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RESEARCH ARTICLE

Re-evaluating Oriental Metarbelidae (Lepidoptera: Cossoidea): Morphology, Cladistics, and Taxonomic Implications for *Psychidarbela* and Ratardidae

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Abstract

Metarbelidae are an intriguing group of Cossoid moths that have recently received considerable attention. Although several new genera have been described from the Oriental region in recent years, the morphological diversity of the family remains poorly investigated. In addition, the unusual genus *Psychidarbela* and the rarely encountered diurnal family Ratardidae share several features overlapping with Metarbelidae. Consequently, Oriental Metarbelidae have remained difficult to delimit, and apomorphic characters are challenging to identify. In this study, we address this gap through an examination of the morphological characters of all Oriental genera. Using a maximum parsimony cladistic analysis based on 39 characters, we find Ratardidae nested within Metarbelidae. Accordingly, we synonymize the two families and recognize Ratardidae, **stat. nov.**, following the ICZN principles of priority. Furthermore, we establish the family-group name Psychidarbelidae Roepke, 1938, **stat. nov.**, for the genus *Psychidarbela*. Detailed morphological features supporting this arrangement are discussed. This proposal aims to improve diagnostic clarity and stabilize classification; however, it is tentative, and a comprehensive molecular analysis will be required to finalize broader phylogenetic relationships.

Keywords
Parsimony, apomorphy, gnathos, venation, genitalia

Introduction

Cossoidea are a phenetically diverse assemblage of Lepidoptera, comprising the largest heteroneurous group outside the Macrolepidoptera (Minet 1991; Edwards et al. 2003). Although historically difficult to classify precisely – particularly due to overlapping morphological and ecological features shared with Sesioidea – the current view of Lepidoptera classification treats Cossoidea as separate from Sesioidea (Minet 1991; van Nieukerken et al. 2011; Kawahara et al. 2019; Mayer et al. 2021; Rota et al. 2022; Chen et al. 2025). Moths of this superfamily are mostly xylophagous as larvae, and a number of species are regarded as economically important pests of commercial trees (Choochuen and Foit 2025).

The Metarbelidae, an intriguing group within Cossoidea, has recently received considerable attention. The family has been studied extensively by Ingo Lehmann, Wolfram Mey, and Polina Pavlova et al. in Africa (Lehmann 2008, 2009, 2010a, 2010b, 2011, 2012, 2014, 2019a, 2019b, 2025; Mey 2005, 2012, 2018, 2024; Lehmann & Rajaei 2013; Lehmann et al. 2018, 2023; Pavlova et al. 2025, 2026a, 2026b) and by Roman Yakovlev and colleagues in the Oriental region (Yakovlev and Zolotuhin 2020; 2021a, 2021b, 2021c, 2021d, 2022; Yakovlev et al. 2022a, 2022b, 2022c, 2022d, 2023, 2025, 2026; Yakovlev and Hulsbosch 2024). The history of Metarbelidae classification, particularly in the Oriental region, is summarized by Yakovlev et al. (2020). Although molecular phylogenetic hypotheses have been generated for many Lepidoptera lineages, Cossoidea has remained largely unstudied. In most molecular phylogenetic studies of Lepidoptera, Cossoidea – especially Cossidae – has been recovered as non-monophyletic (Wahlberg et al. 2013; Heikkilä et al. 2015; Kawahara et al. 2019; Mayer et al. 2021; Rota et al. 2022; Chen et al. 2025). Surprisingly, Metarbelidae has rarely been included in molecular phylogenetic analyses, with the exception of a single species, *Squamura maculata* (Mayer et al. 2021), reflecting a broader pattern of underrepresentation of microlepidopteran lineages in molecular studies (Wright et al. 2026).

Lehmann (2019) provided the first cladistic hypothesis of Metarbelidae, based primarily on Afrotropical taxa and a comprehensive set of morphological characters, establishing a baseline for the family that subsequently prompted studies of Oriental taxa. Currently, more than 44 species are known from the Oriental region, belonging to 17 genera. Although new genera continue to be described and Lehmann (2019) redescribed the family, relationships among Oriental genera remain poorly understood. These taxa share several unique apomorphies, suggesting an origin from African ancestral lineages (Lehmann 2019). Based on available molecular data, the origin of Metarbelidae has been estimated at approximately 90–100 Ma (Mutanen et al. 2010; Wahlberg et al. 2013).

