The King’s Lace Bug *Recaredus rex* Distant, 1909 (Hemiptera: Heteroptera: Tingidae): Systematic Position, First Palaearctic and Afrotropical Records, and Ecological Niche Modelling

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**Simple Summary:** Lace bugs (Tingidae) are known for their spectacular bodily appearance; the pronotum and hemelytra of the adult specimens are lacelike, with a delicate network of areolae that resemble lace. The species are phytophagous and always feed on a specific plant or groups of closely related plants. Therefore, they are recognised as mono- or oligophagous bugs, whose feeding activities may cause significant injury to plant pods and leaves. Lace bugs are distributed worldwide and reported in all continents except Antarctica. Although most of the lace bug species are distributed in a particular zoogeographical region, some genera are widely known from the Holarctic region. However, species with a Palaeotropical distribution are scarce. In this study, based on new records and ecological niche modelling, we indicate that *Recaredus rex*, one of the most enigmatic lace bugs, has a possible Palaeotropical distribution. Moreover, we hypothesise that *R. rex* is an oligo- or polyphagous species. In addition, the systematic position of the genus *Recaredus* is discussed.

**Abstract:** The systematic position and actual distribution of *Recaredus rex*, for a long time one of the most enigmatic lace bug genus and species, is very obscure because only the type specimen and three other individuals from India are known to date. In the present paper, we report the first records of *R. rex* from the Palaearctic region (Iran) and tropical Africa (Ghana). Based on the occurrence localities and climatic variables, we predict potentially useful ecological niches for this species using Maxent software. The areas with the best environmental conditions for *R. rex* indicated in our studies suggest its possible Palaeotropical distribution. Moreover, we regard these results as a good starting point for further searches for specimens of this species. This might help verify the hypothesis of the broad Palaeotropical distribution of *R. rex* and its oligo- or polyphagy. In addition, the lace bug genus *Recaredus*, based on the diagnostic characteristics provided for the tribe Acalyptaini, and the structure of *aedeagus*, is transferred from the tribe Ypsotingini to the Acalyptaini. A key to all genera currently included in the latter tribe is also provided.

**Keywords:** lace bugs; systematic position; new tribal assignment; distribution; niche modelling; feeding habit; Ghana; India; Iran; Palaeotropics

1. Introduction

*Recaredus rex* was described by Distant [1] from West Bengal (India) as a genus and species new to science and was named after the Visigothic King of Hispania and Septimania (Reccared I or Recared I (559–601); in Latin: *Recaredus* or *Recaredus, rex* Visigothorum) [2–4]. This Oriental genus was diagnosed, besides other characteristics, as having a “Head distinctly produced and deflected between the bases of the antennae, and also with a distinct lateral curved robust spine between the antennae and eyes” [1,5]. This unique head armoury (bringing to mind a crown worn by the King Recared I in his portrait [6]) most probably inspired Distant to give such an unusual name to this new lace bug.
For a long time, the species was known only from its original short description [1] repeated in the “Fauna of British India” [5], supplemented by a line drawing of the type specimen. In its description, Distant [1,5] suggested that “this genus apart from the structure of the head has a considerable resemblance to Acalypta Westwood, 1840, a Palaearctic genus”. No type material or other specimens of this species have been recorded since its original description. Therefore, _R. rex_ was regarded as one of the most enigmatic Oriental lace bugs [7].

However, all authors [8–11] hypothesised the systematic position of the genus within the family Tingidae based only on its original description and without any explanation for such acts. In the first checklist of the Tingidae genera of the world [8], _Recaredus_ was placed within the subfamily Tinginae. Three years later, Drake [9] transferred this genus from the Tinginae to the subfamily Cantacaderinae, where it was maintained during the revision of the lace bug genera of the world [10]. However, a few years later [11], _Recaredus_ was reassigned to the subfamily Tinginae and classified within the tribe Tingini, but without any comments or explanations.

Only in the 21st century was the type material of _R. rex_ discovered [7]. Moreover, three other specimens from India were studied, which enabled redescribing the genus and species and disclosing their systematic position within the family [7]. As a result of those studies, _R. rex_ was suggested to represent the tribe Ypsotingini (_sensu_ Froeschner [12]), being closely related to _Derephysia_ Spinola, 1837 and _Kalama_ Puton, 1876 (both representing the tribe Ypsotingini at that time). However, Golub and Golub [13] indicated that three genera of Ypsotingini (_Derephysia, Kalama, Dictyonota_ Curtis, 1827) and the genus _Acalypta_ Westwood, 1840 (classified to date within the tribe Tingini) have several essential features in common. Therefore, they united those four closely related genera into a tribe under the resurrected valid name Acalypthin _[Acalyptaini; ICZN Case 3813]_ [14].

