A Review of the *Nilothauma pictipenne* Group
and a description of four new Afrotropical species of *Nilothauma* Kieffer, 1921
(Diptera: Chironomidae: Chironominae)

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DEDICATION

This Thesis is dedicated to my late Parents

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This is to certify that this thesis has not been submitted for a degree to any other University. It is entirely my own work and all help has been duly acknowledged.

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ABSTRACT

A revised generic diagnosis of the genus *Nilothauma* Kieffer, 1921a, is given. Four new Afrotropical species, *N. loba* sp. n., *N. tricaudata* sp. n., *N. flabella* sp. n., and *N. insolita* sp. n., are described as male imagines. *N. pictipenne* Kieffer, 1921a, is redescribed as male and female imagines. Two Neotropical species (*N. aleta* Roback,1960 and *N. duena* Roback, 1960) are regarded as *nomina dubia* and placed in *Paratendipes*.

A key to male imagines of the *Nilothauma pictipenne* group is given and the phylogenetic relationships of the *Nilothauma* group of genera (*Nilothauma*, *Neelamia* Soponis, 1986 and *Paranilothauma* Soponis, 1986), of the different species groups of *Nilothauma* , and of the *Nilothauma pictipenne* group are discussed. The genus *Paratendipes* Kieffer, apparently forms the sister group of a group consisting of the genera *Paranilothauma*, *Neelamia* and *Nilothauma*. Within *Nilothauma*, four species groups are recognized with the *babiyi* group forming the sister group of the remaining groups. The *bicorne* group apparently forms the sister group of the *mirabile* and the *pictipenne* groups combined.

Paratendipes is cosmopolitan. The Neotropical group of genera (*Neelamia* and *Paranilothauma)* appear to have split off very early with the fragmentation of Pangaea. The species of *Nilothauma* treated here fall into four species group of Megagaeic lineages and are confined to the Holarctic, Sino-Indian, Afrotropical and Australian zoogeographical regions for freshwater fauna. The *babiyi* group is made up of 2 Afrotropical, 1 Holarctic and 1 Sino-Indian species. *N. babiyi* (Rempel, 1937) and *N. japonicum* Niitsuma, 1985, limited to North America (Holarctic region) and Japan (Sino-Indian region) apparently are sister species. The *N. babiyi* group apparently first speciated with the fragmentation of Megagaea. In the *bicorne*

group, *N. bicorne* (Townes, 1945) and *N. brayi* (Goetghebuer, 1921) occur in the Holarctic region. However, *N. brayi* has also been described from Japan in the Sino-Indian zoogeographical region. This group is also of a Megagaeic lineage with some dispersal probably haven taken place. The *mirabile* group consisting of *N. mirabile* (Townes, 1945) and *N. hibaratertia* Sasa, 1993, present in North America and Japan respectively is distributed in the Holarctic and East Asian regions. The *pictipenne* group is made up of 2 species (*N. nojirimaculata* Sasa, 1991, and *N. hibaraquarta* Sasa, 1993) from the Sino-Indian region and 5 species (*N. pictipenne, N. loba, N. tricaudata*, *N. flabella* and *N. insolita*) from the Afrotropical region. The phyletic interrelationship of the *Nilothauma* group of genera suggests the early splitting of their common ancestor into the Neotropical group (namely *Neelamia* and *Paranilothauma*) and the Megagaeic lineage group during the fragmentation of the super-continent Pangaea. The Megagaeic lineage group is made up of *Nilothauma* species with further fragmentation and possible dispersal into the Holarctic, Sino-India, Afrotropical and Australian regions.

The distributions and ecologies of the different species of the genus are outlined.

CHAPTER ONE

INTRODUCTION

The dipteran family Chironomidae (commonly known as non-biting midges) belongs to the suborder Nematocera. Members of the family are the most widely distributed and frequently the most abundant group of insects in freshwater, with representatives in both terrestrial and marine environments (Oliver, 1971; Pinder, 1986; Armitage *et al.*, 1995). In spite of their wide distribution and abundance in diverse habitats, the systematics, detailed ecology and life cycles of many species of Chironomidae are unknown. As such, most general faunistic works either ignore the family entirely or deal with them superficially (Pinder, 1983). Chironomids constitute an important component of freshwater fauna in the Afrotropical Region (Petr, 1970a; Amakye, 1980). It has been reported by Amakye & Samman (1980) that in many aquatic ecosystems in the West African subregion at least 50% of the total benthic macroinvertebrate species recorded belong to the family Chironomidae.

Most of the major studies of the family Chironomidae in the Afrotropical Region have been limited to standing waters like lakes, reservoirs and also large rivers. Freeman (1955, 1956, 1957,1958) has described chironomids of Africa south of the Sahara. McLachlan (1965, 1966,1969) has worked on the benthic fauna of Lake Kariba in Zimbabwe and described some larval and pupal chironomids. Dejoux (1968) carried out studies on Lake Chad and Petr (1969) studied the benthic fauna on the Volta Lake. Many Afrotropical chironomid genera and species of small rivers and streams, especially in forest areas, remain undescribed.

Chironomids have been studied from various parts of Ghana (Amakye, 1993). Thomas (1966) recorded 17 species of chironomids from a small man-made lake. Petr (1970b) reported 52 species of chironomids from light trap collections made from the Volta Lake, while Whyte (1971) studied the ecology of chironomids and recorded 69 species in a small tropical man-made lake, the Danfa Reservoir, situated on the Accra plains of Southern Ghana at the bottom of the Akwapim range of hills. Of the 69 species recorded, 26 were supposedly new species. 5 of these supposedly new species belong to the subfamily Tanypodinae, 2 belong to the subfamily Orthocladinae whilst 15 and 4 belong to the tribes Chironominae and Tanytarsini respectively. Both tribes are in the subfamily Chironominae. However, Whyte (1980) recorded only 34 positively identified species of chironomids in his studies that covered the entire country. Hynes (1972) collected chironomid larvae in his studies of the benthos of the upper reaches of the Pawnpawn River in the Eastern Region of Ghana which were identified only to the subfamily level. In most of these studies, the collected specimens were not identified to species due to the lack of readily available identification keys at that time. However, the availability of keys of Chironomidae larvae (Wiederholm, 1983), pupae (Wiederholm, 1986) and adult males (Wiederholm, 1989) of the Holarctic region these days has remedied the situation.