Another family of interest is Ratardidae, a rare diurnal group of Cossoidea restricted to the Oriental region. The family currently comprises eleven described species in four genera, all endemic to tropical Asia with much diversity seen in India, Taiwan, Borneo and Sumatra islands, Malayan Peninsula, and the Philippines (Heppner 2017; Yakovlev 2018, 2022a). Ratardidae shares key characteristics with Metarbelidae, including features of the male genitalia (gnathos and subscaphium) and female ovipositor lobes (Holloway 1986; Kobes and Ronkay, 1990; Sugi 1995; Lehmann 2019; Lehmann et al. 2023). The family is likely phylogenetically younger than Metarbelidae (Lehmann et al. 2023). Holloway (1986) proposed synonymizing the two groups, but due to the absence of male genitalia data (only studied later by Owada 1993), no formal conclusion was reached.

Another problematic Oriental group related to Metarbelidae is the genus *Psychidarbela* Roepke, 1938. Xylophagous like most other Cossoidea, this genus exhibits acute sexual dimorphism, unusual antennal morphology, and reduction of R1 veins on the forewings in both sexes (Roepke 1938). Originally described within Cossidae, *Psychidarbela* was suggested to merit its own subfamily, Psychidarbelinae (Roepke 1938). The genus was not included in Schoorl's (1990) cladistic analysis, leaving its precise relationships within Cossidae uncertain. Males of this genus, with transparent wings, resemble Limacodidae genera such as *Pseudonagoda* and *Calauta*. Nonaka (2021) described another species mistakenly as a new genus, *Laonagoda*, within Limacodidae from Laos. Yakovlev et al. (2023) synonymized *Laonagoda* under *Psychidarbela* and placed the genus in Metarbelidae, although the apomorphic features supporting this placement were not explicitly discussed.

As a result, Oriental Metarbelidae remains problematic to define. Although many genera have been described, the distribution of apomorphies remains uncertain. It is unclear whether Ratardidae and *Psychidarbela* belong within Metarbelidae or represent separate Cossoid lineages.

The aim of this study is not to conclusively revise Cossoidea classification – a task requiring robust molecular and morphological analyses – but to review current knowledge of Oriental taxa and generate a preliminary phylogenetic hypothesis based on available morphological data, testing previous hypotheses regarding the classification of Oriental Metarbelidae. This study also aims to provide a baseline for future molecular studies and to test previous hypotheses regarding the classification of Oriental Metarbelidae.

Materials and methods

Taxon sampling: All currently recognized Oriental genera of Metarbelidae, including *Psychidarbela*, were included in the analysis. To provide a broader phylogenetic context and evaluate evolutionary relationships, early-diverging African lineages of the family (*Teragra*, *Metarbelodes*, and *Dianfosseya*) (Lehmann 2019) were incorporated. Two genera of Ratardidae (*Ratarda* and *Sumatratarda*) were included to test their potential relationship with Metarbelidae. Outgroups comprised two genera of Limacodidae (*Calauta* and *Pseudonagoda*), one genus of Cossidae (*Phragmataecia*), one genus of Dudgeoneidae (*Dudgeonea*), and one genus of Tortricidae (*Homona*). Limacodidae were specifically included to test their potential affinity with *Psychidarbela* (Figs 1–10).

Character matrix: Largely following Lehmann, 2019, but with a simplified set of characters. The morphological characteristics were retrieved from published literature along with the examination of fresh samples. The following is a summary of the characters and states:

Behavioral:

1. Activity: nocturnal (0), diurnal (1)

Ratardid genera are diurnal (Heppner & Wang, 1987). While metarbelid genera are nocturnal in having drab wing coloration. The genera *Orgyarbela* and *Vietarbela* due to having bright coloration may represent diurnal habit that requires further validation. Therefore, we keep them as unknown (?) character.

Head:

2. Male antennae: Simple filiform (0); basally pectinate, distally filiform (1); bipectinate with branches gradually reduced towards apex (2); bipectinate with nearly uniform branches (3); serrated (4).
3. Female antennae dimorphism: no (0), yes (1)
4. Labial palps: 2 segmented (0), 3 segmented (1)

Thorax:

5. Forewing with accessory cell: absent (0), present (1)
6. Forewing cellular veinlet: absent (0), bifurcated (1), vestigial (2)

Vestigial=present as a reduced single line (never bifurcated), absent=no trace at all.

7. R1 in forewing: absent (0), present (1)

Absent in *Psychidarbela* (=*Laonagoda*).

8. FW R3–R5 stalk type: R4+R5 stalked, R3 separate from base (0); R4+R5 stalked, R3 from base of stalk (1); R4+R5 stalked, R3 from middle of stalk (2); R3+R4 stalked, R5 arising near middle of stalk (3); R3–R5 all arising from same base (4)

Although Roepke (1938) illustrated males of *Psychidarbela* as lacking the R5 vein on the forewing (while it is present in females), Nonaka (2021) depicted R5 in males of *Laonagoda* (now synonymized with *Psychidarbela*). Careful examination of specimens indicates that R5 is indeed present in males of *Psychidarbela*. The R3 vein, however, remains obscured beneath the black scales along the costal margin, which previously led to misidentification of R5 as M1 by Roepke (1938).

