

Distribution and habitats of Joppeicidae (Heteroptera)*)

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The family Joppeicidae contains only one species. *Joppeicus paradoxus* Puton, 1881. Its taxonomic position changed several times; nowadays it is currently regarded as a family of Cimicomorpha. It is a primitive, relict family, and its cladistic affinities are obscure. China (1955) thought that it was related to the ancestors of Reduviidae, while in a recent monographic treatment by Davis & Usinger (1970) it has been concluded that Joppeicidae appear to be related to the cimicoid families s. lat., especially to the Tingidae.

Owing to the unique position of this family, any information on its distribution, habits and habitats is of considerable interest. So far it has been known from Israel, Egypt and the northernmost (Nubian) part of the Sudan only. A few distributional records have been published, only occasionally including scattered data on habitats, and the species was rarely collected. Recently the family has been subjected to an extensive morphological study, and two comprehensive papers dealing with its morphology and cladistic affinities were published by China (1955) and Davis & Usinger (1970); the latter authors furnished also many data on its laboratory ecology, behaviour and juvenile stages.

Prof. R. L. Usinger, who personally collected *Joppeicus paradoxus* in Egypt, wanted to summarize the data on its distribution and bionomics; death prevented him from doing so. On the suggestion of Dr. N. T. Davis I am attempting to complete this plan; all available literary data are condensed here, complemented by information furnished by Prof. Usinger's field notes and letter, by unpublished notes on specimens in collections, and by my own field records of the occurrence of this species in Egypt and the Sudan.

*) A 2nd contribution to N. E. African fauna based on material collected by P. Štys in 1965—68.

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Data on the distribution and bionomics of *Joppeicus paradoxus* Put.

A) Review of literature

- 1) Puton (1881): Israel: Jaffa*), lgt. Abeille de Perin.
- 2) Bergroth (1898): Egypt: Mariout (nr. Alexandria), lgt. M. Letourneux, coll. Mus. nat. Hist. nat. Paris.
- 3) Bergevin (1912): Egypt: Mariout (nr. Alexandria), under a big stone; Alexandria — Nouzha garded, 1. 1911, under the bark of *Ficus sycomorus* (L.) (as „*Sycomorus antiquorum*“), lgt. Bergevin (non-labeled Bergevin's specimens found in Mus. Zool. Univ. Helsinki).
- 4) Priesner & Alfieri (1953): Egypt: “Everywhere in the Delta and the deserts**”, not rare, occasionally abundant under fallen leaves, detritus of desert shrubs or under bark of *Ficus sycomorus* (L.) and *Acacia nilotica* (L.). All over the country, all the year.”
- 5) Linnavuori (1961): Israel: Eres (= Erez, N. of Gaza), 13. 11. 1952, lgt. Bytinski-Salz, under the bark of *Ficus sycomorus* (L.).
- 6) Wagner (1963): Sudan, N. Province (“Nubia”***): W. bank of 2nd Nile Cataracts, 24. 1. and 10. 2. 1962; all from *Acacia seyal* Del.
- 7) Usinger (1966): Egypt: “found in the nests of mammals”, “reared through several generations in bed bug colonies”.
- 8) Davis & Usinger (1970): Egypt: Abu Rawash (nr. Cairo), 7. 11. 1963, deep in crevices in a small rocky hill. Data on the ecology of a laboratory colony (started from Abu Rawash sample): Fed on “early instars of various cimicids”, 1st and 2nd instars of *Periplaneta americana* (L.); regularly breeding. Also attacking larvae of *Tenebrio molitor* (L.) and *Galleria mellonella* (L.), and nymphs of *Oncopeltus fasciatus* (Dallas). “They appear to have no prey specificity and in nature probably feed on whatever small insects they encounter”. Cannibalism rare. Development completed in about 9 weeks under 27 °C and 70% RH (eggs hatched after ca. 2 weeks, duration of each nymphal instar ca. 10 days). Data on feeding and mating behaviour.

*) Originally quoted as in Syria; this often subsequently repeated or quoted as from „Palestine“. Actually no record from within the boundaries of present Syria or Jordan is known.

**) No localities given. Linnavuori (1964) in the analysis of distributional patterns of Egyptian Heteroptera classifies it as occurring in the Nile region only.