By the end of 1993, 87 species in 31 genera belonging to 3 subfamilies had been recorded from Ghana. The subfamilies are represented by 12 species (14%) of Tanypodinae, 6 species (7%) of Orthocladiinae and 69 species (79%) of Chironominae (Amakye, 1993). In all the studies previously undertaken in Ghana, the genus *Nilothauma* has not been recorded among the chironomids collected (Amakye, 1993).

The family Chironomidae is currently divided into eleven subfamilies. These are: Chironominae Macquart, 1838; Tanypodinae Thienemann et Zavrel, 1916; Diamesinae Kieffer, 1923; Orthocladiinae Edwards, 1929; Podonominae Thienemann, 1937; Aphroteniinae Brundin, 1966; Telmatogetoninae Brundin, 1966; Prodiamesinae Sæther, 1976; Buchonomyiinae Brundin et Sæther, 1978; Chilenomyiinae Brundin, 1983; Usumbaromyiinae Andersen et Sæther, 1994.

The majority of species of Chironomidae from Africa south of the Sahara fall into the subfamily Chironominae, a fact which is in accordance with the work of entomologists in the Palaearctic Region, who have found that species of this subfamily are especially typical of warm water environments (Freeman, 1957) and also seem to prefer standing or slow flowing water (Freeman & Cranston, 1980). Members of the subfamily are found in all zoogeographic regions except the Antarctica (Cranston *et. al.*, 1989). The subfamily is quite homogenous and is recognised in the adult stage by the following features: Wing lacking mediocubital (MCu) crossvein; radius$_{2+3}$ (R_{2+3}) present; if absent, then R_1 and R_{4+5} narrowly separated by no more than width of a vein; foreleg with first tarsomere longer than or subequal to tibia (leg ratio subequal to or greater than one); spurs of mid and posterior tibiae often comb-like, consisting of fused spines; male hypopygium with gonostylus virtually fused to gonocoxite, with little or no flexion permitted [even in the few genera (*Stictochironomus* Kieffer, *Sergentia* Kieffer, and *Phaenopsectra* Kieffer) with flexible gonostylus, the angle of flexion rarely allows folding inwards]. The female genitalia lacks gonostyli and ovipositor; 2-3 seminal capsules present; tergite VIII well developed; gonocoxite IX separated from tergite IX; tergite IX large, nearly always more than 1.5 times as long as gonococoxite IX, hood shaped with setae evenly distributed at least on posterior half.

Three tribes are recognised within the subfamily Chironominae: Pseudochironomini of more recent designation (Sæther, 1977), for *Pseudochironomus* Malloch, *Manoa* Fittkau, and *Riethia* Kieffer, primarily in the Neotropical and Nearctic regions, but with wider representation in the Australian regions and 1-2 Palaearctic species; and the worldwide Chironomini and Tanytarsini. The phylogenetic positions of the tribes have been provided by Sæther (1977).

The genus *Nilothauma* belongs to the tribe Chironomini. Members of this tribe are characterised by the wing membrane being bare or if it carries macrotrichia then the squama has a marginal fringe of long setae, and the cross-vein radius-media (R-M) is oblique to the direction of vein R_{4+5}. The tribe was divided by Kieffer (1921a,b) into two groups depending on whether the posterior tibia had one or two spurs in association with the combs. This system of dividing the bulk of the species was also adopted by Edwards (1929) and Goetghebuer (1937-1954) and for many genera it is satisfactory. Freeman (1957) also adopted Kieffer's original method of dividing the tribe, but modified some of the definitions because of the presence of single spurred species within genera which are normally two-spurred.

Nilothauma, in the adult stage, comprises a distinct and relatively easily recognizable group of species. The adult male of *Nilothauma* can be distinguished from other genera of Chironomini [except *Paranilothauma* Soponis, 1986; *Neelamia* Soponis, 1986; and some *Paratendipes* Kieffer, 1911] by the following characters: Male antenna with 13 flagellomeres, female usually with 6 flagellomeres, antennal ratio (AR) low to very low (less than 0.35); anterior tibia with long, curved spur; terminal combs of middle and posterior tibiae fused or separated, middle tibia with one, posterior tibia with two spurs; VR (venarium ratio) high, squama bare; transverse sternapodeme lacking. *Nilothauma* differs from *Paranilothauma*, *Neelamia* and *Paratendipes* by the presence of at least one anal projection on tergite IX.

The genus *Nilothauma* is known from the Holarctic, Neotropical, Australian, and Afrotropical regions. Up to now twelve species of the genus have been described world wide. Six are Palaearctic, three Nearctic, two Neotropical, one Afrotropical, and one species described only as larva, is known from Western Australia.

Adult taxonomy of *Nilothauma* has been fairly well described. The six Palaearctic species have been described by Goetghebuer (1921), Niitsuma (1985), and Sasa (1990, 1991, 1993). The three Nearctic species have been dealt with by Rempel (1937) and Townes (1945), while Roback (1960) has described the two Neotropical species. However, the two Neotropical species (*N. aleta* Roback, 1960 and *N. duena* Roback, 1960) are here regarded as not belonging to *Nilothauma* since they lack any projection on tergite IX. The type studied is lost and they have to be regarded as *nomina dubia* in the genus *Paratendipes*.