9. Fully developed CuP of forewings: absent (0), present (1)
10. Hindwing frenulum in males: absent (0), present (1)
11. Hindwing cellular veinlet: absent (0), forked (1), unforked (2)
12. Condition of Sc+R1 and Rs in HW of males: free (0), Sc+R1 connected to Rs with a cross vein (1)
13. CuP in HW: absent (0), present (1)
14. Hindwing anal veins: single (0), two (1)
15. Fore and hindwing area: unequal (0), almost equal (1)
16. Male wings: scaly (0), transparent (1)
17. Male wings with distinct androconial scales along cubitus and middle area: absent (0), present (1)

Abdomen in general:
18. Tympanal organ at base of abdomen: absent (0), present (1)
19. Abdominal tuft: Absent (0), present (1)

Male genitalia:
20. Uncus type: undivided (0), divided (1)
21. Tegumen and vinculum: separable (0), fused (1)

Unseparable/fused condition of tegumen and vinculum is seen in all lineages of Cossoidea.

22. Uncus with apical hook: absent (0), present (1)

Present in Cossidae and Dudgeonidae.

23. Saccus: ill defined (0), moderate (1), robust (2)
24. Uncus and tegumen joint: separable (0), fully connected (1)
25. Shape of uncus: Spatulate (0), spatulate with caudal process (1), pyramidal M shape (2), broad M (3), laterally sclerotized membranous (4), apex pointed (5), Y shaped (6), spatulate with partially divided (7), fully divided (8), Lizard head (9), fishtail (10)
26. Gnathos arm: absent (0), connected beak like (1), bridged with subscaphium (2), bridged without subscaphium (3)
27. Gnathal sclerotized tongue (**if 26:2**): absent (0), present (1)
28. Lateral gnathal process: absent (0), present (1)
29. Lateral gnathal process shape (**if 28:1**): tongue/ ribbon like moderately sclerotized (0), broader leaf like (1), bifurcated (2), spiny (3), ribbed (4)

Although Heppner (2024) noted that *Vietarbela* is the only genus in Metarbelidae with a bifurcated lateral gnathal process, this feature is also present in *Hollowarbela kinabalua*, suggesting possible affinities between the two genera. This relationship is further supported by their shared character states, 25(0) and 33(1).

30. Length/width of valva ratio: almost equal (0), medium (1), almost twice (2)
31. Costal and saccular margin: parallel (0), converging (1)
32. Tip of valva: rounded (0), pointed (1)
33. Saccular margin in valva: undifferentiated (0), moderately differentiated without harpe (1), completely differentiated with harpe (2)
34. Basal valval bridge: absent (0), present (1)

Present in Tortricidae, Limacodidae, not in Cossoidea
35. Juxtal horn: absent (0), present (1)

Present in Limacodidae.
36. Cornutus in vesica: absent (0), present as a spinous field (1), present as 1-2 strong spine (2)
37. Shape of aedeagus: Tubular with apex base similar in width (0), nail shaped with swollen base (1)

Female genitalia:
38. Ovipositor lobe in female genitalia: Broad, flat, setose (0); short, telescopic, with slightly sclerotized, setose, non-piercing (1); short, telescopic and 8 shaped (2), very long, telescopic and piercing (3), broad, setose, not flattened (4)
39. Corpus bursae: simple (0), signate (1), scobinate (2)

Phylogenetic analysis: A morphological character matrix was compiled in Mesquite 3.81 (Maddison & Maddison 2023). Cladistic analyses were conducted in TNT version 1.6 using the custom script guoyi.run version 0.1.7 (Zhang 2025). Maximum parsimony analyses were performed under extended implied weighting (EIW) with a K value of 12, following the recommendations of Goloboff et al. (2018) and the implementation described by Zhang (2025). The script provides an automated pipeline for tree search, consensus construction, support estimation, and character optimization within the TNT environment. Clade support was assessed using three resampling approaches implemented in the script: jackknifing, bootstrapping, and symmetric resampling, each with 1,000 replicates. Apomorphic character-state changes were mapped onto the consensus tree following standard TNT optimization procedures as implemented by the script. In addition, overall tree statistics, including tree length (TL), consistency index (CI), and retention index (RI), were calculated to evaluate character fit and homoplasy in the dataset. The tree was visualized in WinClada v.1.00.08 (Nixon and Nixon 2002), and a publication-quality figure was prepared in Inkscape.

