

THE DISTRIBUTION OF THE COSMOPOLITAN GENUS *ANAX* LEACH AND ITS PROBABLE ORIGIN (ANISOPTERA: AESHNIDAE)

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Received February 2, 1978

The genus includes approx. 30 spp. The largest number of these occur in southern Asia and in Africa, 4 are known from America and 2 from Europe, while in Australia the representatives occur in the northern part of the continent only. The majority of spp. have either a very local or a very extensive range. The original (Paleocene) territory of the genus (southern Asia - southern Europe and northern Africa - southern North America) has been split up by continental drift in the Neocene, giving rise to 3 apparent focal regions, viz. Eastern Asiatic, Euro-African and American. It is stressed that the pattern of the dispersal of *Anax* is similar to that of the zygopteran *Enallagma*.

INTRODUCTION

The genus *Anax* Leach is almost cosmopolitan. However, it is not found in either the far north of Europe (AGUESSE, 1968) or in northern Asia (BELYSHEV, 1973), whereas in the New World only a single species reaches as far north as Alaska (NEEDHAM & WESTFALL, 1955; WALKER, 1958). In the southern hemisphere it is absent in the southern part of the Neotropical region, and in Australia it occurs only in the northern tropical state of Queensland (FRASER, 1960).

The genus includes about 30 species. We stress this approximation, since there is still work to be done on the taxonomy. Sometimes *Hemianax papuensis* (Burm.) has been placed in the genus *Anax* (LIEFTINCK, 1953). Some authors assume that there is a subspecies, *A. parthenope geyeri* Buchholz in northern Africa (AGUESSE, 1968), but for this region the nominate form was also introduced, hence this subspecies may be considered as a species in the zoogeographical respect. There are doubts as to whether *A. piraticus* Kenn. is a separate

species (KENNEDY, 1934). Some workers believe that *A. longipes* Hag. and *A. concolor* Br. are separate species, others consider them as being only subspecifically distinct. A similar situation prevails with respect to *A. nigrolineatus* Fras. and *A. nigrofasciatus* Oguma, which again are sometimes considered as subspecies only (ASAHINA, 1962). Also there are a number of other cases. We have examined 30 species, but it should be stressed that the neotropical fauna is insufficiently known and possibly certain species have been omitted. However, our conclusions still hold good. In the Neotropical region fairly complete data are available only for Venezuela (Dr. J. Racenis, unpublished), Peru (RACENIS, 1959), Chile (NEEDHAM & BULLOCK, 1943; FRASER, 1957) and Cuba (ALAYO, 1968), but there is some information on the Central American countries (Dr. D.R. Paulson, unpublished), Argentina and Brazil (FRASER, 1947; LONGFIELD, 1929; SJÖSTEDT, 1918).

REVIEW OF THE REGIONAL FAUNAS

In the Australian faunal area the genus is alien. From New Guinea two species, *A. gibbosulus* Ramb. and *A. guttatus* (Burm.), reach to the northern (tropical) part of the Cape York Peninsula, Queensland (FRASER, 1960).

In the New World the *Anax* species occur in the northern hemisphere i.e. in southern North America and north of the Meridional; extending slightly south of the equator. Of the four American species, *A. amazili* (Burm.), *A. longipes*, *A. walsinghamsi* McLach. and *A. junius* (Drury), only the latter is typical for the Boreal region, ranging from Alaska to Mexico. The other three are found both in the Boreal and in the Meridional faunal regions, usually in the vicinity of the contact zones between the regions.

Only two species are known in Europe (AGUESSE, 1968), *A. imperator* Leach and *A. parthenope* Sel. These are centred in the southern half of the continent, but are widely distributed.

In Asia the species of the genus occur only to the south of Siberia (BELY-SHEV, 1973). In Boreal Asia there are only two species, *A. imperator* and *A. parthenope*. To these can be added *A. immaculifrons* Ramb., an Indian species, reaching to Afghanistan (SCHMIDT, 1961).