Kieffer (1921a) described the single previously known Afrotropical species, *Nilothauma pictipenne*, which was redescribed by Freeman (1957). According to Freeman, the Afrotropical species is extremely similar structurally to *N. brayi* (Goetghebuer, 1921), but differs in the presence of wing markings.

The descriptions of the species were without adequate quantitative data, were very general and rarely accompanied by adequate illustrations. The descriptions were also based on phenotypic characters such as colour and size. Description of species using colour is subjective. Colouration and size are not very good features as they are highly variable. The extent to which colour can be relied on depends on the knowledge of the influence of ontogenetic and environmental factors (Wiley, 1981). Traditionally, gross features of adults' external morphology such as wing venation, hairiness and colour patterns were important in discrimination of species. This can result in placing many different species under one particular species. As the relative lengths of the segments of legs and antennae often varied in a species-specific manner, morphometrics were used in chironomid studies (Cranston, 1995). The drawings made by previous authors were not detailed enough to illustrate the subtle features needed to discriminate species.

The inadequate descriptions coupled with the great species richness of Chironomidae has necessitated the redescription of the only previously described Afrotropical species of *Nilothauma* by Freeman (1957). This is needed for the construction of up-to date keys and for proper phylogenetic analysis of the genus. The current conventional approach to taxonomic descriptions of Chironomidae which involves measuring and counting of important morphological features of a number specimens backed by detailed and clear drawings is used in this study. The methods of taking measurements and ratios generally follow Sæther (1969, 1971, 1980a, 1990b) and Schlee (1966).

During the collection done in streams and rivers of some forest areas in Ghana in connection with the Norwegian Universities Committee for Development, Research, and Education (NUFU) Project, three new species of *Nilothauma* were found. The NUFU Project is a collaborative programme between the Museum of Zoology, University of Bergen Bergen, Norway; Department of Zoology, University of Ghana, Legon; and the Institute of Aquatic Biology, Ghana. The fourth new species of the genus is a male imago from Tanzania logged at the Museum of Zoology, University of Bergen. Not many specimens were collected. This may be partly due to the collecting methods used and the localities sampled.

This thesis reviews the *Nilothauma pictipenne* group with the description of four new Afrotropical species of *Nilothauma*. A key for adult males of the *Nilothauma pictipenne* group is given and the systematic relationships of the species of *Nilothauma* and the *Nilothauma* group of genera (*Nilothauma, Neelamia* and *Paranilothauma*), as well as their zoogeography, are presented.

Chironomids

Geographically, chironomids are the most widely distributed of free-living holometabolous insects. It has been estimated that there are about 15, 000 species of chironomids world-wide (Armitage *et al.*, 1995). Of this number, about 6, 000 species have been described and about 500 species are Afrotropical (Sæther pers. comm.). In normal freshwater habitats they show a large range from arctic and alpine glacier water to tropical ponds, from extreme oligotrophy to extreme eutrophy. There are stenotopic as well as eurytopic species (Oliver, 1971; Pinder, 1986; Sæther, 1979a, 1980b, 1983; Armitage *et al.*, 1995). In the northern hemisphere, a diverse community of chironomids exists at Lake Hazen (81^{o} 49' N) at Ellesmere Island (Oliver & Corbett, 1966). The Antarctic mainland in the southern hemisphere is home to three species, with *Parochlus steinenii* (Gercke) and *Belgica antarctica* Jacobs reaching 62^{o} S and 68^{o} S, respectively (Usher & Edwards, 1984; Edwards & Usher, 1985). These represent the southernmost, free-living, holometabolous insect species (Williams & Feltmate, 1992; Oliver 1971).

Chironomid species can be found in habitats with wide ranges of temperature, pH, oxygen concentration, salinity, current velocity, depth, productivity, altitude and latitude. In grossly polluted environments chironomids may be the only insects present (Armitage *et al.*, 1995). Among benthic fauna the predictable responses of populations of certain species of chironomids to different levels of a variety of nutrients and pollutants has resulted in the use of larval chironomids as biological indicators of water quality (Oliver, 1979). Chironomids are low in the food chain and therefore make up most of the diets of many other aquatic invertebrates, fishes and birds in some localities. In addition, there are many terrestrial, semi-terrestrial and also some that are marine.

Chironomids occupy a key position from an ecological perspective and are very valuable indicator animals in biogeographical, fauna-historical, and phylogenetic analyses. They are easy to collect, and differ from most other groups of insects, all stages are known for most genera. Fossils of chironomids show that the family constitutes a very old group with most present genera represented already between the Jurassic and the Cretaceous periods (Brundin, 1976). They thus are extraordinarily well suited as test animals for hierarchical and biogeographical reconstructions as well as for indicators of environmental deterioration. The science of limnology, some would even say of ecology, was given an early impetus by the use of chironomid communities as indicators of the trophic state of freshwaters (Brundin, 1949, 1956; Sæther, 1979a, 1980b). The theory of plate tectonics (continental drift) provided an explanation for the transantarctic relationships of chironomids (Brundin, 1966) and a major contribution to the general acceptance of the theory.

Chironomids are most familiar to us as adults because of the habit of many species forming aerial mating swarms beside productive standing waters. However, there are some species that mate on the ground or water surface. Swarming period is commonly controlled by light intensity, with twilight swarming being common, but the response may also be modified by temperature (Oliver, 1971). Males are attracted to females that enter the swarm by the sound produced by the females' wings. Males remain motionless on the ground until stimulated to swarm by the sound of a nearby female. Swarming could also be induced by humming the appropriate note.

Aquatic habitats are strongly preferred by chironomids for the development of the immature stages. These range from flowing waters (trickles, torrents, seeps to more unexpected habitats, such as temporary rain-pools, plant-held waters (phytotelmata) and even the thin film of water on high-altitude glaciers (Kohshima, 1984; Sæther & Willassen, 1987). They may be parasites, symbionts, or live in hot springs, hypersaline waters etc.