Morphological Matrix

Homona	0001001001001100000000001003-0-0002100001
Teragra	030112131020110000101001520???00000????
Dianfosseya	0301121300211100001110012201320010001??
Metarbelodes	0301121310211100001110013200-2001000120
Calauta	011102131120110100110010043-0-211111004?
Pseudonagoda	01?102131120110100100010041-0-11121110??
Ratarda	131002120121111000111001620111002002120
Sumatratarda	1310021201211110001110016201120020021??
Phragmataecia	011111111110110000000012050-0-2000000030
Dudgeonea	040111141110110001000012151-0-2000000010
Orgyarbela_	?30002120021110000111001A201010020001??
Hollowarbela	0300021200211100001010010201210010001??
Encaumaptera	0300021200211100001010019201010010021??
Indarbela_	030002120021110000111001620101002000120
Lutzkobesia	03000212002111000011100162010100200?1??
Squamicapilla	0300021200211100001110016201010020021??
Squamura	0300021200211100001110016201010020021??
Stueningeria	0300021200211100101110016201010020021??
Ghatarbela	0300021200211100001110018201010020001??
Micrarbela	0300021200211100001110017201010020021??
Marcopoloia	030002120021110000111001620101002002120
Tearbela	0300021200211100001110016201010020021??
Aukorbela	0300021200211100001010011211410000001??
Laonagoda	020002030120000100101011521142010000020
Psychidarbela	020002030120000100101011521142010000020
Vietarbela	?30002120021110000101001020121001000120
Siamella	0300021200211100001010015211410010001??
Tagoria	030002120021110000101001620101002000122.

Results and discussion

The broader aim of the present study is not to advance taxonomic changes solely on the basis of the following cladistic analysis, but rather to review the genera in light of the currently available morphological evidence. The cladistic results are used here primarily as a framework for assessing generic limits, identifying diagnostic characters, and highlighting major patterns of relationship, rather than as the sole basis for formal nomenclatural decisions. Accordingly, the emphasis of this work is on clarifying the composition and diagnosis of the genera, drawing attention to problematic placements, and providing a foundation for future studies. Any far-reaching taxonomic conclusions should therefore be regarded as provisional until they can be tested with broader sampling and, ideally, robust molecular data.

Phylogenetic relationships

Figure 15 shows the strict consensus tree of the 24 most parsimonious trees obtained from the analysis using extended implied weighting (K = 12). The maximum parsimony analysis did not fully resolve the relationships among the Oriental genera of Metarbelidae. The genera *Hollowarbela*, *Encaumaptera*, *Aukorbela*, *Vietarbela*, and *Siamella* retain a polytomous early diverging sister group position to all other genera, while *Tagoria* forms as sister lineage to the rest of the genera that all forms another polytomous clade.

In contrast, the African genera *Teragra*, *Metarbelodes*, and *Dianfosseya* were consistently recovered as the early diverging lineages of Metarbelidae, in agreement with Lehmann (2019), further supporting the hypothesis that the Oriental genera originated from African ancestral lineages.

The genus *Psychidarbela* (=*Laonagoda*) was confirmed as belonging to Cossoidea, forming a sister group to the remaining Metarbelid genera. Interestingly, the Ratardid genera *Ratarda* and *Sumatratarda* were nested within the unresolved polytomy of Oriental Metarbelidae, suggesting a close relationship with this group. The oriental clade of the metarbelid genera including *Ratarda* and *Sumatratarda* has a moderate support of jackknife/bootstrap/symmetric resampling = 58/48/53.

The apomorphies of Oriental Metarbelidae

1. The family was comprehensively defined by Lehmann (2019). In our study, character state 12(1), the presence of a crossvein between Sc+R1 and Rs in the hindwing, appears to be an apomorphic feature of the family. It is present in all Oriental genera, as well as in the African genera examined here, except for the earliest-diverging genus, *Teragra*.

2. In addition, all Oriental genera of Metarbelidae share a unique forewing venation pattern, characterized by R4 and R5 stalked, with R3 arising from the middle of the stalk (state 8:2) (Figs 3–4). Early diverging African genera, however, differ in exhibiting state 8:3, characterized by R3 and R4 stalked, with R5 arising near the middle of the stalk (Fig. 9).

3. The absence of a hindwing frenulum in males is another apomorphic feature shared by all metarbelid genera.

4. All Oriental genera of Metarbelidae lack a well-defined saccus in the male genitalia (state 23:0), although saccus is present in some African genera and is well developed in most Cossidae and Dudgeoneidae.

5. Although the vesica of the aedeagus usually lacks cornuti in Metarbelidae, when present they are always represented by one or two strong spines (state 36:2).

6. The aedeagus itself is usually divided into a swollen base and a tapered apex, giving it a nail-shaped appearance (state 37:1), a feature previously recognized by Holloway (1986) and Kobes & Ronkay (1990).

7. In addition, the antennae in Oriental Metarbelidae differs from those of other cossoid lineages in being bipectinate with nearly uniform branches throughout the length (state 2:3).