***) Both localities are situated in the inundation zone of the present Aswan Dam, practically at the boundary between the Sudan and Egypt.

B) Unpublished data

a) Collection of the Department of Entomology, British Museum (Nat. Hist.)

1) Egypt: Wadi Tir (nr. Cairo), 22. 12. 1932, lgt. Priesner; El Merg (?) (nr. Cairo), lgt. Priesner.

2) Ethiopia: Bako (37. 02 E., 9. 08 N.), "Maize, Mudpot Farm, Sample No. 31", McFarlane, 1968.

b) Collection of Dr. E. Wagner, Hamburg

3) Egypt: Wadi Tir (nr. Cairo), 27. 12. 1932, lgt. Priesner; Heluan (= Helwan), 2. 3. 1933, lgt. C. Koch; "Deschena" (= ? Dishna, N. of Luxor), lgt. J. Sahlberg.

c) Records of the late Prof. R. L. Usinger (the data sub 5—7 come from Usinger's field notes made during his stay in Egypt in July 1959; I bear the responsibility for their excerption and stylization, and for any possible error in transcription)

4) Letter of 1st February, 1966: Egypt: "It had been previously found under bark, where I assume it was preying on subcortical insects; but my findings were invariably in nests and burrows of rodents and bats... I suspect they [Joppeicidae] are general predators."

5) Egypt: Western Desert, nr. Abu Rawash (nr. Cairo), 14. 7. 1959, lgt. Usinger, adults and nymphs "of all sizes", in litter and faeces of the bat *Tadarida aegyptiaca aegyptiaca* (Geoffr.)* in a deep narrow fissure in a rocky outcrop inhabited by the above bat, together with *Stricticimex namru* Usinger*) (Cimicidae), Dermestid larvae, "three species of tick" (probably *Argas* spp.) and "small shiny globose beetles"; undoubtedly a breeding site. Nymphs of *Joppeicus paradoxus* from the same locality and associated with the same species of bat and bed bug also in coll. N. A. M. R. U., Cairo.

6) Egypt: Sahara City (nr. Cairo), 5. 1958, lgt. Kaiser, coll. Chicago Nat. Hist. Museum; 25 specimens taken in flight, "biting through shirt".

7) Egypt (records from coll. Ministry of Agriculture, Cairo): Alexandria — Nouzha garden, 2. 3. 1929, lgt. Priesner; Alexandria — Mazari, July, at light; Abu Kir (nr. Alexandria), June; Burg El Arab (nr. Alexandria), 25. 3. 1935, lgt. Priesner; Cairo — Shubra, October, under bark of *Acacia nilotica* [L.].

d) Author's finds (all lgt. and coll. Štys)

8) Egypt: Giza (nr. Cairo), 8. 7. 1966, 2 ♂♂, 5 ♀♀, 2 first instar nymphs. Edge of sandy desert with no vegetation except for *Alhagi maurorum* Medic. (Viciaceae, det. O. Kassas), in semi-caves in eroded limestone rocks with dusty and sandy ground covered with fallen pieces of rock, human faeces and paper litter; adults and nymphs under stones and particularly under the papers; adults very active, quickly running, with a negative phototaxis and showing a cataleptic reaction when tou-

*) Identification according to Usinger [1960, 1966].

ched. Associated fauna: larvae and adults of Dermestidae and Tenebrionidae. Undoubtedly a breeding site.

9) Sudan: Khartoum Province, Shambat (15.40 N., 32.32 E.), Sample No. 337, 12. 8. 1966, 1 ♀, edge of an irrigated field with *Medicago sativa* L., under prostrate *Portulacca quadrifida* L. (det. A. Pettet). Collected unawares among numerous nymphs and adults of *Piesma llnnavuorii* Štys together with a few nymphs of *Phorticus* sp. (Nabidae). The site was several times visited, but no further specimens were found.

10) Sudan: Khartoum, Sample No. 4, 4. 9. 1965, 1 ♀, street alley of *Ficus senegalensis* Miq. along the Blue Nile embankment; sieved from a leaf litter accumulated at the foot of this tree. Associated fauna: *Collembola*, Embioptera, *Dasychnemus sahlbergi* Bergr. (Reduviidae: Holoptilinae), Carabidae, Tenebrionidae, larvae of Dermestidae, ants.