Practically all ecological niches in fresh water are inhabited by chironomid larvae, often at high densities (Freeman & Cranston, 1980). The larvae often show a distinct preference for certain types of substrate, although sediments are usually the preferred habitat, and this creates distinct microdistribution patterns (Williams & Feltmate, 1992). For instance, the larvae of *Nilothauma* are found in littoral and sublittoral sediments of standing and flowing waters (Cranston *et al.*, 1989). According to

Brundin (1949) the larvae reach their maximum abundance in the lower littoral zone of lakes.

Chironomid larvae are not restricted to sediments or other surfaces exposed to free-water; many can develop in marginal and interstitial aquatic habitats, and a substantial number of genera include species that are considered to be fully terrestrial. The terrestrial habitats used by chironomid larvae predominantly are humic soils, but decaying vegetation and even, exceptionally, living green house vegetation (Cranston, 1987) may be used. One of the most unusual biotopes adopted by some terrestrial chironomids is fresh cow dung. However, outside the temperate northern hemisphere, the larval ecologies of terrestrial chironomids are poorly known (Armitage *et al.*, 1995).

The chironomid fauna of the different zoogeographical regions have been investigated with highly differing intensity. The least examined region is the Oriental, and within the Palaearctic region, China especially is poorly investigated. The Afrotropical region is relatively well investigated concerning larger widespread species, not well at all concerning the smaller, more localised species found, for instance, in rain forest areas.

CHAPTER TWO

MATERIAL AND METHODS

Material

The material examined consists of the following Ghanaian male imagines of new species of *Nilothauma* : 1 of *N. tricaudata*, 1 of *N. flabella* and 1 specimen of *N. insolita*.

In addition one male imago of a new species from Tanzania (*N. loba)* lodged with the Museum of Zoology, University of Bergen, is described.

Imagines of *Nilothauma pictipenne* were borrowed from The Natural History Museum (British Museum), London, for comparison and to ascertain the validity of the new species described.

The holotypes of the new species (on slides) are deposited at the Museum of Zoology, University of Bergen (ZMBN). Paratypes are placed at the Zoology Department, University of Ghana, Legon, Accra, and at the Zoologisches Staatssammlung, Munich.

Methods

Field methods

Adult chironomids were collected by the use of Malaise traps, light traps and aerial sweep nets. Larvae and exuviae were collected from around the weeds within the river and from the periphery of the rivers by means of pond nets and dip nets. Collection of larvae and exuviae in flowing water mostly was by drift netting supplemented by dip nets and pond nets.

Aerial sampling

Malaise trap

The Malaise traps used for the collections were made of black nylon fabric with a white plastic container at the end of the net to receive the catch. To set up the Malaise trap, two wooden poles were used. A long pole was fixed firmly into the ground. To this was tied the front part of the Malaise trap with the plastic container positioned vertically on the pole. The second pole was fixed about two and half metres away from the first pole. The rear of the net was then tied to this pole. The longer sides are opened, partioned in the middle by another piece of net material. The front and back sides were spread out sideways and pegged to the ground using plastic pegs. The central part dividing the net into two was also pegged to the ground so that it is vertical. When fixed in position, the Malaise trap is tent shaped with one end of the roof of the net sloping upwards to the innermost corner at which there is a common aperture from both sides of the net leading into the plastic container (Plate 1). Having fixed the net in position, the plastic container was screwed open and the lower part half-filled with seventy-five percent (75%) ethanol to preserve trapped insects. Flying insects enter the net through the opened sides and are directed by the sloping end into the plastic container.

A number of these traps were usually set up along the banks of rivers or streams and left for a week. At the end of the week the contents were emptied into plastic containers and taken to the laboratory for sorting out of chironomids.

Light trap

Adult chironomids were also collected with light traps at night as flying insects are attracted to light at night. The light trap used (Fig. 1 A) consisted of a bulb connected to a generator with a white screen directly behind the bulb. The trap used a 250 watt mercury vapour and tungsten bulb as the mercury vapour bulbs alone are too bright for some species of chironomids. The illumination of the light relative to the surroundings interfered with the normal photic orientation and therefore results in the

Plate. 1. Malaise trap in a small stream in a moist evergreen forest at Kakum.

insects moving towards the light. The screen consisted of white calico material tied to two poles fixed apart into the ground. In front of this was the lighted bulb hung on a short wooden pole. Below the bulb was a large aluminum funnel fixed in the mouth of a plastic bucket. The funnel led into a plastic container with 75% ethanol. Insects that came into contact with the bulb fell through the funnel into the alcohol in the container. The contents of the containers were taken to the laboratory and chironomids sorted out. Chironomids were also picked out from the other insects that landed on the white screen, using pooters and small test tubes containing 75% ethanol.

Aerial sweep net

An aerial sweep net (Fig. 1 B) was used for collecting insects in flight. The sweep net was made of a stout wire ring frame 60 cm in diameter. A white fine nylon net bag mounted on the wire ring had a mesh of 250 μm, 90 cm deep and rounded at the bottom. The rim of the net was mounted onto the wire ring by linen material. The ends of the wire frame were bound into the end of a one metre handle.

After sweeping through the air, the wrist was twisted so that the mouth of the net faced downwards and the tip of the net swung over the wire ring to trap the insects in the net. The white colour of the net has the advantage that the captured insects can be seen clearly. Trapped insects were removed from the net by working the insects into a fold of the net, inserting a bottle containing 75% ethanol into the net and getting the insects directly into the bottle.

Aquatic sampling

Samples were taken from weeds along the fringe of the river or stream bottom using pond nets and dip nets.

Dip net

A dip net (Fig. 1 C) was used to sample pupal exuviae on the water surface along the fringes of rivers and streams. The net consisted of a conical net bag about 10 cm in diameter and 20 cm deep attached to a stout metal ring of about 6.5mm thick.