The 8 shaped ovipositor lobe, as seen in this study, is probably not a unique apomorphy of Metarbelidae/ Ratardidae, as it is shared by *Psychidarbela* as well, which seems to represent a non-metarbelid cossoid lineage discussed below.

Position of *Psychidarbela*

The genus *Psychidarbela* was recovered as the sister lineage to Metarbelidae and lacks the key apomorphies that characterize Oriental metarbelid genera. Unlike Oriental Metarbelidae, *Psychidarbela* exhibits the forewing venation pattern in which R3 and R4 are stalked and R5 arises near the middle of the stalk (state 8:3) (Figs 7–9). This is a homoplasious trait that is also seen in African genera studied here (Fig. 9), as well as in Limacodidae. In addition, the tubular, non–nail-shaped aedeagus, the absence of a crossvein between Sc+R1 and Rs in the hindwing, the moderately developed saccus, and the presence of a frenulum in males further distinguish this genus from Metarbelidae.

Despite these differences, *Psychidarbela* shares several features with Metarbelidae, including 8-shaped ovipositor lobes in females (state 38:2), a subscaphium fused with the gnathal bridge (state 26:2), and laterally ribbed gnathos arms, as seen in the metarbelid genera *Aukorbela* and *Siamella*. The latter trait is of particular interest, as it is consistently associated with two additional features: a highly sclerotized, broad, triangular- or tongue-like structure, apparently modified from the boat-shaped subscaphium seen in most Metarbelidae; and an elongated valva, nearly twice as long as wide. This pattern probably suggests that these features are ontogenetically correlated, which may warrant further investigation.

Unlike any Oriental cossoid family, *Psychidarbela* possesses the following autapomorphies:

a. absence of R1 in the forewing in both sexes (state 7:0);

b. sexual dimorphism characterized by transparent-winged males (state 16:1).

c. absence of CuP in hindwings (state 13:0).

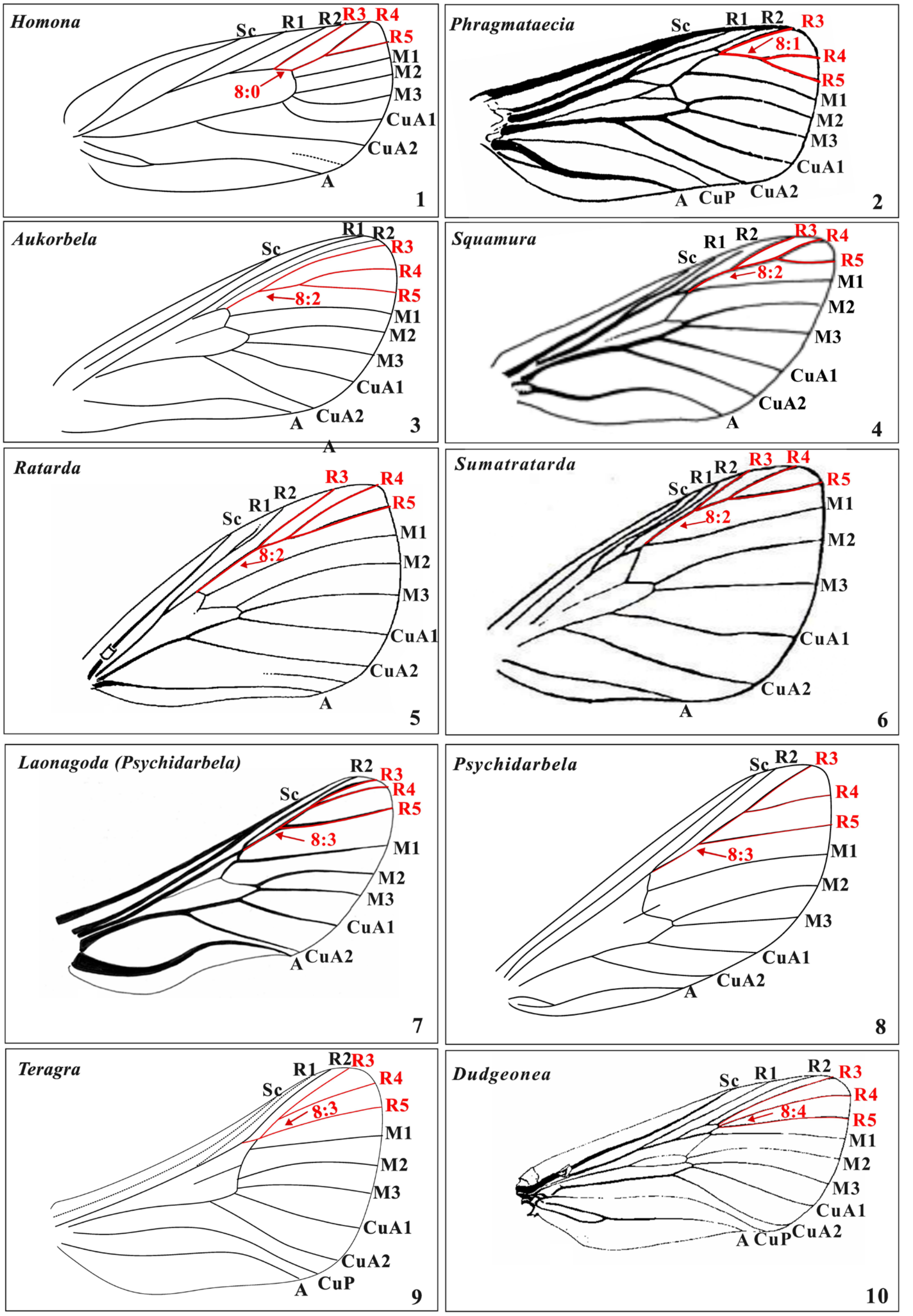
d. a single anal vein (state 14:0), which is always two (state 14:1) in the majority of oriental metarbelid genera along with other cossoids.

