



On the status of the genera complex *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* (Heteroptera: Tingidae: Tinginae) having common morphological and karyological features

О статусе комплекса родов *Acalypta*, *Dictyonota*, *Kalama* и *Derephysia* (Heteroptera: Tingidae: Tinginae), имеющих общие морфологические и кариологические особенности

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Abstract. A complex of morphological features of the genera *Dictyonota* Curtis, 1827, *Kalama* Puton, 1876 and *Derephysia* Spinola, 1837 (Heteroptera: Tingidae: Tinginae), inconsistent with the characters of the tribe Ypsotingini Drake et Ruhoff, 1965, is discussed. The common morphological features of these genera together with those of *Acalypta* Westwood, 1840, which do not correspond to the characters of *Tingis* Fabricius, 1803, as the type genus of the tribe Tingini Laporte, 1832, are presented. The data on the sex chromosome system X0/XX of these four genera, radically different from that of all the other 17 so far karyotyped Tinginae genera (XY/XX), are summarised. The closely related genera *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* are united in a tribe under the resurrected valid name Acalyptini [Acalyptaini; ICZN Case 3813, in press] Blatchley, 1926 according to the principle of priority (ICZN, Article 23). A diagnosis of the resurrected tribe Acalyptini based on morphological and karyological characters and an improved key to the genera *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* are given.

Резюме. Обсуждён комплекс морфологических особенностей родов *Dictyonota* Curtis, 1827, *Kalama* Puton, 1876 и *Derephysia* Spinola, 1837 (Heteroptera: Tingidae: Tinginae), не соответствующих признакам трибы Ypsotingini Drake et Ruhoff, 1965. Представлены общие морфологические особенности этих родов и *Acalypta* Westwood, 1840, не соответствующие признакам *Tingis* Fabricius, 1803, типового рода трибы Tingini Laporte, 1832. Обобщены данные о половой хромосомной системе этих четырех родов (X0/XX), кардинально отличающейся от таковой всех других 17 изученных к настоящему времени родов Tinginae (XY/XX). Таксономически близкие роды *Acalypta*, *Dictyonota*, *Kalama* и *Derephysia* объединены в трибу с восстановленным валидным названием Acalyptini [Acalyptaini; ICZN Case 3813, in press] Blatchley, 1926 в соответствии с принципом приоритета (МКЗН, статья 23). Даны диагноз восстановленной трибы Acalyptini на основе морфологических и кариологических признаков и усовершенствованный ключ для определения родов *Acalypta*, *Dictyonota*, *Kalama* и *Derephysia*.

Key words: morphological and karyological features, restoration of tribe, diagnosis, key, lace bugs, Acalyptini, *Acalypta*, *Dictyonota*, *Kalama*, *Derephysia*

Ключевые слова: морфологические и кариологические особенности, восстановление трибы, диагноз, ключ, клопы-кружевницы, Acalyptini, *Acalypta*, *Dictyonota*, *Kalama*, *Derephysia*

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Introduction

There is no consensus on the classification of the subfamily Tinginae (Heteroptera: Tingidae) at the suprageneric level. Various numbers of tribes and other family-group taxa were recognised in this subfamily by different authors. The lists of all the previously proposed tribes and genera groups of different ranks were provided by Drake & Ruhoff (1965) and Péricart & Golub (1996).

The tribe Acalyptini Blatchley, 1926 was created for two genera, *Acalypta* Westwood, 1840 and *Drakella* Bergroth, 1922. Drake (1928) reduced *Drakella* to a synonym of *Acalypta*. Later, Drake & Ruhoff (1965) included *Acalypta* in the tribe Tingini Laporte, 1832.

The tribe Ypsotingini Drake & Ruhoff, 1965 originally included two Oriental (*Ypsotingis* Drake, 1947 and *Dictyotingis* Drake, 1942), two Australian (*Chorotingis* Drake, 1961 and *Euaulana* Drake, 1945) and three Holarctic genera (*Biskria* Puton, 1874, *Dictyonota* Curtis, 1994 and *Derephysia* Spinola, 1837). Later the genus *Biskria* was synonymised with *Dictyonota* (Golub, 1975), and the subgenus *Kalama* Puton, 1876 of the genus *Dictyonota* was erected as the valid genus *Kalama* (Péricart, 1982). Froeschner (2001) retained in the tribe Ypsotingini the indicated Oriental and Australian genera as well as three widespread Holarctic genera: *Dictyonota*, *Kalama* and *Derephysia*.