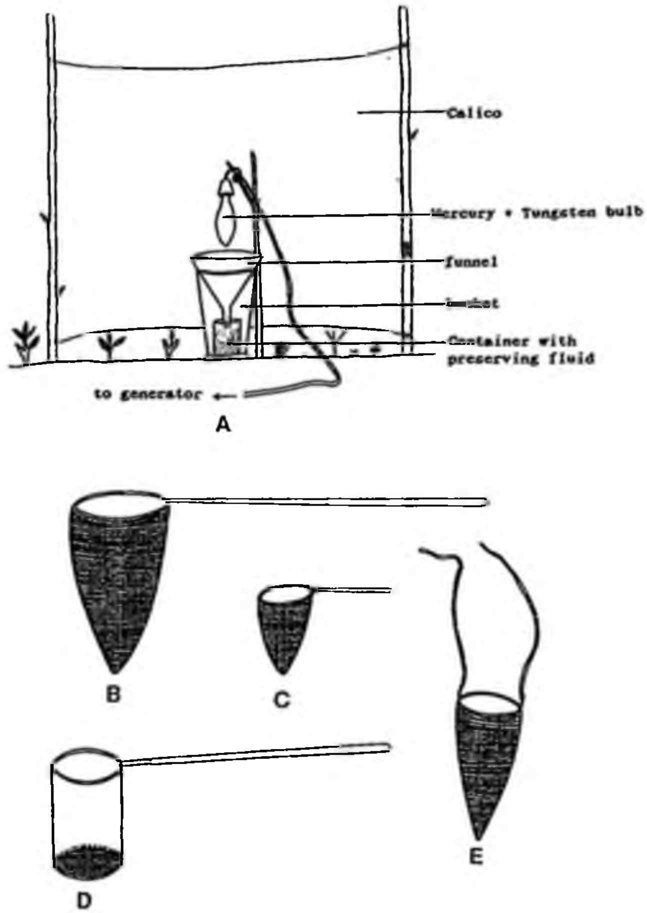

Fig. 1. Equipment used for collecting chironomids. (A) Light trap with white screen. (B) Aerial sweep net. (C) Dip net. (D) Pond net. (E) Drift net.

which is firmly fixed to a stiff, wooden handle of about 50 cm long. The net had a mesh size of 250 μm plankton net cloth.

Pond net

The pond net used was cylindrical in shape (Fig. 1 D). It was made of linen material mounted on a metal ring frame of diameter 30 cm with a circular metallic gauze bottom of mesh size 250 μm.

Samples were collected by dipping the net into rivers or streams and collecting mud and debris from the bottom. The net was lifted from time to time to allow water drain through the metallic gauze bottom. Larvae and exuviae collected in the net as the water drained out. The contents of the net were emptied by turning it inside out into a shallow, white, rectangular tray: shallow so that the water was never too deep to see what was in the tray, and white so that the fauna would show up clearly. Live chironomid larvae in the tray were noticed by their wriggling movements after allowing the contents to settle for about five minutes. The larvae were picked up from the tray by a wide-mouth pipette into bottles containing water from their immediate environment. This was to reduce the environment shock the larvae would experience. Dead larvae and exuviae were picked with forceps and put into vials containing 75% ethanol.

Drift net

The drift net (Fig. 1 E) used was similar to the dip net used for sampling along the fringes of the river except that it did not have a handle. The drift net had a mesh size of 250 μm plankton net cloth. It was woven in such a way that the mesh remained in place against the pressure of water. The net was made of a metal ring frame 30 cm in diameter with a net bag of 75 cm deep. It had strings attached to the metal ring which were used to fix it in position. The nets were fixed in the river or stream water with the mouth facing the direction of the current. As the water passed through the net, fauna in the running water collect in the net. The contents were emptied from time to time as the net got full of debris into a shallow, white rectangular tray for sorting. Live larvae collected were put into vials filled with water from their environment and placed into a portable ice chest. Many species are temperature intolerant and die at temperatures above that of their normal environment. The larvae were transported to the laboratory in the ice chest. A vacuum flask, filled with water from the larvae's immediate environment is also ideal for transporting the larvae. Dead larvae and exuviae sorted out were put into vials containing 75% ethanol.

Laboratory methods

Rearing of larvae

In the laboratory, the live larvae collected in the field were placed singly, in individual 50 mm petri dishes. Each petri dish contained about 30 mm^3 of water from the river the larvae were collected. The covers of the petri dishes had small pegs on them so that they were not in direct contact with the rims of the lower ones. This was to allow aeration of the water. The petri dishes were arranged on a table in an air-conditioned room with a temperature of about 24 ^{o} C to provide a stable environment.

The dishes were checked daily for emerged adults. Dishes with emerged adults were allowed to stand for a day to enable the cuticle to harden for the preparation of good slides. The petri dishes with the adults were then put into a freezer for about half an hour to make them immobile so that the adults were easily collected. Dead larvae and exuviae were also removed for mounting.

Sorting

Insects collected in the field through light traps, Malaise traps and preserved in 75% alcohol, were sorted out in the laboratory using a low power stereo-microscope.

Slide preparation

Due to the often minute dimensions of the features used to discriminate genus, species, and for phylogenetic analysis it was necessary to make microscope slides of the specimen. The collected specimens were mounted on slides following the procedure outlined by Sæther (1969).

Adults

From the 75% ethanol, the adult wings were carefully detached using fine forceps and dissecting needles ensuring that the squama were removed with the wings. These were placed in glacial acetic acid at room temperature. The adult bodies were then transferred into hot (near boiling) 8% potassium hydroxide for three to forty-five minutes to macerate the musculature. Alternatively the bodies were left in the 8% potassium hydroxide overnight at room temperature.

The adult bodies having been cleared of musculature were then neutralized by transferring to glacial acetic acid at room temperature for at least fifteen minutes. The bodies and wings were next transferred to absolute alcohol for dehydration for at least ten minutes and then to absolute ethyl alcohol layered over cedar wood oil for clearing for at least fifteen minutes.