These autapomorphies, together with the clear morphological differences between *Psychidarbela* and Oriental metarbelid genera, indicate that it is better treated as a distinct group. Roepke (1957) commented that, after examining the genitalia of a number of eastern “Squamuridae” [= Metarbelidae], “it is clear to me that *Psychidarbela* undoubtedly belongs to the Cossidae.” The comment, undoubtedly, stemmed from the fact that the Tegumen and vinculum are fused in *Psychidarbela* as seen in other cossoid families (state 21:1). However, *Psychidarbela* differs from all cossid subfamilies in the absence of R1 on forewings, absence of CuP on both wings, the vestigial and non-bifurcated condition of the cellular veinlets in both wings (a feature also seen in all Metarbelidae), and the form of the female ovipositor lobes which is piercing and telescopic in all cossid subfamilies known so far. Although the non-monophyletic condition of Cossidae is well documented, and we included solely the genus *Phragmataecia* (Zeuzerinae) as an exemplar of the family in our analysis, the abovementioned condition of morphological features observed in Psychidarbela almost readily set it apart from Cossidae.

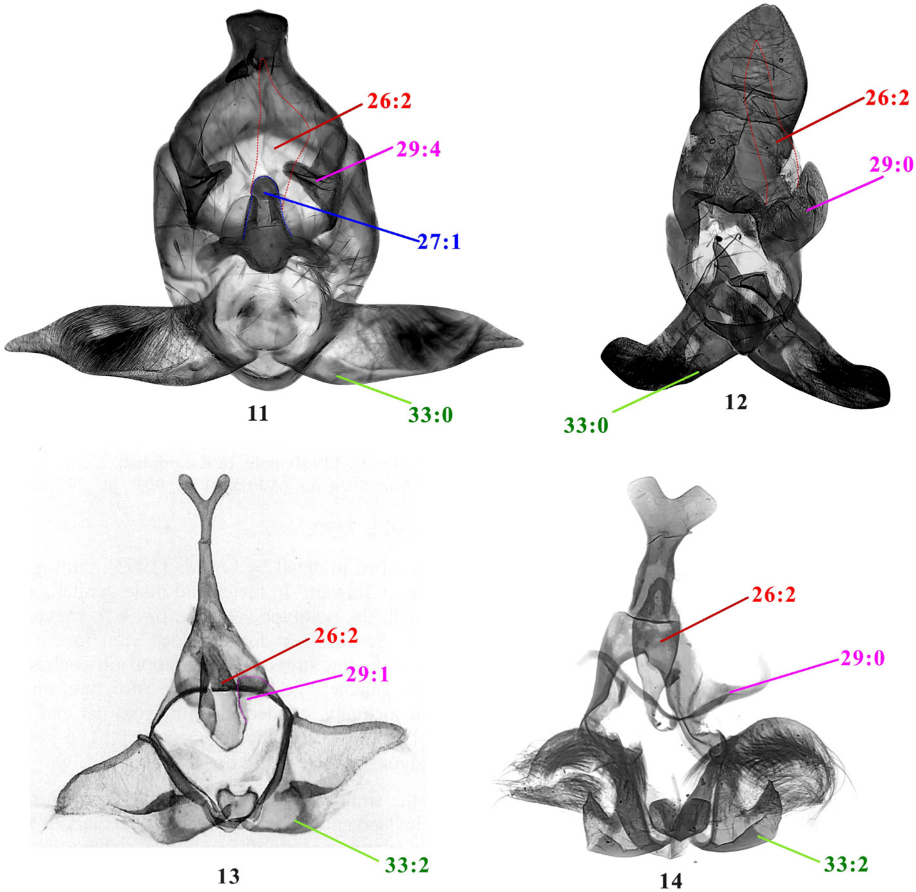
Accordingly, the original opinion of Roepke (1938), who erected the subfamily Psychidarbelinae, deserves support. Nevertheless, placing the genus within Cossidae would make the concept of that family difficult to define because of the anomalous morphology of Psychidarbela discussed above. On the basis of all currently available evidence, it is therefore proposed that the genus be elevated to a monogeneric family of its own, Psychidarbelidae Roepke, 1938, **stat. nov.** However, its affinities with other cossoid families remain unclear, and whether it constitutes a highly divergent lineage of Cossidae or even Metarbelidae can only be determined through comprehensive molecular study. Based on the morphological evidence presently available, the objective of this proposal is not to introduce an artificial reclassification, but to provide a classification that is both stable and diagnosable. We therefore propose that *Psychidarbela*, rather than being treated as incertae sedis within Cossoidea, be recognized as a separate monogeneric family. Nevertheless, a definitive resolution will depend on robust molecular evidence, which is currently lacking.