Thus, the authors who developed the modern classification of Tinginae tribes, Drake & Ruhoff (1965) and Froeschner (2001), recognised three tribes within Tinginae: Tingini Laporte, 1832, Litadeini Drake et Ruhoff, 1965, and Ypsotingini Drake et Ruhoff, 1965, the former tribe comprising the vast majority of recent genera in the world Tinginae fauna. The Litadeini, which was initially described as a monotypic tribe, currently includes 13 genera whose species are distributed in the Neotropical, Oriental and Ethiopian Regions, in Madagascar and Oceania (Froeschner, 2001).

However, a number of subsequent authors who used the system of the whole subfamily Tinginae did not recognise any tribes within the subfamily Tinginae (Péricart, 1983; Péricart & Golub, 1996, and others).

Guilbert included both the Litadeini and Ypsotingini in the Tingini based on his analysis of the

evolutionary and phylogenetic significance of the morphological features of imagines (Guilbert, 2001) and larvae (Guilbert, 2004). Guilbert et al. (2014), based on the results of cladistic analysis using a complex of morphological and molecular data, confirmed the opinion of Guilbert (2004) and defined the tribes Ypsotingini and Litadeini as synonyms of Tingini. These authors considered only two tribes within Tinginae: Tingini and Phatnomini. Lis (1999) had previously excluded Phatnomini from Cantacaderinae, including them in the Tingidae as Phatnominae and raised Cantacaderini to the family rank. The systematic position of Phatnomini is not discussed here, since it has been reviewed by Golub (2001), Guilbert (2004), Schuh et al. (2006), Guilbert et al. (2014), and Golub & Popov (2016).

Below we present the results of comparative analysis of the common morphological and karyological features of the genera *Acalypta* Westwood, 1840, *Dictyonota* Curtis, 1827, *Kalama* Puton, 1876, and *Derephysia* Spinola, 1837, and also the characters of the tribes Ypsotingini and Tingini in which they were placed by the previous authors, in an attempt to clarify their position in the suprageneric classification of Tinginae.

Material and methods

Our present contribution is based on the study of the extensive material on the species in question from different regions of the Palearctic, as well as single specimens of some species from the Nearctic [*Acalypta parvula* (Fallén, 1807), *Kalama tricornis* (Schrank, 1801), and *Derephysia foliacea foliacea* (Fallén, 1807)] and Oriental [*Dictyotingis monticula* Drake, 1956] Regions, kept in the Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia (ZISP) and in the private collection of the first author. Altogether, 1.5 thousand specimens of Tingidae were studied.

Photos of some specimens were taken using an MBS-10 stereoscopic microscope, and the digital images were processed using the freeware stacking program CombineZP and Adobe Photoshop CS5. The material used for chromosome analysis is listed in Table 1.

For karyological analysis the male specimens were fixed in a field in 3:1 Karnoy solution (96% ethanol: glacial acetic acid) and stored at 4 °C. In

Table 1. Material used for chromosome analysis, with publications in which the chromosome number was reported for the first time

| Species | Locality and dates of collecting (all in Russia) | Number of males/ chromosomal plates | References |
|---|---|---|---------------------------|
| <i>Acalypta carinata</i> (Panzer, 1806) | Voronezh Prov., 30.IV.2017 | 1/35 | Grozeva, Nokkala, 2001 |
| <i>Derephysia</i> (<i>Paraderephysia</i>) <i>longispina</i> Golub, 1974 | Voronezh Prov., 7.VI.2017 | 22/76 | Golub et al., 2018 |
| <i>Dictyonota strichnocera</i> Fieber, 1844 | Voronezh Prov., 20.VI–1.VII.2017 | 3/62 | Golub et al., 2018 |
| <i>Tingis (Tingis) cardui</i> (Linnaeus, 1758) | Env. of Inzer Settlm., South Ural Nature Reserve, Bashkortostan, 4.VIII.2014 | 2/19 | Golub et al., 2015 |
| <i>Tingis (Tropidocheila)</i> <i>reticulata</i> Herrich- Schaeffer, 1835 | Voronezh Prov., 20.VI–4.VII.2017 | 20/65 | Golub et al., 2018 |
| <i>Tingis (Neolasiotropis)</i> <i>pilosa</i> Hummel, 1825 | Voronezh Prov., 8.VI–25.VI.2017 | 10/22 | Golub et al., 2018 |

a laboratory, the testes were dissected in a drop of 45% acetic acid and squashed on the slide. Coverslips were removed using the dry ice technique. The preparations were stained by the Feulgen-Giemsa method according to Grozeva & Nokkala (1996). The chromosome slides were analysed under a Leica DM 6000 B microscope (Leica Microsystems Wetzlar GmbH, Germany) with a 100× magnification. Images were captured with a Leica DFC 345 FX camera using Leica Application Suite 3.7 software with an Image Overlay module.