11) Sudan: Blue Nile Province, Gezira, Dolga (14.49 N., 33.13 E.), Samples Nos. 258, 259, 8. 2. 1966, 1 ♀, 1 fifth instar nymph and numerous exuviae; small, mixed, planted, park-like irrigated wood with *Acacia* undergrowth, under stripes of loose bark of a well insulated stem of the tree *Azadirachta* (= *Wizzardia*) *indica* A. Juss. (Meliaceae). Associated fauna: small spiders (*Scytodes* sp., Sicariidae, det. J. Buchar), adults and larvae of Dermestidae, Undoubtedly a breeding site. The site was visited again 10. 2. 1966; 1 pregnant ♀, 2 very small nymphs and numerous exuviae found on the same species of tree under the same conditions; material lost.

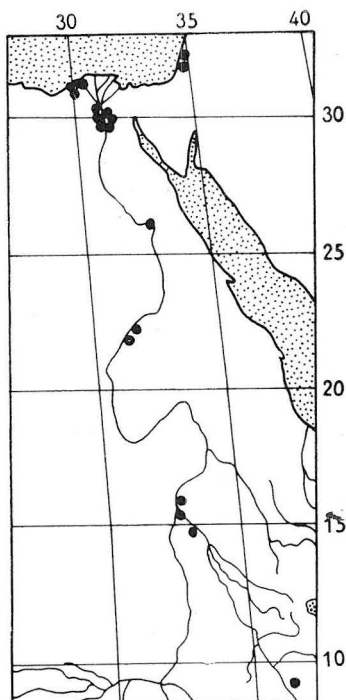
Discussion

a) Present distribution of *Joppeicus paradoxus* Put.

All the above records undoubtedly refer to one and the same species. Prof. Usinger and I compared my specimens from C. Sudan with the material from Egypt and found no differences; the Sudanese females were only slightly darker. Mr. Dolling kindly compared the Ethiopian specimens in the British Museum (Nat. Hist.) with the Egyptian ones and failed to find any difference.

The range of *Joppeicus paradoxus* may be characterized, as follows (see also the Map): S. Israel, the Nile Delta, the Nile Valley in Egypt and the Sudan up to Khartoum, the Blue Nile Valley in the Sudan, and — because of an isolated record from Bako — probably the entire region of the Blue Nile drainage system in W. Ethiopia*). In the absence of any further evidence I must take Priesner's & Alfieri's (1953) comments on its occurrence in Egypt "everywhere in ... the deserts" and "all over the country" for an overstatement, since all the Egyptian localities recorded are either in the Delta or in the Nile Valley or very close to them, at most at the very edge of the desert; the same applies to the Sudanese localities. The range in Egypt may be wider, and Priesner's & Alfieri's (1953) opinion is supported by the extension of *Joppeicus paradoxus* into S. Israel, but its distribution must be at present regarded as basically associated with the Main and Blue Niles.

*) Through Bako itself is situated probably in the northernmost part of the drainage system of the Omo river which flows into the Lake Rudolf.



Distribution of *Joppeicus paradoxus* Put.

Joppeicus paradoxus probably does not occur in North Africa west of Egypt, since not a single record is known from there; neither was the species ever encountered there by Dr. H. Eckerlein during his numerous recent collecting trips. It seems to be abundant at some localities around Cairo and Alexandria only, whereas it is apparently rare in other parts of its range, as documented by Dr. Linnavuori's failure to find this species in all countries concerned at the time of his extensive collecting; I failed to find it in Jordan and Ethiopia and collected it three times only in the Sudan during three years, although I knew suitable habitats and paid them special attention.

It is amazing how many vegetation zones are comprised by the more or less meridional range of *Joppeicus paradoxus*. Starting from the North it is found on the southern border of the Mediterranean evergreen maquis, then in the Desert district and in the Semidesert (= Acacia Desert Scrub) district, on the southern border of which there is situated the southernmost Sudanese locality of the species. The localities in this area are, however, situated on the edges of these districts or in the close vicinity of the Nile, whose banks are either cultivated and irrigated, providing relict habitats for an originally more hygrophilous flora, or occupied in the Central Sudan by a thorny bush; both these types of the Nilotic habitats should probably be better regarded as special floral districts.