Since we were able to study the samples of _R. rex_ from India and recently discovered its Afrotropical and Palaearctic specimens, we decided to verify whether the genus _Recaredus_ should also be classified within the tribe Acalypthin. Moreover, its new country records suggest a not strictly Oriental but much broader area of occurrence. Because _R. rex_ specimens were found in the territory of three countries that are not directly adjacent, we considered generating the species potential distribution map using the ecological niche modelling (ENM) methods. Ecological niche modelling (ENM) is a method that allows an area of high habitat suitability to be estimated for a species based on data on its occurrence and environmental conditions [15,16].

In true bugs (Hemiptera: Heteroptera), ENM has also been used, but not so often. This method was applied several times to invasive alien species [17–21] and agricultural pests [22,23] and incorporated in ecological studies of various types [24–31].

2. Materials and Methods

2.1. Specimens Examined

Indian specimens of _R. rex_ come from the entomological collection at the National Pusa Collection (New Delhi, India—NPCI). The African specimen from Ghana belongs to the Museum and Institute of Zoology, Polish Academy of Sciences (Warsaw, Poland—ZMPA). The Iranian specimens (Figure 1A–C) were found in the entomological collection of the National Museum of Natural History, Department of Entomology (Prague, Czech Republic—NMPC), and were sampled during the Czechoslovak–Iranian entomological expedition to Iran [32].
Figure 1. (A–C) One of two specimens of *Recaredus rex* sampled during the Czechoslovak–Iranian entomological expedition to Iran in 1977. (A) Habitus, dorsal view. (B) Habitus, lateral view. (C) Head, dorsal view. (D–F). *Ductus seminis* (ds), *endosomal diverticula* (ed) and *endosomal sclerites* (scl). (D) *Recaredus rex* (after [7], modified). (E) *Derephysia foliacea* (Fallén, 1807). (F) *Kalama tricornis* (Schrank, 1801) (after [33], modified).

2.2. Photograph Preparation

All images of the studied specimens were captured with a Moticam 1000 digital camera mounted to an Olympus SZX10 microscope using an Images Plus 2.0 software (Motic Asia, Hong Kong, China). Multiple focal planes were merged using Helicon Focus 7.7.5 software (Helicon Soft Ltd., Kharkiv, Ukraine).

2.3. Ecological Niche Modelling (ENM)

Many methods have been used for ENM, but the maximum entropy algorithm implemented in the Maxent software is suggested to perform better than other algorithms [34–37]. In our study, we used the machine learning algorithm of the Maxent tool [38]. It estimates suitable and unsuitable areas for species based on maximum entropy for presence-only and environmental data [34] and is less sensitive to sample size [39]. Small samples are a significant limitation for building an ecological niche model. We use the recommendations to optimise the model for small samples [40–43] in order to obtain the most statistically significant and helpful results based on a few sites.

2.3.1. Occurrence Data

To model the niche in Maxent, all available information on the presence of *R. rex* (two sites from India [7] and two new sites described in this paper—one from Ghana and one from Iran; Figure 2) were used. The distance between the sites in India is over 480 km;
therefore, there is no risk of spatial autocorrelation. The data were georeferenced in Google Earth 9.158.0.0 [44].

Figure 2. Maxent ecological niche modelling results for *Recaredus rex*. Red and dark orange colours mark areas with high habitat suitability for the species. Literature sites (India) are marked with black stars, while new locations (Iran, Ghana) are marked with green stars.

2.3.2. Environmental Variables

WorldClim 2.1 climate data for 1970–2000 [45] were used as environmental variables: 19 bioclimatic variables, elevation data, monthly climate data for precipitation, solar radiation, and minimum, maximum, and mean temperature. Both versions of the variables (with WGS84 Coordinate Reference System), 30 arc-seconds spatial resolution and 2.5 arc-minutes spatial resolution, were converted to ASCII format in the ArcGIS Desktop 10.7.1 software [46].

