2015; Savatenalinton, 2018). These subapical setae are apparently absent in Zonocypridini and in many genera of Cypridopsinae based on current information. Thus far, 23

cypridopsine genera have been recorded worldwide (Meisch et al., 2019; Almeida et al., 2021; Jacobs & Martens, 2022). Seventeen of these genera do not have subapical setae: Klieopsis Martens et al., 1991 (see Martens et al., 1991), Plesiocypridopsis Rome, 1965, Sarscypridopsis McKenzie, 1977 (see Meisch, 2000), Potamocypris (see Martens, 1982; Horne & Smith, 2004), Pseudocypridopsis Karanovic, 1999 (see Karanovic, 1999), Siamopsis Savatenalinton, 2017 (see Savatenalinton, 2017), Tanganyikacypridopsis Martens, 1985 (see Martens, 1985), Brazilodopsis Almeida, Higuti, Ferreira & Martens, 2021, Parananopsis Almeida, Higuti, Ferreira & Martens, 2021 (see Almeida et al., 2021), Malawidopsis Jacobs & Martens, 2022 (see Jacobs & Martens, 2022); no information on these setae has been reported in six genera: e.g., Austrocypridopsis McKenzie, 1982, Cavernocypris Hartmann, 1964, Tungucypridopsis Victor, 1983. The absence of subapical setae thus seems to be a common feature of the T1 protopodite of Cypridopsinae and could be regarded as a synapomorphy for the subfamily. This could be potentiality confirmed by re-examination of all cypridopsine taxa. It is also important to note that this character also shows a dissimilarity between Pseudocypretta and Cypretta and thus strengthens the exclusion of *Pseudocypretta* from Cyprettinae.

T3: The occurrence of a terminal segment is a key character for the classification of Cypridoidea at the family level (see Karanovic, 2012; Horne *et al.*, 2019). The presence of a distinctive terminal segment and the absence of a pincer organ are typical characters of Candonidae, but it can also be recognized in some representatives of Cyprididae, namely the cypridopsine *Neocypridopsis* Klie, 1940 (see Karanovic, 2012; Savatenalinton, 2018), *Cyprettadopsis* (see Savatenalinton, 2020), and *Pseudocypretta* (Ma & Yu, 2020; herein). Such features suggest a close relationship among these genera, and especially between *Cyprettadopsis* and *Pseudocypretta*.

Zoogeographical distribution

Pseudocypretta maculata is endemic to the Oriental region and P. lineata has been recently recorded from the Palaearctic region, whereas another cyprettadopsinid genus, Cyprettadopsis, is endemic to Thailand (Savatenalinton, 2020). Pseudocypretta mac*ulata* has so far been recorded from Java and Sumatra (Klie, 1932), India (Battish, 1978, 1982; Victor & Fernando, 1979), Malaysia (Victor & Fernando, 1981a), and Thailand (Savatenalinton & Suttajit, 2016). The lineage of Cyprettadopsini is so far restricted to the Oriental and Palaearctic regions whereas its closest tribe, Zonocypridini, has at least three lineages: Afrotropical-Palaearctic, Neotropic, and Oriental, represented by Zonocypris, Cabelodopsis and Thaicypridopsis, respectively. Thaicypridopsis, which is the only zonocypridinid genus in Southeast Asia, is endemic to Thailand (Savatenalinton, 2018). In the Oriental region, the oldest Zonocypridini fossils are the Cretaceous Zonocypris from India (Mazzini, 2011); no fossil records of Zonocypridini have so far been reported from Southeast Asia. Southeast Asian genera may thus be assumed to have evolved from an ancestor in the Indian subcontinent, but data on species distribution are still lacking and more research is needed to confirm the origin of the clade.

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