The adult bodies were then dissected in cedar wood oil using a stereoscopic microscope before mounting. This was a strategy to prevent losing some of the body parts during the transfer stages. The antennae (with pedicel) were removed, then legs from the left side, head, thorax and abdomen.

Parts of the same specimen were mounted under a stereo-microscope in Canada balsam on the same slide using the five cover slip method outlined by Sæther (1969). The head was orientated to lie horizontally with its anterior side up and the thorax laterally with the legs spaced out. The abdomen was mounted with the dorsal side up for males and ventral side up for females. To prevent compression of the structures of the head and thorax, the cover slip was not placed directly on the specimen. Two layers of mountant were allowed to harden and the cover slip placed on the specimen with the addition of a third layer.

The diagram shown (Fig. 2) on page 19 illustrates the procedures followed for preparations of chironomids on slides at the Museum of Zoology, University of Bergen, Bergen, Norway.

Larvae and pupae

Larval heads and pupae were first cleared of musculature in hot (near boiling) 8 % potassium hydroxide for three to forty-five minutes and together with the pupal exuviae were treated like the adult bodies.

Larval and pupal exuviae

Larval and pupal exuviae were placed directly into glacial acetic acid and treated like the adult bodies.

Adults obtained from laboratory rearing and their associated larval and pupal exuviae were mounted on one slide using seven cover slips [the extra two cover slips for pupae and larval exuviae] to prevent future loss of association. The cephalothorax of pupal exuviae was separated from the abdomen and the two sides spread out horizontally in order that the features of the abdominal segment as well as that of the cephalothorax itself could be easily distinguished.

Identification

Having made slides, the chironomids were identified by means of a phase contrast microscope (Laborlux k) using the identification keys in Pinder and Reiss (1983, 1986) and Cranston *et al.*, (1989).

Calibration of microscope

Measurements were taken using a phase contrast microscope (Laborlux K) equipped with a drawing tube. An eye piece scale was calibrated using a calibrated micrometer slide. The slide scale of 2 mm long was subdivided into 20 units of 0.1 mm each. Gradations on the eye piece scale were matched with those of the micrometer scale. The point where both intervals coincided perfectly was read for both scales. This procedure was carried out for each magnification of the microscope. The length corresponding to 0.1 unit of the eye piece was calculated for each magnification using simple proportion (Table 1).

Table 1. Conversion of gradations on measuring piece to calculated values in mm and μm.

Magnification of objective lens	4x	10x	25x	40x
Reading on eye piece scale /units	0.5	0.5	1.6	1.0
Reading on calibrated scale /mm	0.1	0.04	0.05	0.02
Calculated value on eye piece scale/mm	0.2	0.08	0.03125	0.02
Calculated value on eye piece scale /μm	200	80	31.25	20.0