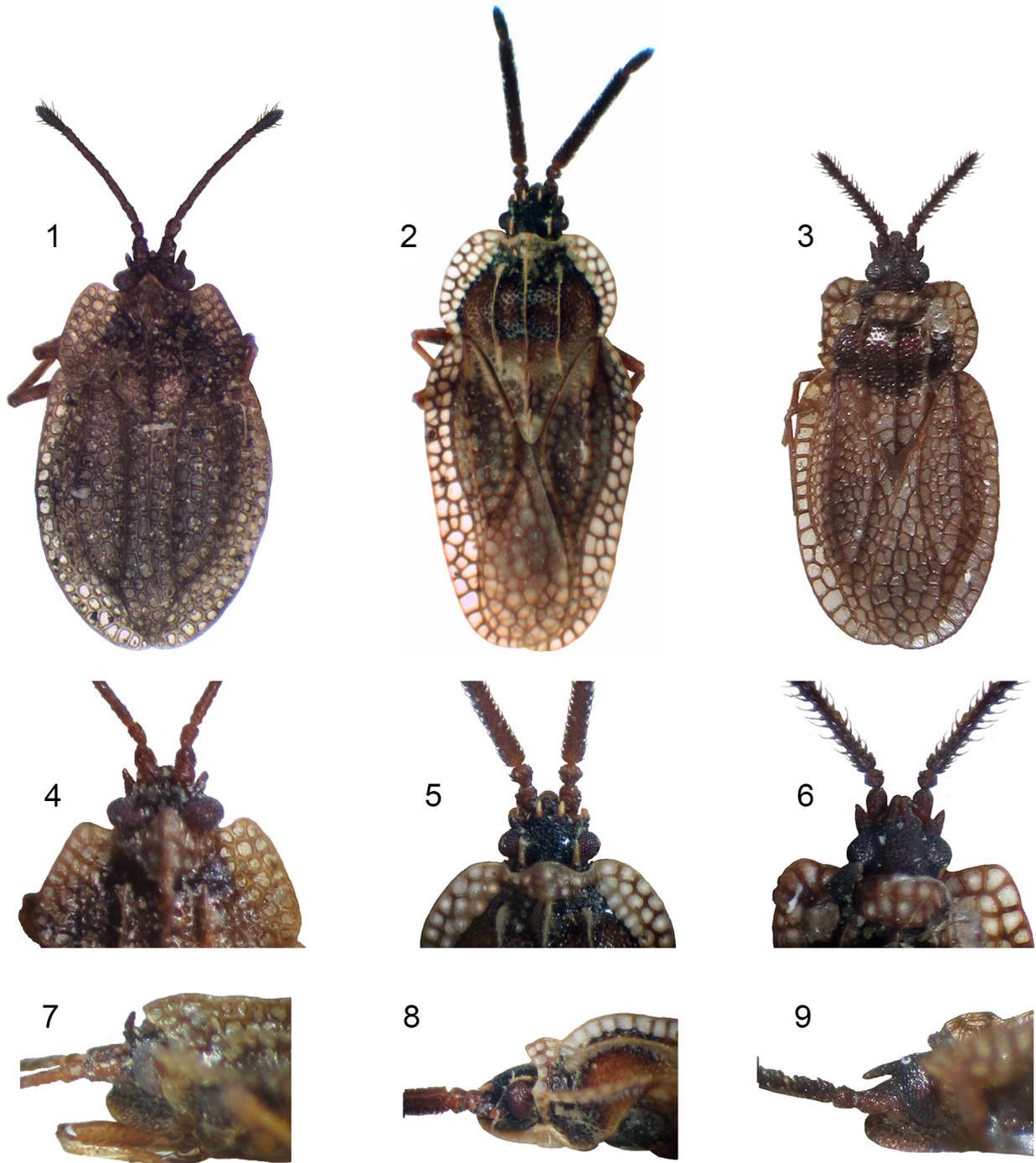
Results

The following are the results of studying the main features based on which the genera *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* were included by different authors in the tribes Ypsotingini and Tingini, as well as the essential karyological character, namely the type of sex chromosome system.