The locality Bako in Ethiopia (in an area of 1500—2000 m altitude) is, however, in the district of Dry Mountain Grassland, and if the range of *Joppeicus paradoxus* from the Sudan to Bako is continuous, it must also pass through the Tropical Grassland (= Acacia Short Grass Scrub & Acacia Tall Grass Forest) and Ethiopian Forest districts.

The same applies for the distribution of *Joppeicus paradoxus* considered from the viewpoint of zoogeographical classification. It is a shared Palaearctic-Ethiopian species occurring in the Sumerian and Saharian districts of the Mediterranean subregion of the Palaearctic, and in the Sudanese Arid, Sudanese Savanna (?) and Abyssinian Highland districts of the Ethiopian region.

b) Bionomics of *Joppeicus paradoxus* Put.

The bionomics of *Joppeicus paradoxus* may be summarized as below, taking into account both the data contained in this paper and the results of Davis' & Usinger's (1970) laboratory studies.

Habitats. Macrohabitats: gardens, fields, planted woods, street alleys, etc. in the Nile Delta and Valley, and protected habitats (caves, fissures in rocks) in the surrounding desert and semidesert habitats; perhaps partly synanthropic ("mudpot farm"). Microhabitats: under loose scaly bark of trees (recorded: *Ficus sycomorus*, *F. senegalensis*, *Acacia nilotica*, *A. seyal*, *Azidarachta indica*), under prostrate herbs (*Portulacca quadrifida*), under leaf litter of *Ficus* (and probably other trees and shrubs as well), under stones, in rock crevices inhabited by bats (*Tadarida a. aegyptiaca*), among human and bat faeces, under paper litter, often on dusty and sandy ground, in burrows of rodents (? *Meriones* sp.).

Food. In the field recorded as occurring in association with larvae and adults of Dermestidae and Tenebrionidae, Carabidae, ants, Embioptera, Cimicidae, Piesmatidae, Reduviidae, Collembola, bat ticks and subcortical spiders. Laboratory experiments have shown that it feeds (and can be bred) on nymphs of bed bugs and cockroaches, and attacks larvae of Heteroptera, Coleoptera and Lepidoptera. Field observations suggest that the most probable natural prey are nymphs of Heteroptera, larvae of Dermestidae and other generally distasteful insects, little looked for by other predators. Apparently Usinger's opinion that *Joppeicus paradoxus* is a general non-specialized predator is right.

Generation cycle. In Israel, Egypt and the Sudan probably without any definite cycle; the available records of adults (at some occasions taken together both with old and very young nymphal instars) are from almost all months of the year (except for April, June and October).

Behaviour. Very active, with a negative phototaxis during the day, with cataleptic reactions when disturbed, capable of running quickly, probably flying to light, rarely biting man.

Conclusion. *Joppeicus paradoxus* is a general predator living in sheltered situations in various types of habitats in the Nile Valley and its vicinity. It is generally associated with microhabitats little frequented by other insects, occurs frequently in extreme situations (like among hu-

man and bat faeces), and apparently it is well adapted for life under variable and extreme conditions where it can feed on generally distasteful groups of insects with little competition by other predators. If this is the true ecological niche of this species, we might assume that it was pushed into it from habitats with a richer food supply by competition of other, more successful, predators. Its non-specialized food regime might have caused both its incapability to compete as well as its ready adaptation to diverse and extreme conditions and utilization of little exploited sources of food.

c) Past distributional history of Joppeicidae

Linnavuori (1963) included *Joppeicus paradoxus* among the endemic species of Israel, endemic in a broad sense, having spread also to the adjacent countries. Later (Linnavuori, 1964) he modified his opinion and regarded it as an Eremian element applying this term again in a broad sense to all species adapted to life in the desert transitional Palaearctic-Ethiopian belt disregarding "whether they have spread southwards into Tropical Africa or not". Though the presently known range of this species may be characterized as largely restricted to the vicinity of the Main and Blue Niles, it would still fit Linnavuori's broad definition of an Eremian element. *Joppeicus paradoxus* is, however, a single surviving representative of the family Joppeicidae, and this type of distribution must definitely be regarded as secondary for this family for reasons given below.

