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Recent nomenclatural history of the genus *Locusta*

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The migratory locust, *Locusta migratoria* (Linnaeus, 1758), is an Orthopteran species of the Acrididae family, subfamily Oedipodinae (Cigliano et al., 2022). It is one of about a dozen species of short-horned grasshoppers characterized by a phase polyphenism, being able to present either in a solitary phase, or in gregarious phase that can form dense, mobile adults' swarms and huge hopper bands. It is the most widely distributed locust species, extending all over the Old World, from sea-level to more than 4,000 m in Central Asian mountains. The migratory locust is a major pest in many tropical regions and some temperate areas and regarded as the most important agricultural pest in some countries. Magnitude of plagues and destruction they cause are due to its gregariousness, mobility, voracity and size of swarms. Sudden and severe damage can be caused to a wide variety of crops, even if this species is essentially graminivorous. The outbreaks can result in substantial effects on national and regional food security and agricultural and agropastoral livelihoods when they reach upsurge or plague levels. In addition, social costs to the local human population during outbreaks can be enormous, but difficult to estimate. In most cases, water — rainfall or flooding — is a key factor for population dynamics and outbreak determinism. However, human activities (over-grazing, deforestation, irrigation, dams...) can play an important role in promoting or impeding the process of multiplication and gregarization. Today, the migratory locust seems to be better controlled, but outbreaks/upsurges continue to occur regularly despite multiple prevention and control operations (Lecoq, 2023).

The migratory locust belongs to a monotypic genus and has been described under many different names, up to 20, corresponding to species or subspecies levels. Some subspecies were never even named and were simply referred to by their geographic origin. A certain confusion continues to reign between those in favor of a simplification of the nomenclature on the basis of recent data provided by molecular biology, and those in favor of maintaining the status quo or even increasing the number of subspecies. Part of the confusion was caused by the fact that solitary and gregarious populations were considered to be different species. Uvarov (1921) was the first to realize that *Locusta danica* represented the solitary phase of *L. migratoria*. However, in the 1980s, 12 subspecies were still recognized as valid (COPR, 1982). These subspecies were thought to represent discrete geographical races, because specimens were usually collected from populations associated with widely separated outbreak areas (Uvarov, 1966). Recently, Defaut et al. (2012, 2013) considered one of these subspecies, *Gryllus cinerascens* Fabricius, as a valid species, *Locusta cinerascens*, distinct from *Locusta migratoria* Linnaeus, on the basis of their morphological characteristics and ecology, but this strongly needs to be confirmed as recent observations indicate that the distinction between *cinerascens* and *migratoria* seems very blurred (Bonifait, 2019). Overall, the names of these multiple subspecies are still frequently used in various parts of the world but correspond more to a facility to specify a geographical origin than to a biological reality in a locust species that is otherwise known for its very pronounced phase polyphenism and its strong dispersal abilities (Lecoq, 2023).

Since the 1980s, several authors have questioned the validity of these distinctions into as many subspecies. Thus, Farrow & Colless (1980) demonstrated the inadequacy of classical morphometrics for classifying geographical races at the subspecific level. Migratory locusts from the tropics and southern hemisphere were considered by these authors to be a single pantropical, polymorphic, non-diapausing subspecies, *L. migratoria migratorioides* (Reiche and Fairmaire, 1849) and morphometric variation within it was attributed to climate and habitat variations, degree of isolation of populations and variations in population size and density. The second subspecies *L. migratoria migratoria* (Linnaeus, 1758) was considered to be an embryonic diapausing subspecies distributed in temperate zones. This demonstration based on numerical taxonomy analyses applied to some morphometric parameters has been masterfully confirmed by recent molecular biology analyses by Chapuis et al. (2008), Tokuda et al. (2010), Ma et al. (2012), Ma and Kang (2013), Lee et al. (2016). In particular the work of Ma et al. (2012)—based on samples from the whole range of the migratory locust— represent the most in-depth, comprehensive investigation to date of the global-scale phylogeography of this species. For these authors, morphometry, distribution, number of generations and diapause eggs are not sufficiently clear to identify the subspecific status of a given migratory locust population. The evidence they gathered, using a molecular approach with a

phylogeographic and evolutionary perspective, show high levels of genetic differentiation among worldwide populations of the migratory locust, and that most of the molecular variations is present between two main lineages—the Northern and Southern lineages—which cover distinct climatic regions on the planet, namely the temperate and tropical zones, respectively. The adaptive differentiation of the two lineages, driven by different selective pressures in their respective distribution areas, counteracts the considerable dispersal ability of the locusts and likely accounts for the maintenance over time of the south–north cleavage pattern. Other factors, such as geographic barriers and temperature, also play important roles in maintaining the present phylogeographic patterns of the migratory locust (Ma et al., 2012). Clearly, even if additional investigations are required, this study does not support the previously defined subspecies of the migratory locust and provides a genetic basis for a phylogeography-based subspecific taxonomy. Overall, all these recent molecular studies confirmed the already old conclusions of Farrow and Colless (1980), challenged the long-held view of multiple subspecies in *Locusta migratoria* and clearly divided it into only two main subspecies:

- *L. m. migratoria* (Linnaeus, 1758). Synonyms: *cinerascens* (Fabricius, 1781) ; *australis* (Saussure, 1884) ; *brasiliensis* (Walker, 1870) ; *danica* (Linnaeus, 1767) ; *gallica* Remaudière, 1947 ; *remaudierei* Harz, 1962 ; *rossica* Uvarov & Zolotarevsky, 1929 ; *solitaria* Carthy, 1955.
- *L. m. migratorioides* (Reiche and Fairmaire, 1849). Synonyms: *affinis* (Sjöstedt, 1931) ; *burmana* Ramme, 1951 ; *capito* (Saussure, 1884) ; *manilensis* (Meyen, 1835) ; *morio* (Sjöstedt, 1931) ; *punctifrons* (Dirsh, 1961) ; *tibetensis* Chen, 1963 ; arabian spp. (COPR, 1982) ; indian spp. (COPR, 1982) ; australian spp. (COPR, 1982).

The Tibetan populations, still considered by some authors as a valid subspecies (Zhang et al. 2009; Tu et al. 2012; Dong et al. 2015; Jyoti et al. 2020), are however extremely close to *L. m. migratorioides* according to phylogenetic analysis (Ma et al., 2012, 2013) and should instead be considered synonyms of this subspecies.

The distribution range of *Locusta migratoria* with indication of the approximate boundary between the two subspecies now to be recognized, *L. m. migratoria* and *L. m. migratorioides*, is shown in figure 1 as well as the location of the main outbreak areas from which invasions can start under favorable ecological conditions.

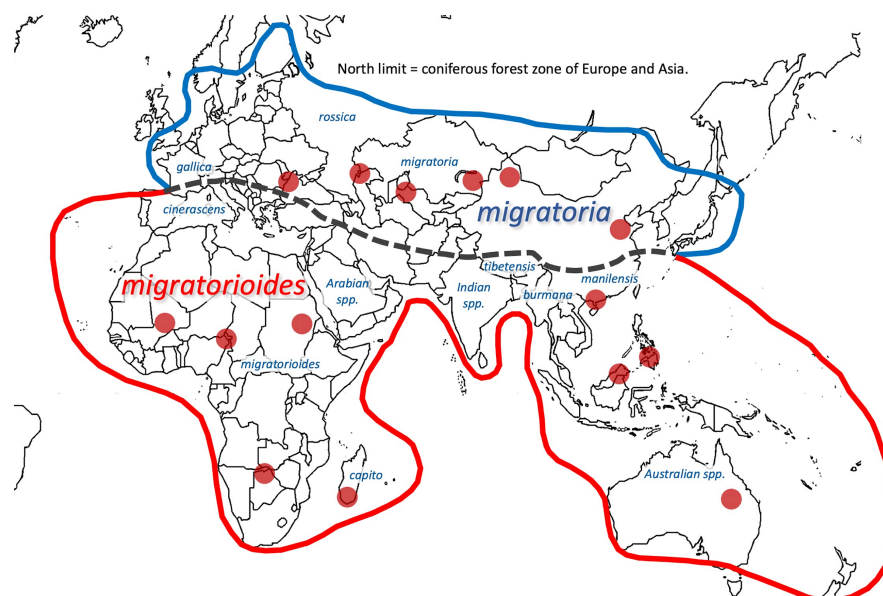


Figure 1. Distribution range of *Locusta migratoria* with indication of the approximate limit between the two subspecies, *L. m. migratoria* and *L. m. migratorioides*. From Ma et al. (2012) modified according to Latchinsky et al. (2002), Latchinsky and Sivanpillai (2010), and GBIF (2022) for the Northern limit. The main subspecies recognized until the work of Ma et al. (2012) are mentioned in small type. The red circles indicate the location of the main outbreak areas of the migratory locust.

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