The tribe Ypsotingini, to which the genera *Dictyonota*, *Kalama* and *Derephysia* formerly belonged, was distinguished from Tingini (and also from Litadeini) by the following features: “Head

very long, greatly extended in front of the eyes, usually surpassing apex of first antennal segment, sometimes even that of the second; all tarsi slender as in Tingini” (Drake & Ruhoff, 1965). Froeschner (2001) emended the defining characters of this tribe. In his key to the tribes of Tinginae, Froeschner (2001) indicated only one differential characteristic of this tribe: “Head very long, prolonged in front of antennal insertions, subporrect; apex of antennal I (sometimes also that of II) not surpassing apex of clypeus” (Froeschner, 2001, p. 2). The morphological diagnosis of this tribe was formulated as follows: “This tribe is recognized within the family by the combination of the reduced, depressed clavi coupled with the porrect, elongate head reaching or almost reaching apex of antennal segment I” (Froeschner, 2001, p. 15).

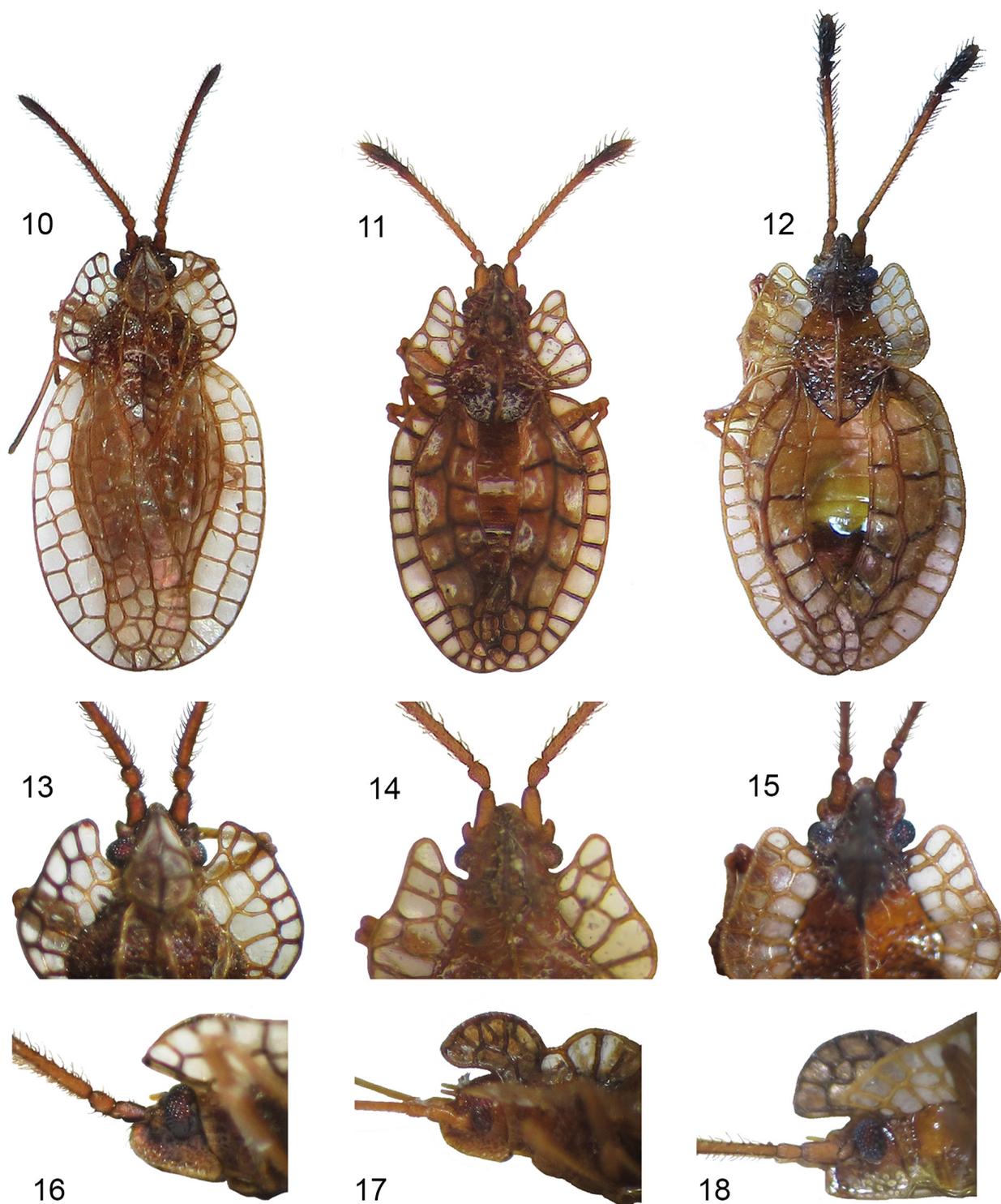
In fact, our study of these characters has shown that the ratio of the head and antennal segment I varies among the different species of *Dictyonota*, *Kalama* and *Derephysia* and most often does not correspond to the diagnostic characters of Ypsotingini. In particular, in the type species of these genera, namely *Dictyonota strichnocera* Fieber,