Variable selection was performed to exclude variables that were highly correlated. First, in ArcGIS, the variables with 2.5 arc-minutes spatial resolution were normalised to compare variables with different units. Then, the MaxentVariableSelection vignette [47] for R 4.0.0 [48] was used to extract environmental variables for occurrence and background locations (background data were generated by Maxent 3.4.1 software), removing highly correlated variables (contribution threshold 5, correlation threshold 0.8) and selection of most accurate beta-multiplier settings. Thirty arc-seconds version of selected variables (Table S1) was used in Maxent analysis.

2.3.3. Model Optimisation and Maxent Settings

Maxent software was used to predict *R. rex* presence probability (main settings: auto features, 25 random test percentages, ten bootstrap replicates, maximum test sensitivity plus specificity threshold rule). Modelling was conducted for beta-multiplier from 1.0 to 3.5 (in increments of 0.5). Even though the MaxentVariableSelection vignette indicated 1.0 as the most accurate beta-multiplier, the beta-multiplier 1.5 was selected as it gave a lower standard deviation for the receiver operating characteristic curve and environmental variables response curves, with the same average training AUC (average area under the curve) for the replicate runs. Higher beta-multipliers generated overfitted models.
2.4. Output Visualisation and ENM Map Preparation

The point-wise mean picture of the model, obtained as a result of calculations in Maxent, was converted in ArcGIS to TIFF format. The results and occurrence data were plotted on the Natural Earth map [49] with the world administrative boundaries [50]. The jackknife test plot was prepared in R. The environmental variables response curves were generated in Maxent.

2.5. Tribal Classification of the Subfamily Tinginae

Since there is no shared view on the tribal classification of the subfamily Tinginae, several different approaches to this problem exist (a detailed review can be found in [13]). Sometimes, the subfamily is not subdivided into lower taxonomic units, e.g., [51,52], or only two tribes, Phatnomini and Tingini (including genera of Litadeini and Ypsotingini) [53–55] are recognised. Some authors, however, accept its traditional subdivision into three tribes, namely Ypsotingini, Tingini, and Litadeini [7,11,12,33]. Nevertheless, the complete list of all previously suggested intra-subfamilial taxa of the Tinginae is much longer; they are summarised in the World [11] and the Palaearctic [52] family catalogues.

For the present study, we accept the conventional grouping of the Tinginae genera into three tribes (Ypsotingini, Tingini, Litadeini), with the Acalyptaini, recently recognised as a separate tribe for the genera excluded from the Tingini [13].

3. Results and Discussion

3.1. Material Studied, First Country Records and Geographic Coordinates

**INDIA**: West Bengal, Pareshnath, 4.000–4.400 ft, 12.iv.1909 (Zoological Survey of India, Kolkata; not examined, see [7]).

**INDIA**: 1 ex.: 14. VIII. 1910, Potato tuber, Mullyah, Bettiah, J. R. No: 927, l. no: 853; Recaredus, A. Hakk det., 1. 1. 63; 1 ex.: 17. VIII. 1910, Potato tuber, Mullyah, Bettiah, J. R. No: 927, l. no: 853; Recaredus, A. Hakk det., 1. 1. 63; 1 ex.: Bettiah, Behar and Oriissa, On stored potatoes, H. L. Dutt, Recaredus, A. Hakk det., 1. 1. 63, coll. unknown (NPCI).

**GHANA**: 1 ex.: Legon, Botanical Garden, 22–28 IV 1965, at light, leg. M. J. Prószyński, 1963 (ZMPA). **First country record; new to tropical Africa.**

**IRAN**: 2 exx.: S. Iran, Abbassi, Bang-e Tang, 6 km W. of Geno, 410 m, 50 km N. of Bandar Abbas, 7–9. 05. 1977, Loc. no 323, Exp. Nat. Mus. Praha—Figure 1 (NMPC). **First country record; new to the Palaearctic Region.**

We provide all the geographic coordinates for each locality used for ENM in Table 1.

| Position Number on the Map | Country | Locality Data | Coordinates |
|---------------------------|---------|---------------|-------------|
| 1                         | India   | West Bengal: Pareshnath, Bankura district | 22°57′21.3″ N, 86°44′51.4″ E |
| 2                         | India   | Bihar State: Bettiah, West Champaran district | 26°48′05″ N, 84°30′10″ E |
| 3                         | Iran    | Hormozgan province: Abbassi, Bang-e Tang | 27°27′ N, 56°18′ E |
| 4                         | Ghana   | Accra Metropolis district: Legon | 5°39′ N, 0°11′ W |