In south and southeast Asia (i.e. within the Oriental region of the Meridional kingdom), 17 species are known: *A. bacchus* Hag., *A. fumosus* Hag., *A. gibbosulus*, *A. goliathus* Fras., *A. guttatus*, *A. immaculifrons*, *A. junius*, *A. maclachlani* Foerst., *A. nigrofasciatus*, *A. nigrolineatus*, *A. papuensis* (Burm.), *A. panybeus* Hag., *A. parthenope*, *A. piraticus* (?), *A. pugnax* Lieft., *A. selysi* Foerst. and *A. strenuus* Hag.

In New Guinea and the adjoining islands (LIEFTINCK, 1949) six species occur: *A. fumosus**, *A. gibbosulus*, *A. guttatus*, *A. maclachlani**, *A. pugnax** and *A. selysi**. The four marked with an asterisk are endemic for the island or

still occur in the Moluccas or Bismark Archipelago. *A. guttatus* is distributed very widely and *A. gibbosulus* is also known in the Sunda Archipelago (LIEFTINCK, 1953) and in northern Australia (FRASER, 1960).

In Hindustan (FRASER, 1933-1936; KUMAR, 1973) six species are known: *A. guttatus*, *A. immaculifrons*, *A. nigrolineatus*, *A. parthenope*, *A. indicus* Lieft. and *A. marginope* Baijal & Agarwal. Of these, only *A. nigrolineatus* is endemic for India. *A. immaculifrons* is common in China and enters the Boreal to some extent, while *A. guttatus* is widely distributed in the area of the Pacific and Indian Ocean. The areas of *A. indicus* and *A. marginope* are not known to us. It should be noted that such a widely distributed species as *A. imperator* reaches northwestern India only and does not extend into the peninsula.

There is one species group also in eastern Asia, i.e. in China (NEEDHAM, 1930), Japan (ASAHINA, 1965), the Philippines, Malaysia and the Sunda Archipelago (LIEFTINCK, 1953, 1954, 1962, 1974). Ten species are known from this territory, viz. *A. bacchus**, *A. gibbosulus*, *A. goliathus**, *A. guttatus*, *A. immaculifrons*, *A. junius*, *A. nigrofasciatus**, *A. panybeus**, *A. parthenope* and *A. papuensis*. The endemics are marked with an asterisk. *A. junius* reached there from America. *A. guttatus* and *A. parthenope* are characterized by a wide distribution, while *A. gibbosulus* and *A. immaculifrons* are widely distributed within the Oriental region, reaching New Guinea and Hindustan.

Now we must examine the fauna of Africa, or rather the Ethiopian region (PINHEY, 1962). There are two species which occur only in the Boreal region of this continent: *A. parthenope* and *A. imperator* (if *A. p. geyri* is not a separate species). From eight Ethiopian species: *A. bangweuluensis* Kimm., *A. chloromelas* Ris, *A. congoliath* Fras., *A. imperator*, *A. parthenope*, *A. speratus* Hag., *A. tristis* Hag. and *A. tumorifer* McLach., all except the first two mentioned, were not endemic to northern Africa. Formally, *A. guttatus*, known from the Seychelles, should be also referred to this group.

It will be noted that a series of purely African taxa has very narrow areas. Thus, *A. bangweuluensis* has been recorded only from Zambia and Botswana, *A. congoliath* only from Zaire and northwest Zambia, and *A. tumorifer* only from Madagascar. Thus there are three widely distributed species in the Ethiopian region.

THE RANGE OF INDIVIDUAL SPECIES

Having dealt with the regional faunas, we will now examine the regions of individual species. On the one hand, there are highly localized areas which can be divided into two groups. Firstly, there are endemics of the islands: New Guinea, the Hawaiian Islands, Guam and Madagascar. Secondly, there are continental-restricted endemics: southern China, Hindustan, Zaire river basin, Cape Province. The reasons for the existence of so many restricted, localized regions

of such excellent fliers as the dragonflies of the genus *Anax* are obscure.

On the other hand, there are widely distributed species. The area of *A. guttatus* is extremely interesting, extending through the whole region of the Pacific and Indian Oceans (BELYSHEV, 1968). This species is known from the Tuamotu Islands in the east to the Seychelles in the west. From the northern extremity of Australia in the south it reaches to the north of the Marianas. Most of the oceanic islands are inhabited by this species (LIEFTINCK, 1962). It occurs also in the peninsulas or even on the mainland coasts, but it is always absent within the continents. Hence it is an oceanic species.