1) Joppeicidae have numerous autapomorphic characters, some characters more plesiomorphic than the other Cimicomorpha (e.g. the number of dorsal scent glands), some very primitive cimicomorphan characters e.g. the type of insemination and fertilization), but only very few synapomorphies shared with the other cimicomorphan families. We can thus agree with Davis's & Usinger's (1970) opinion that the family "must have diverged very early in the evolutionary history of the cimicomorphan line". Since all major cimicomorphan families have fossil records dating back from Jurassic to Palaeogenic times, we can assume that also Joppeicidae must have existed at some time during that period, if not earlier.

2) There is no other similarly ancestral and relict Hemipteran group which would have its range restricted to the area inhabited by Joppeicidae. The only primitive group with a range restricted to the Eremian zone is the most primitive pentatomoid family, the Thaumastellidae. It ranges, however, from Algeria to S. Iran, and as unpublished observations by Linnavuori, Schaefer and Štys show, it extends in Africa much further southwards than it was expected before. Consequently, its past distributional history was probably different from that of Joppeicidae.

3) The above discussion of bionomics of *Joppeicus paradoxus* has shown that the ecological niche occupied at present is probably secondary. The species is rare throughout its range, more frequently occurring around Cairo and Alexandria only.

4) The most pertinent facts from the geological history of the areas involved are, as follows. Still in the Middle Pliocene (about 4 000 000

years ago] the Nile Valley from the Delta to the Tropic of Cancer was a marine estuary; then a period of sea subsidence followed until the present land-sea boundary was roughly established some 100 000 B.C. There were no deserts or semideserts along the Nile; the climate became arid, and the present eremic climatic and biotic patterns have been formed only after the last pluvial period (50 000 B.C.) (Linnavuori, 1964). In Pleistocene the Abyssinian Highlands were subjected in the highest altitudes to a certain degree of glaciation, and the life conditions became adverse to the originally much richer biota, the primary reason being the cooling of the climate, the other one — according to different authorities — either the arid conditions due to the shifting of prevalent winds, or an extensive fall of volcanic dust during the last phases of plutonic activity in the area. Both the flora and fauna have been, however, definitely impoverished during that period (Mani, 1968).

We are thus facing a rather unusual situation: an obviously old, relict, monotypic family occurs in an area definitely atypical for such a taxon. Moreover, most of its range has been only recently established as a terrestrial habitat, and it has been subjected to recent far-reaching climatic and biotic changes. The situation is the more curious considering that the only place of a really frequent occurrence of Joppeicidae is the Nile Delta and its vicinity, i.e. the most recently formed part of the area.

The following hypothesis might explain this situation. We may assume that the original area where Joppeicidae survived were the Abyssinian Highlands. During the Pleistocene deterioration of life conditions the Joppeicidae were unable to compete with more vigorous predators under the conditions of increased food competition, and were pushed into extreme, newly formed habitats, being — as non-specialized predators — able to utilize any possible kind of prey. They were pushed into warmer Sudanese lowlands and followed the course of the Nile; a part of the population was forced into temporary habitats in the Nile Delta and moved with it northwards. The competition pressure combined with the capacity for survival of those fragments of population which had been brought into the Delta by floods might have been the cause of the shift of the main bulk of population into the Delta and vicinity and of only rare occurrence of surviving relict colonies along the long stretch of Blue and Main Niles. An obvious alternative hypothesis would be that Joppeicidae had been a group originally widely distributed in N.E. Africa Savanna district, which was pushed into the Nile Valley by the post-pluvial dessication of climate; this would not, however, explain the fact of their unequal abundance within their range.

S u m m a r y

1) The distribution of *Joppeicus paradoxus* Put., the only species of the family Joppeicidae, is reviewed and complemented. It occurs in S. Israel, Egypt, the Sudan and W. Ethiopia, all the localities not being far from the Main and Blue Niles.

2) The data on its habitats and probable natural prey are reviewed and discussed. It is concluded that Joppeicidae are non-specialized gene-

ral predators feeding on small insects and living in diverse, often extreme habitats, particularly in such where little food competition occurs. This ecological niche is probably secondary.

3) The past distributional history of Joppeicidae is discussed. Their original range is supposed to have been in the Abyssinian Highlands, the Pleistocene climatic changes being responsible for the formation of present distributional patterns.

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