3.2. Ecological Niche Modelling

Maxent’s modelling results (Figure 2) indicate very high habitat suitability for *R. rex* along the Middle Eastern and Northeast African coastlines, bordering the Red Sea, Arabian Sea, and the Persian Gulf. Good environmental conditions for this species can be noted primarily along the eastern shore of the Indian Peninsula, in Bangladesh, in the Indus Valley Plain of Pakistan, in Saudi Arabia’s Al-Ahsa Governorate, and in the western part of the Sahara Desert ecoregion (in Mauritania, Mali and Algeria).
The mean AUC for ten replicate Maxent runs is 0.990, and the standard deviation is 0.003. The environmental variables response curves (Figure 3) and the jackknife test of variable importance (Figure 4) indicate that the most substantial impact on the Maxent prediction has a minimum temperature in September—a decrease in the average temperature this month below 27 °C significantly reduces the habitat suitability for this species. The elevation is also essential—the suitability of a location is better in the case of areas located at or below sea level.

![Figure 3. The environmental variables response curves. The mean response of the 10 replicate Maxent runs (red) and the mean +/- one standard deviation (blue) show how each environmental variable affects the Maxent prediction.](image-url)
Figure 4. The jackknife test of variable importance. The grey colour indicates using a variable in isolation, and the blue colour specifies the modelling without the selected variable. The higher the score for the first (with only variable) and the lower for the second (without variable), the more critical the selected environmental variable is for the model (AUC—average area under the curve).

The obtained results indicate that the most crucial factor contributing to the high level of habitat suitability for *R. rex* is the temperature in September above 27 °C, especially in areas with low altitudes. The areas with the best environmental conditions for *R. rex* indicated by Maxent can be a starting point for further searches for other specimens of this species.

3.3. Systematic Position and New Tribal Assignment

When Golub and Golub [13] restored the tribe Acalyptaini, they provided a set of diagnostic morphological characters enabling its separation from other tribes of the subfamily Tinginae. All of these were also found in *R. rex*, as follows: the head with two frontal tubercles (the median spine or tubercle is lacking); the buccal laminae not closed anteriorly; the paranota only slightly oblique; the posterior process of the pronotum flat, and the opening of the metathoracic scent glands without peritreme.

Moreover, the structure of aedeagus in *R. rex*, especially its bifurcate ductus seminis and small endosomal diverticula ([7], and Figure 1D–F), suggest a close relation of Recaredus to the four genera constituting at present the tribe Acalyptaini (*Acalypta*, *Derephysia*, *Dictyonota*, and *Kalama*) [13]. Though their male genitalia were not analysed when the tribe was restored [13], we consider bifurcate ductus seminis and small endosomal diverticula as good diagnostic characteristics for this tribe [7,33].

Therefore, considering all the characters mentioned above, we propose transferring the genus *Recaredus* from the tribe Ypsotingini to the Acalyptaini (new tribal assignment).

3.4. Taxonomy

Order **Hemiptera** Linnaeus, 1758
Suborder **Heteroptera** Latreille, 1810
Infraorder Cimicomorpha Leston, Pendergrast et Southwood, 1954
Superfamily Tingooidea Laporte, 1832
Family Tingidae Laporte, 1832
Subfamily Tinginae Laporte, 1832
Tribe Acalyptaini Blatchley, 1926

Acalyptini Blatchley, 1926: 451, 479. Junior homonym of the Acalyptini Thomson, 1859 (Coleoptera, Curculionidae) [14]. Type genus: Acalypta Westwood, 1840.

Included genera: Acalypta Westwood, 1840. Type species: Tingis carinata Panzer, 1806. Derephysia Spinola, 1837. Type species: Tingis foliacea Fallén, 1807. Dictyonota Curtis, 1827. Type species: Dictyonota strichnocera Fieber, 1844. Kalama Puton, 1876. Type species: Campylostira (Kalama) coquereli Puton, 1876. Recaredus Distant, 1909 (new tribal assignment). Type species: Recaredus rex Distant, 1909.

3.5. Key to the World Genera of the Tribe Acalyptaini

A key to all genera classified currently within the tribe Acalyptaini is provided below. It was adapted from [7,13] and modified adequately to the results of the present study.