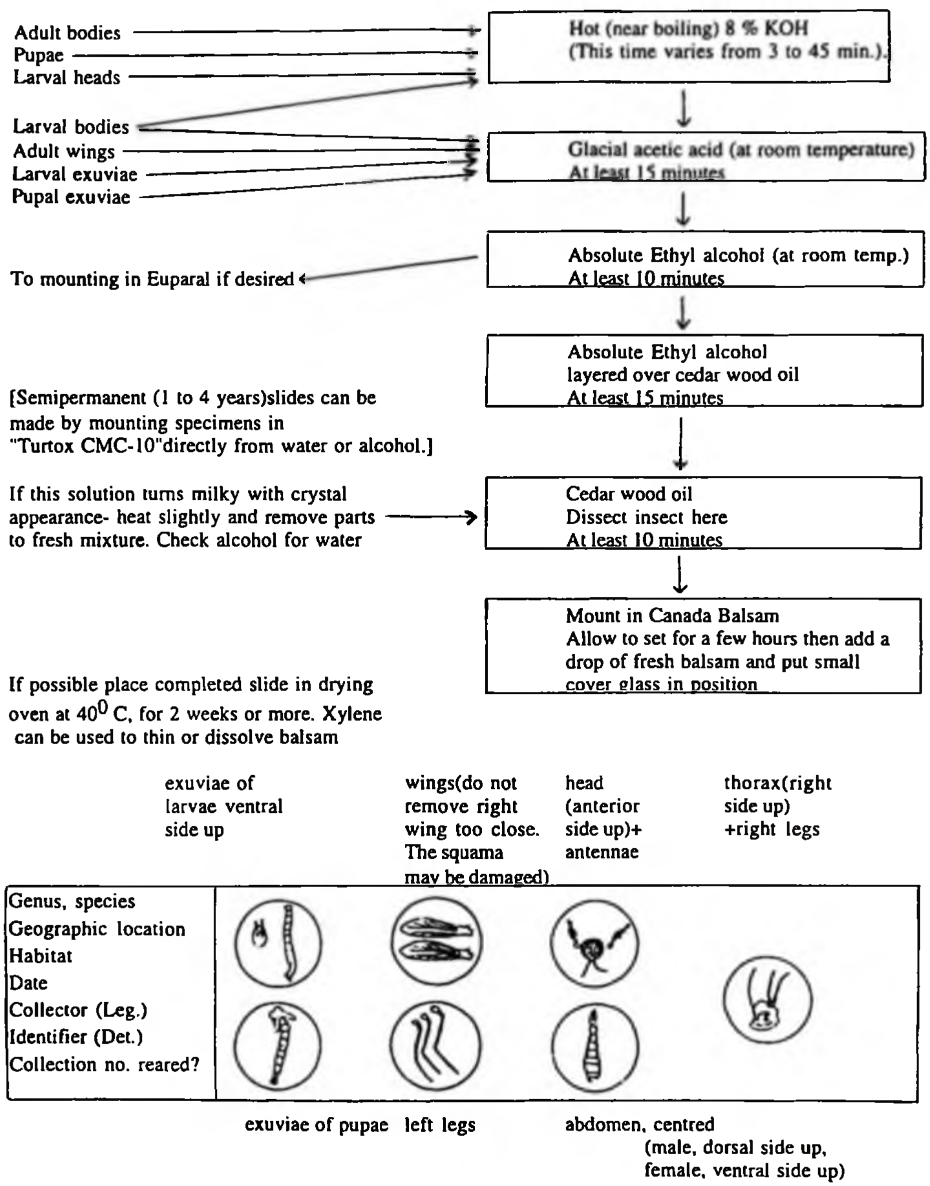

Fig. 2. Scheme of mounting procedures

Morphology and terminology

Morphology nomenclature follows Sæther (1980a) with the additions mentioned in Sæther (1990b) and illustrated in Wiederholm (1983, 1986, 1989). The terminology, as well as some abbreviations commonly used in the study of chironomids will appear from the list of measurements and ratios as well as from Figs 3 and 4.

Measurements and ratios

Measurements and ratios used are described below and shown in Figs 3 and 4. All measurements are given as ranges in mm for the total and wing lengths, in µm for the remaining measurements, followed by a mean when 4 or more specimens are measured, followed by the number measured in parentheses (n).

Measurements

Total length (TL): maximum length of thorax plus the length of abdomen (LAbdomen) measured from concave end of midline of tergite 1 to apex of gonostylus (Fig. 3 E).

Length of thorax (LThorax) is measured from postnotum to apex of scutum in lateral view (Fig. 3 D).

Wing length (WL) is measured from arculus (Ar) to the apex of the wing (Fig. 3 C).

Media length (LM) is measured from arculus to the outer margin of radius - media (RM) (Fig. 3 C).

Cubitus length (LCu) is measured from arculus to the outer margin of the cubital fork [FCu] (Fig. 3 C).

Radius, R, R_1, R_{4+5} setae were counted.

Flagellomeres (Fm) 1-12 were measured from base of first flagellomere which is sunken into the apical depression on the pedicel (Fig. 3 B).

Clypeus setae, dorsocentrals (Dc) and acrostichals (Ac) were counted (Fig 3D).

Temporal setae [IV = inner verticals; OV = outer verticals; PO = postorbitals] were counted.

Tentorium length (LTe) is the longitudinal length of tentorium (Fig. 3 A).

Sieve pore width is the width at area with several holes in the middle of tentorium in the broad part just anterior to narrowing.

Posterior tentorial pit width is the width at the hole in the tentorium near the dorsal, slender end.

Stipes length (LSt) is the longitudinal length of the stipes (Fig. 3 A).

Stipes width is the width at widest part of the stipes.

Palp segment lengths (Pm 1-5) were measured from the base to the apex of each segment (Fig. 3 A).

Length of the longest sensilla clavata (SCl) on each third palpal segment was taken from the base to the apex (Fig. 3 A).

Leg lengths were measured according to Schlee (1966) and not as total lengths (Fig. 3).

Lfe = length of femur; Lti = length of tibia; Lta_1 = length of tarsomere 1; Lta_2 = length of tarsomere 2; Lta_3 = length of tarsomere 3; Lta_4 = length of tarsomere 4; Lta_5 = length of tarsomere 5).

Length of spurs on the legs and width at apex of fore- mid- and hind tibia were measured.

The length of the projections of the male tergite IX are measured as shown in Fig. 4 B (anterior projection = LAP, median projection = LMP, g = length of anterior projection from base to apical division of projection).

The widths of the projections of male tergite IX are measured as shown in Fig. 4 B (f = width of anterior projection at base, h= width of posterior projection at base, i = width of posterior projection at apex).

The anal point length is measured as shown in Fig. 4 A (LAnp), the basal width as in Fig. 4A (d), and the apical width as in Fig. 4 A (e).

The length of the gonocoxite (LGc) is measured as shown in Fig. 4 B.

The length of the gonostylus (LGs) is measured as shown in Fig. 4 B.

The length of the superior volsella is measured as a+b in Fig. 4 A.

The length of the median volsella is measured as c in Fig. 4 A.

The length of the inferior volsella (LIVo) is measured as shown in Fig. 4 A.

The length of the phallapodeme (LPha) is measured as shown in Fig. 4 B.

Ratios

AR, antennal ratio: length of apical elongated flagellomere (Fig. 3 B, LFm_{13}) divided by combined length of basal flagellomeres (Fig. 3 B, LFm_{1-12}).

TL /WL: total length to wing length.

VR, venarum ratio: ratio of length of Cu (Fig. 3 C, LCu) to length of M (Fig. 3 C, LM).

WL / Pfe: ratio of wing length to length of profemur measured along median line.

LR, leg ratio: ratio of metatarsus (tarsomere 1) to tibia.

BV (Beinverhaltnisse): ratio of combined length of femur, tibia and basitarsus to combined length of tarsomeres 2-5.

SV (Schenkel-Schiene-Verhaltnis): ratio of femur plus tibia to metatarsus.

BR (seta ratio): ratio of longest seta of ta_1 to width of ta_1 measured one-third from apex.

HR, hypopygium ratio: ratio of length of gonocoxite to length of gonostylus.

HV, hypopygium value: total length divided by length of gonostylus times 10 for convenience.

Abbreviations and special terms

(Ap= antepronotum; CP= cibarial pump; Scts = Scutellars; Pc = Pedicel; Pa = Prealars)

Shagreen (spine pattern): pattern of spinules or minute tubercles on abdominal segments.