Figs 1–9. *Acalyptini* spp., habitus (1–3); head and pronotum dorsally (4–6) and laterally (7–9). **1, 4, 7,** *Acalypta carinata* (Panzer); **2, 5, 8,** *Dictyonota strichnocera* Fieber; **3, 6, 9,** *Kalama tricornis* (Schrank).

1844, *Kalama tricornis* (Schrank, 1801) and *Derephysia foliacea foliacea* (Fallén, 1807), as well as in *D. cristata* (Panzer, 1806), the type species of the subgenus *Paraderephysia* Péricart, 1978 of the *Derephysia*, and in other species of these genera, the apex of antennal segment I distinctly surpass-

es the apex of clypeus (Figs 1–21). This difference from the main character of the tribe Ypsotingini is observed in all the known species of the genera *Kalama* and *Derephysia*. Only in a few species of *Dictyonota*, the head is indeed quite elongated, as indicated earlier (Golub, 1975; Péricart, 1983),



Figs 10–18. *Acalyptini* spp., habitus (10–12); head and pronotum dorsally (13–15) and laterally (16–18). **10, 13, 16,** *Derephysia (Derephysia) foliacea foliacea* (Fallén); **11, 14, 17,** *D. (Paraderephysia) cristata* (Panzer); **12, 15, 18,** *D. (P.) longispina* Golub, 1974.



Figs 19–21. Acalyptini spp., pronotum and basal part of right hemelytron. **19**, *Dictyonota strichnocera* Fieber; **20**, *Kalama tricornis* (Schrank); **21**, *Derephysia (Derephysia) foliacea foliacea* (Fallén). *cl* – clavus.

but it is still not as elongated as in *Ypsotingis sideris* Drake, 1947, the type species of this genus (Froeschner, 2001, Fig. 20).

As for the reduction of the clavus in species of the genera included in the tribe Ypsotingini (Froeschner, 2001), this feature applies only to the brachypterous forms of the *Dictyonota*, *Kalama* and *Derephysia* species. In species where macropterous specimens exist, including the type species of these genera, they have normally developed clavi (Figs 19–21). The wing polymorphism features in Tingidae, including species of the genera discussed, were described by Péricart (1983). Therefore, the reduction of the clavus cannot be used as a character for suprageneric differentiation of taxa within Tinginae.

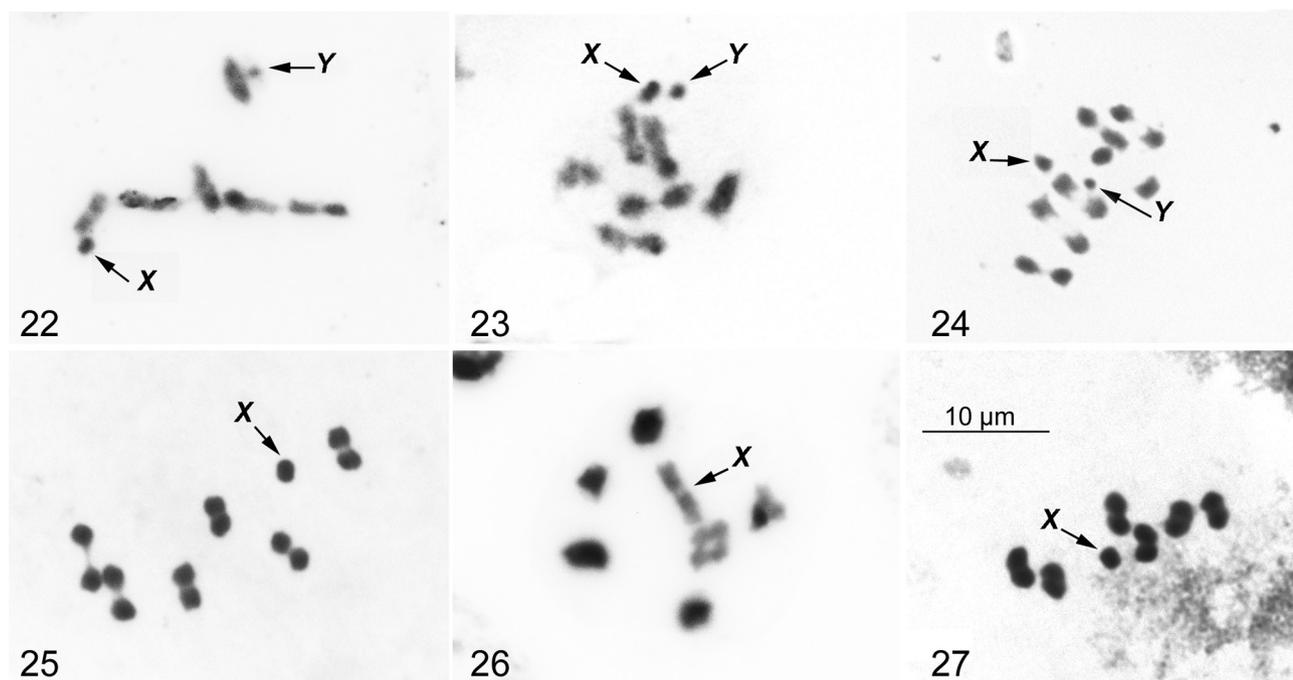
Other morphological characters of *Dictyonota*, *Kalama* and *Derephysia* are also inconsistent with the features of *Ypsotingis* species and, therefore, with those of the tribe Ypsotingini as a whole. All the *Dictyonota*, *Kalama* and *Derephysia* species share the following diagnostic features: head with four or two spines or tubercles and without medial frontal (mediocentral) spine; bucculae opened anteriorly; paranota horizontal or only slightly oblique, not reflexed and not forming cysts; methathoracic gland peritreme absent.