A. panybeus is also distinctly maritime, though to a lesser extent, and it has not been reported from oceanic islands. Its area is situated along the eastern Asiatic islands and peninsulas: Japan, the Philippines, Malaysia and the Sunda Islands, but does not cover the continental regions of eastern Asia.

Finally, *A. junius* also has a distribution connected with oceanic regions (BELYSHEV, 1966). However, it cannot be called either oceanic or maritime, since it is widely distributed in Northern America and was carried by hurricane winds to the Hawaiian Islands and then to northern China.

Undoubtedly these oceanic regions are of great importance in the dispersal of dragonfly species with the help of air currents of the hurricane kind (BELYSHEV, 1966). All three species are to be found along the main hurricane directions. This should be taken into consideration in any discussion of species dispersal of the genus under study.

The two vast regions of the relatively northern species which occur within the Boreal faunal kingdom are of interest. They mainly inhabit the Subholarctic region and partially enter the Holarctic region.

A. imperator is distributed from southern Sweden in the north to the Cape of Good Hope in the south. Longitudinally this species has been reported from the Atlantic Ocean to the mountains of Central Asia. Attention must be drawn not only to the vast spatial area and distribution across landmass zones, but also to the fact that the species does not yet reach Hindustan. This can be easily explained by its late dispersal to the east. Its subspecies, *A. i. mauricanus* Ramb., occurs in the extreme south of Africa (PINHEY, 1951), but this is impossible to understand at present, since it is difficult to suppose that the centre of origin was in southern Africa.

The second species, *A. parthenope*, is also widely distributed longitudinally, but not in a latitudinal direction. It has been reported from the Atlantic to the Pacific Ocean and from Siberia (BELYSHEV, 1973) to India (FRASER, 1933-1936) and tropical Africa (PINHEY, 1962). This species has reached India, but has not succeeded in populating the whole of Africa.

SPECULATIONS ON THE HISTORY OF THE DISTRIBUTION
OF THE GENUS

We have now elucidated the zoogeography of the genus thoroughly, i.e. its distribution, centres of speciation, faunistic complexes and connections of individual territories. Supported by these data, we can conceive the history of the development of the distribution of the genus.

There is no doubt that the genus *Anax* is quite tropical with only a very small number of species entering the moderate latitudes, and then only to a limited extent.

In the Palaeocene the genus occupied a fairly narrow tropical zone. It ranged from south-eastern Asia (according to present definition), through southern Europe and northern Africa and to southern North America, including the adjacent parts of Central America.

In the Neocene the original territory was split up by continental drift, Europe and America maintaining contact only in the north, where the *Anax* species were absent. Also the influence of developing aridity in many areas of Asia and northern Africa should be taken into account.

Thus separate foci of speciation arose: Eastern Asiatic, Euro-African and American. Some time later, glaciation destroyed the European species or drove them back to the region of present day equatorial Africa.

Almost throughout this period the genus was lacking in one part of the former Gondwana, i.e. in Australia and India, while in the other part, Africa and Southern America, some species only occurred in the zone contiguous to Lavrasia. The invasion of India took place in several stages. Firstly *A. nigrolineatus* reached Hindustan, having originated from a forespecies which inhabited or still inhabits south-eastern Asia.

The Hawaiian endemite, *A. strenuus*, evolved from the American *A. junius*, due to its early arrival in the islands, while the subsequent immigrants of the same retained the original specific features (BELYSHEV, 1966).

In view of the uncertainty as to the taxonomic status of the Islands of Guam endemite, *A. piraticus*, we refrain from further discussion on it.

Until paleontological material will have become known, the above considerations on the history of the dispersal of the genus *Anax* should be regarded as a working hypothesis only. A similar history could be put forward for *Enallagma* Charp., another tropical genus of almost cosmopolitan distribution. Whereas the *Anax* dragonflies are excellent fliers, able to actively cover great distances, the members of the zygopteran *Enallagma* have but weak flying capacity, and can be carried from one territory to another only passively, with the help of wind. Nevertheless, the patterns of dispersal of the two genera resemble each other.

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