Position of Ratardidae

The two ratardid genera examined here differ from the Oriental metarbelid genera mainly in their diurnal habit, broader wing shape, presence of a male frenulum, and female antennal dimorphism. In nearly all other respects, however, Ratardidae is morphologically inseparable from Oriental Metarbelidae. Although support for the relevant polytomous clade is low (jackknife/bootstrap/symmetric resampling = 26/21/28), both *Ratarda* and *Sumatratarda* are recovered within the Oriental metarbelid assemblage and share with it a number of distinctive character states, including the presence of a crossvein between Sc+R1 and Rs in the hindwing (character 12:1); the distinctive forewing venational pattern in which R3 arises from almost the middle of the R4+R5 stalk (character 8:2); a poorly defined saccus and nail-shaped aedeagus in the male genitalia; well-developed harpe on the valva; similarly pectinate male antennae; an 8-shaped ovipositor lobe; a Y-shaped uncus, also present in several Oriental metarbelid genera such as *Squamura*, *Stueningeria*, and *Indarbela* (character 26:6) (Figs 11–14); and a similarly boat-shaped subscaphium connected to the gnathal bridge, a condition seen in all Metarbelidae (Figs 13–14).



Figures 1–10. Forewing venation showing character 9 and its states. **1.** *Homona coffearia*; **2.** *Phragmataecia castaneae* (from Arora 1976); **3.** *Aukorbela golovizini*; **4.** *Squamura kinabalua* (from Holloway, 1976); **5.** *Ratarda excellens* (from Owada 1993); **6.** *Sumatratarda diehli* (from Kobes and Ronkay 1990); **7.** *Laonagoda pellucida* (from Nonaka 2021); **8.** *Psychidarbela kalshoveni*; **9.** *Teragra* sp.; **10.** *Dudgeonea leucosticta* (from Edwards et al. 2003). [Fig. 8 female, rest males].



Figures 11–14. Male genitalia with character states. **11.** *Aukorbela golovizini*; **12.** *Encaumaptera arora*; **13.** *Ratarda excellens* (from Sugi 1995); **14.** *Stueningeria htetae*.

These results strongly suggest that Ratardidae does not represent an independent cossoid lineage, but rather a specialized, probably more recently derived diurnal lineage within Metarbelidae as noted by Lehmann et al. (2023). This interpretation aligns with Holloway (1986), who had already recognized the close affinity between the two groups. At the time, however, Holloway refrained from formally synonymizing the two families because male genitalia were not yet available for study. Inoue (1988) later expressed the same view. Holloway (1986) even predicted that ratardid moths would prove to be bark-feeding in their larval stage, as in many metarbelid genera, based on three shared features of the female genitalia. Nevertheless, bark-feeding is not universal within Metarbelidae; for example, *Vietarbela* feeds entirely within the stem rather than bark (Heppner et al. 2024).