On the contrary, the head armature of *Ypsotingis* species, including the type species *Y. sideris*, as well as *Dictyotingis* species, comprises five spines; the medial frontal spine is present (Froeschner, 2001: Fig. 20). The paranota in *Ypsotingis* and *Dictyotingis* species are broadly and strongly recurved, with their free margins turned downward above the pronotal disk and with each paranotum forming the elevated, inflated cyst (Froeschner,

2001: Fig. 20). The buccal laminae in *Y. sideris* are closed anteriorly. The peritreme of methathoracic gland is present in *Dictyotingis monticula*, based on the studied specimen from Thailand (ZISP).

Dictyonota, *Kalama*, *Derephysia*, as well as *Acalypta*, have almost the same differences from the genus *Tingis* Fabricius, 1803, the type genus of the tribe Tingini. An exception is the shape of the paranota, which do not form inflated cysts over the pronotal disk in all species of *Tingis*, including the type species *T. (T.) cardui* (Linnaeus, 1758).

An important feature shared by the four genera in question (*Acalypta*, *Dictyonota*, *Kalama* and *Derephysia*), distinguishing them from all the studied genera of Tingini, is their sex chromosome system. Analysis of all the available karyological data on Tingidae (Nokkala & Nokkala, 1984; Grozeva & Nokkala, 2001; Golub et al., 2015, 2016, 2017, 2018; for other references see: Ueshima, 1979) allows us to conclude that species of these genera differ in their karyotypes from the other karyologically studied Tinginae species. In particular, the family Tingidae as a whole is characterised by the modal karyotype of $2n = 12 + XY/XX$ (male/female). This karyotype was found in most of the karyologically studied lace bug species (in 41 out of 48 studied species and in 17 out of 21 studied genera), including *Tingis cardui* (Linnaeus, 1758), the type species of the type genus of Tingini (Golub et al., 2015), *T. pilosa* Hummel, 1825, the type species of the subgenus *T. (Neolasiotropis)* Wagner, 1961 (Golub et al., 2018), and one member of the subgenus *T. (Tropidocheila)* Fieber, 1844, namely *T. (Tropidocheila) reticulata* Herrich-Schäffer, 1835 (Figs 22–24). Seven other Tingidae species were shown to have karyotypes



Figs 22–27. Male meiotic metaphase plates (MI) of species of the genera *Tingis* Fabricius ($n=6+XY$), *Acalypta* Westwood, *Derephysia* Spinola, and *Dictyonota* Curtis ($n=6+X$). **22**, *Tingis* (*Tingis*) *cardui* (Linnaeus) [after Golub et al., 2015]; **23**, *T. (Tropidocheila) reticulata* Herrrich-Schaeffer; **24**, *T. (Neolasiotropis) pilosa* Hummel; **25**, *Acalypta carinata* (Panzer); **26**, *Derephysia longispina* Golub; **27**, *Dictyonota strichnocera* Fieber. X and Y chromosomes are indicated by arrow. Scale bar: 10 μ m.