1. Each hemelytron with tectiform or almost vesicular elevation. Areolae of hemelytra large ([13], p. 232, Figures 10–18) (Figure 1A–B) . . . 2

2. Hemelytra flat, without tectiform or vesicular elevation [13]. Areolae of hemelytra of moderate size ([13], p. 231, Figures 1–3) . . . 3

3. Subcostal area with a single row of cells ([13], p. 232, Figures 10–12) . . . Derephysia Spinola, 1837

- Subcostal area multiseriate, with three rows of cells ([7], p. 598, Figure 1) ... Recaredus Distant, 1909

3. Head with two frontal spines only [13]. Antennae thin, without tubercles bearing seta on their apices [13]; antennal segment IV distinctly thicker than segment III ([13], p. 321, Figures 1, 4 and 7) . . . Acalypta Westwood, 1840

- Head, besides two frontal spines, usually with two additional occipital spines or tubercles visible from above or covered dorsally by areolate hood (vesicula); but if occipital spines absent (in some Kalama species), then antennae thick, with distinct and often large tubercles bearing seta apically; antennal segment IV not thicker or insignificantly thicker than segment III [13] . . . 4

4. Occipital spines always present, noticeably elongated and usually protruding beyond posterior margin of eyes [13]. Preorbital part of the head often noticeably elongated ([13], p. 231, Figures 2, 5 and 8) . . . Dictyonota Curtis, 1827

- Occipital spines absent or very small, tuberculate, not elongate, located far behind the posterior margin of eyes [13]. Preorbital part of head short ([13], p. 231, Figures 3, 6 and 9) . . . Kalama Puton, 1876.

3.6. Distribution and Biology

To date, R. rex is known only from two localities in India [1,7] and has always been considered an Oriental taxon [1,5,7–11]. Two new records, one from the Palaearctic region and one from tropical Africa, along with the ENM results, suggest a more widespread distribution of this lace bug. The very high habitat suitability for R. rex in some areas of Africa, the Near East, and Southeast Asia (Figure 2) indicates its possible Palaeotropical distribution.

Nevertheless, almost nothing is known about the species’ biology and feeding habits. Nonetheless, the collected data (“potato tubers” and “on stored potatoes” [7]) might indicate that this species is somehow closely related to Solanaceae. This is a little surprising since Solanum tuberosum Linnaeus, 1753, as well as all other species of Solanaceae, are reported as host plants only for New World lace bugs [11]. Therefore, when the predicted Palaeotropical distribution of R. rex is considered, it seems reasonable to believe it is an oligo- or polyphagous species.
Furthermore, even though lace bugs are predominantly mono- or oligophagous [11,51,55], several species can feed on plants of various taxonomic groups. Significantly, it is worth mentioning the Ivy lace bug, *Derephysia foliacea* (Fallén, 1807), a polyphagous species [11,52], which is classified within the tribe Acalyptaini [13], the same as *R. rex* is in this paper. However, one can also find a widely polyphagous lace bug, e.g., *Cochlochila bullita* (Stål, 1873), that has a Palaeotropical distribution [11,52,56–61], the same as suggested for *R. rex* in this paper. The predicted areas of *R. rex* distribution and indicated possible feeding habits could be a starting point for future studies on this species.

4. Conclusions
1. The lace bug genus *Recaredus*, based on the diagnostic characters provided for the tribe Acalyptaini and the structure of *aedeagus*, is transferred from the tribe Ypsotingini to the Acalyptaini.
2. *Recaredus rex*, a lace bug species only known from localities distributed within the Oriental region, are recorded for the first time in the Palaearctic region and the Afrotropics.
3. Ecological niche modelling results and new records of species suggest its possible Palaeotropical distribution.
4. The areas with the best environmental conditions for *R. rex* indicated by Maxent can be a starting point for further searches for specimens of this species. It might help verify the hypothesis of its Palaeotropical distribution and its oligo- or polyphagy.

**Supplementary Materials:** The following supporting information can be downloaded at: [https://www.mdpi.com/article/10.3390/insects13060558/s1](https://www.mdpi.com/article/10.3390/insects13060558/s1), Table S1. Environmental variables for occurrence and background locations used in Maxent analysis.

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**Conflicts of Interest:** The authors declare no conflict of interest.

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