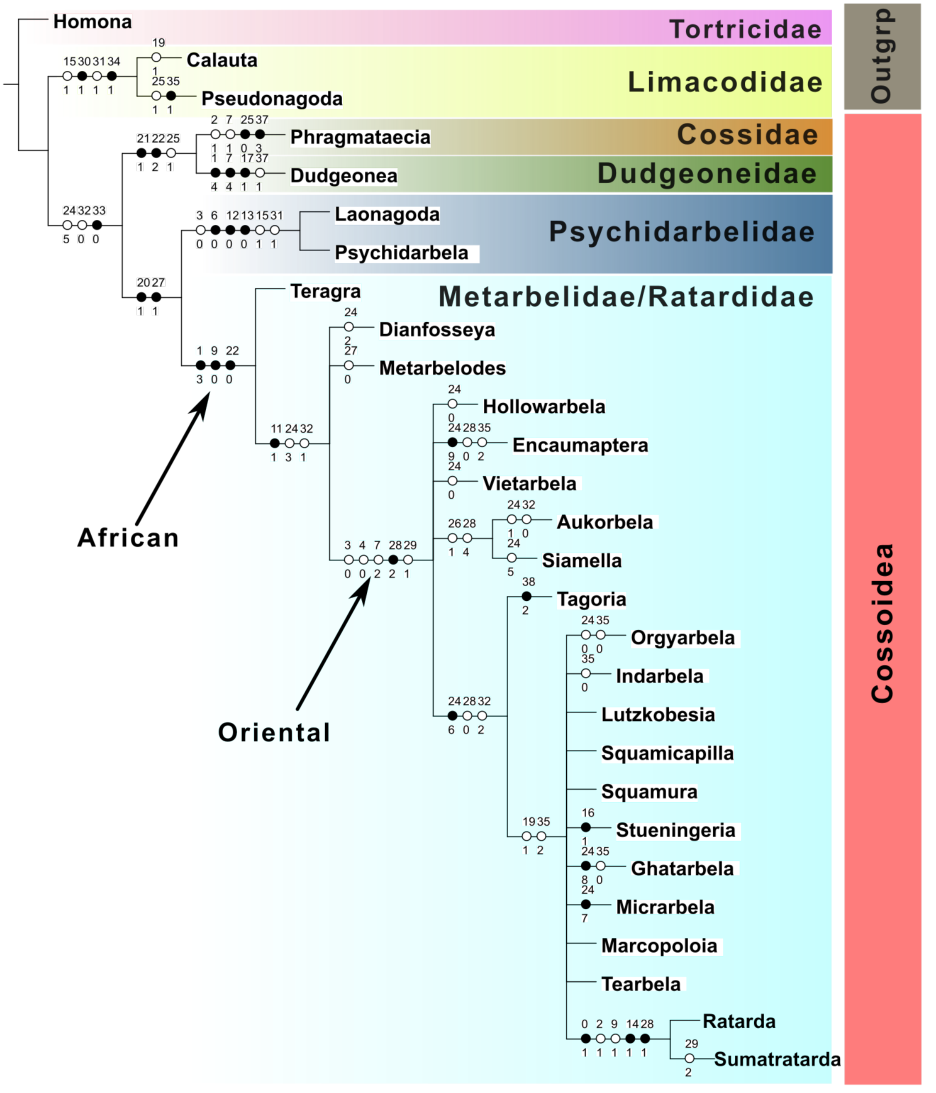


Figure 15. Strict consensus tree of 24 most parsimonious trees obtained using TNT 1.6 under extended implied weighting (K = 12). Apomorphic characters are mapped on the tree. Consistency Index (CI) = 0.683, Retention Index (RI) = 0.775, Tree Length (TL) = 101. Apomorphic characters are mapped onto the tree (read as 0-38, representing 1-39 characters listed above). Black filled circles indicate apomorphic (non-homoplasious) character changes, whereas transparent circles indicate homoplasious character changes.

Kobes and Ronke (1990) further emphasized the similarities between Ratardidae and Metarbelidae, noting the Y-shaped uncus, the fused condition of the uncus and tegumen, the form of the valva together with the presence of a harpe, and the structure of the aedeagus. Their assessment, however, was based solely on the genus

Sumatraratarda. The male genitalia of the genus *Ratarda* were described only later by Owada (1993) and Sugi (1995), and these were found to conform closely to those of *Sumatraratarda*. Together, they share the same apomorphic traits seen in most Oriental metarbelid genera specifically *Indarbela*, *Squamura*, *Stueningeria*, *Lutzkobesia*, *Tearbela*, *Marcopoloia*, and *Squamicapilla*. Although the males and male genitalia of the remaining two ratardid genera (*Callosiope* and *Praesaturnia*) are still unknown, the available female characters likewise support their close relationship with metarbelid genera.

It follows, on the basis of the morphological evidence presently available, that the most parsimonious interpretation is to treat Ratardidae as a synonym of Metarbelidae. Nevertheless, as noted above, Cossoidea has repeatedly been recovered as non-monophyletic, and the metarbelid genus *Squamura* was placed within Cossidae – itself also recovered as non-monophyletic – in the molecular study of Mayer et al. (2021). Despite these findings, the prevailing consensus has been to retain Metarbelidae as a distinct family pending a comprehensive molecular phylogeny of Cossoidea. Accordingly, if Metarbelidae + Ratardidae are regarded as a separate lineage within Cossoidea, outside Cossidae, then under the Principle of Priority of the ICZN the valid family-group name would be Ratardidae Hampson, 1898 as proposed by Holloway, 1986.

Synthesizing the evidence from all previous studies together with our present analysis, we conclude that Metarbelidae should be synonymized with Ratardidae, **stat. nov.**

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