of $2n = 12 + X0/XX$ (male/female). These are: all the four karyologically studied species of the genus *Acalypta* [the type species of this genus, *A. carinata* (Panzer, 1806), *A. marginata* (Wolff, 1804), *A. nigrina* (Fallén, 1807), and *A. parvula* (Fallén, 1807)], *Dictyonota strichnocera* Fieber, 1844 (the type species of this genus), *Kalama tricornis* (the type species of this genus) and *Derephysia (Paraderephysia) longispina* Golub, 1974, the latter two species being the only karyologically studied members of their respective genera (Grozeva & Nokkala, 2001; Golub et al., 2018) (Figs 25–27). Although Southwood & Leston (1959) initially indicated that *Acalypta parvula* had karyotypes with XY/XX (without providing photographs of chromosomes), Grozeva & Nokkala (2001) revealed the X0/XX chromosome system in this species (see also Golub et al., 2018). For *Dictyonota fuliginosa* Costa, 1853, Southwood & Leston (1959) described the XY/XX sex chromosome system; however, this was not supported either by photographs of chromosomes or by the original publication; therefore, the karyotype of this species obviously needs to be reexamined.

Discussion

It has long been known that the genera *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* share significant morphological features such as the head structures (see above) and the absence of the methathoracic gland peritreme (evaporatory area), used in their diagnoses and keys to the genera of Tingidae (Horváth, 1906; Péricart, 1983, and other authors). An important common feature of these genera is the type of sex chromosome system (X0/XX), which distinguishes them from all the other genera studied so far (Grozeva and Nokkala 2001; Golub et al., 2018).

The complex of common morphological features and differences from *Ypsotingis*, the type genus of Ygnotingini, demonstrates the impossibility of preserving *Dictyonota*, *Kalama* and *Derephysia* in this tribe. The same complex of morphological characters, with the exception of the paranotal shape, and the shared type of the sex chromosome system (X0/XX) distinguish these genera, as well as *Acalypta*, from *Tingis*, the type genus of Tingini, and many other genera of this tribe.

In addition, Guilbert and co-authors (Guilbert et al., 2014) recognised Ypsotingini as a junior synonym for Tingini, though *Acalypta*, *Dictyonota* and *Kalama* formed a single clade in all the phylogenetic trees based on morphological and molecular data. The type genus of the tribe Ypsotingini, *Ypsotingis*, and the genus *Derephysia* were not included in this phylogenetic analysis (Guilbert et al., 2014).

It should be noted that the species of some other genera of Tinginae share certain morphological characters with species of *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia*. For instance, two or four head spines occur in species of *Phaenotropis* Horváth, 1906; the methathoracic gland peritreme is absent in species of *Dictyla* Stål, 1874, *Oncochila* Stål, 1873 and some other genera. However, the whole complex of features described above is observed within Tinginae only in the four genera in question, as well as in the genus *Campylosteira* Fieber, 1844 and *Sphaerista* Kiritshenko, 1951; the latter genera is not discussed here due to lack of data on their karyotypes. The occurrence in other Tinginae genera of some individual features characteristic of the species of *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* is obviously the result of homoplasy.

Conclusions

The complex of morphological features shared by the genera *Dictyonota*, *Derephysia* and *Kalama* does not correspond to the main diagnostic characters of the tribe Ypsotingini. Moreover, these genera and *Acalypta* have a common set of important morphological features and a common mechanism of sex determination (X0/XY), which distinguish them from *Tingis*, the type genus of Tingini, and many other studied genera of this tribe. We consider the X0/XX sex chromosome system to be secondary in Tingidae, having derived from the XY/XX system by loss of Y chromosome in males (see also Nokkala & Nokkala 1984, Golub et al., 2018). Thus, karyotypes of representatives of *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* are the derived ones; they have originated from the modal one by losing the Y-chromosome while preserving the autosome number. Blackman (1995), based on the results of studying the distribution of the

X0 chromosomal system in males of Heteroptera, suggested that secondary loss of Y chromosome may have occurred early in the evolution of many families of terrestrial Heteroptera. In any case, the whole complex of taxonomically important common features observed in the genera discussed is most probably not a case of homoplasy but the result of joint evolution of closely related and almost exclusively Holarctic taxa.

Based on the above arguments, we consider the genera *Acalypta* Westwood, 1840, *Dictyonota* Curtis, 1827, *Kalama* Puton, 1876, and *Derephysia* Spinola, 1837 as members of the restored tribe Acalyptini Blatchley, 1926 according to the principle of priority (ICZN Article 23).

Order **Heteroptera** Latreille, 1810

Infraorder **Cimicomorpha** Leston,
Pendergrast et Soutwood, 1954

Superfamily **Tingoidea** Laporte, 1832

Family **Tingidae** Laporte, 1832

Subfamily **Tinginae** Laporte, 1832

Tribe **Acalyptini** Blatchley, 1926, **trib. resurr.**

Acalyptini Blatchley, 1926: 451, 479.

Type genus: *Acalypta* Westwood, 1840.

Included genera: *Acalypta* Westwood, 1840; *Derephysia* Spinola, 1837; *Dictyonota* Curtis, 1827; and *Kalama* Puton, 1876.

Note. Since the name Acalyptini Blatchley, 1926 is the junior homonym of the Acalyptini Thomson, 1859 (Coleoptera, Curculionidae), the solution to emend the stem of the type genus and adopt the entire type genus name *Acalypta* Westwood, 1840 as the stem for the corresponding family-group name Acalyptaini Blatchley, 1926 was proposed for consideration by the International Commission on Zoological Nomenclature (Gapon et al., 2019; Case 3813).

Diagnosis. The main morphological and karyological features of Acalyptini distinguishing this tribe from the complex of other Tinginae genera, at least of the Palaearctic fauna are presented below in the form of a key. The genera *Campylosteira* and *Sphaerista*, which is morphologically very close to the genera of Acalyptini but not studied karyologically, are not taken into account here.

1. Buccal laminae not closed anteriorly. Opening of metathoracic scent glands without peritreme (evaporatory area). Head with two (frontal) or four (frontal and occipital) spines or tubercles, but without unpaired medial frontal (mediocentral) spine. Paranota explanate or only slightly oblique, not reflexed and not forming cysts. Posterior process of pronotum not swelled and not vesicular. Karyotype $2n = 12 + X0/XX$ (male/female) **Acalyptini** (including *Acalypta*, *Dictyonota*, *Kalama*, *Derephysia*)
- Buccal laminae almost always closed anteriorly; if opened, then posterior process of pronotum at apex more or less swelled or vesicular (*Galeatus* Curtis, 1833, *Hyalochiton* Horváth, 1905) or opening of metathoracic scent glands with peritreme (subgenus *Neolasiotropis* Wagner, 1961 of *Tingis*). Peritreme more often present. Head more often with five spines or tubercles: three frontal and two occipital ones. If peritreme absent (*Dictyla* Stål, 1874, *Urentius* Distant, 1903, *Compseuta* Stål, 1873, *Monosteira* A. Costa, 1862, *Agramma* Stephens, 1829, *Magmara* Péricart, 1977, and *Phaenotropis* Horváth, 1906) or in addition head with four or two spinules or without them (*Agramma*, *Magmara*, *Phaenotropis*, and *Compseuta*), then buccal laminae closed anteriorly, paranota widely wrapped on pronotal disk (*Dictyla*, *Urentius*, and partially *Compseuta*), extremely narrow or absent (*Monosteira*, *Agramma*, *Magmara*, *Phaenotropis*, and partially *Compseuta*). Karyotype $2n = 12 + XY/XX$ (male/female) in all studied species, including *Tingis cardui* (type species of *Tingis*) **Tingini** (all Palaearctic genera of Tinginae without Acalyptini, *Campylosteira* and *Sphaerista*)

Below we provide a key to the genera *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia* based on the studied material from the collection of ZISP, with regard to the characters used by previous authors (Horváth, 1906; Kerzhner & Jaczewski, 1964; Wagner, 1967; Péricart, 1983; Golub, 1988).

Key to the genera *Acalypta*, *Dictyonota*, *Kalama* and *Derephysia*

1. Each hemelytron with tectiform or almost vesicular elevation. Hemelytra vitreous, transparent, with large areolae (Figs 10–18) ***Derephysia***
- Hemelytra flat, without tectiform or vesicular elevation, not transparent, their areolae not large 2
2. Head with two frontal spines only. Antennae thin, without tubercles bearing seta on their apices; antennal segment IV distinctly thicker than segment III (Figs 1, 4, 7) ***Acalypta***

- 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 3
3. Occipital spines always present, noticeably elongated and usually protruding beyond posterior margin of eyes. Preorbital part of head often noticeably elongated (Figs 2, 5, 8) ***Dictyonota***
- Occipital spines absent or very small, tuberculate, not elongate, located far behind posterior margin of eyes. Preorbital part of head short (Figs 3, 6, 9) ***Kalama***

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