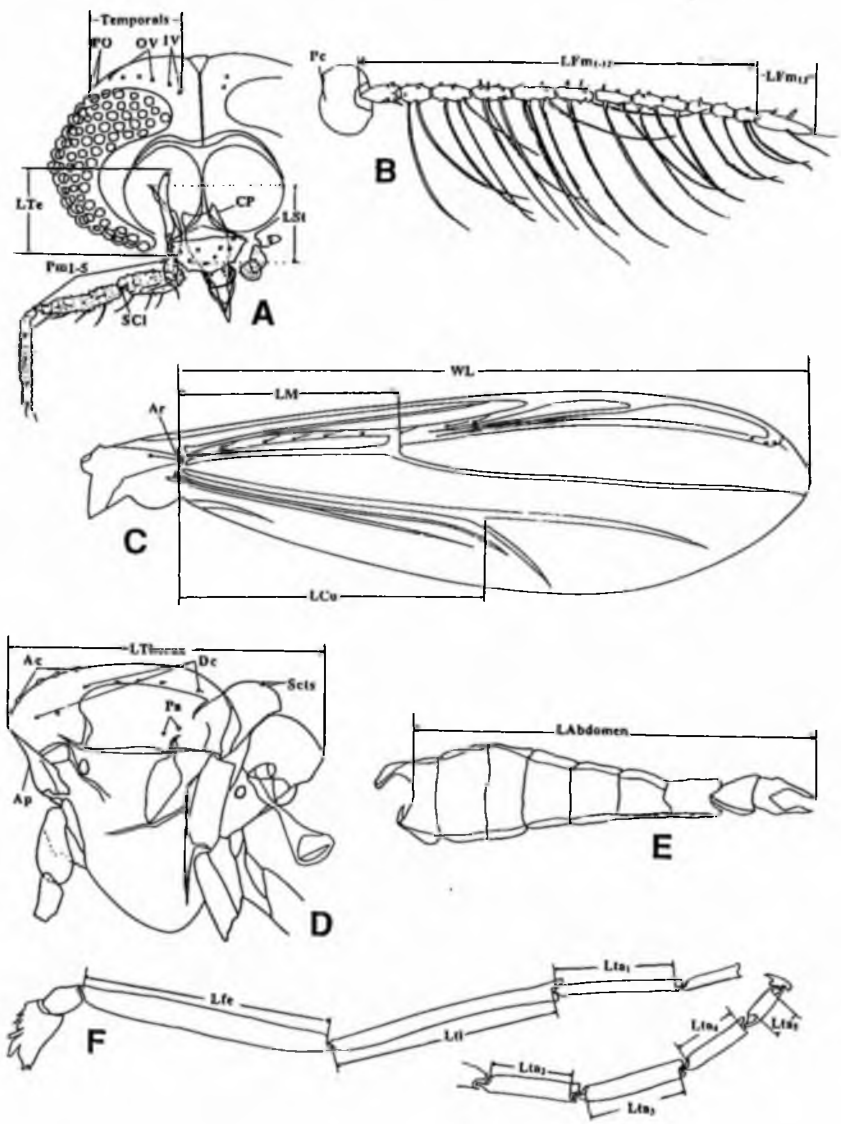

Fig. 3. Illustration of terminology and measurements of *Nilothauma* Kieffer, male imago. — A. Head.— B. Antenna.— C. Wing.— D. Thorax.— E. Abdomen.— F. Leg.

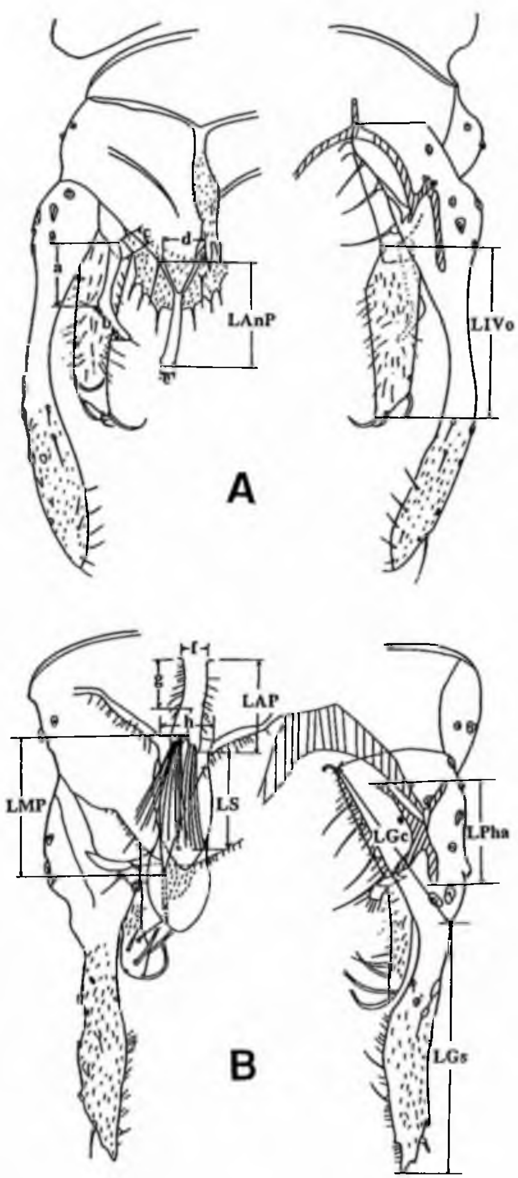

Fig. 4. Illustration of the measurements of *Nilothauma* Kieffer, male hypopygium.—A. sp. n.—B. *N. pictipenne* Kieffer.

Drawings

Drawings of the various structures were made using a phase contrast microscope (Laborlux K) equipped with a drawing tube. The hypopygium was usually drawn under high power (40 X) to get all the details. Pencil drawings made were usually reduced with the aid of a copy machine if too large and fixed into position on A2 sized cards as needed. The drawings on the A2 cards were photocopied onto 2 A3 papers and inked onto a tracing paper using Rotring pens. The drawings on the tracing papers were then reduced to the size required.

The hypopygial figures are drawn to show a dorsal view to the right, the ventral and internal view (of apodemes) to the left.

CHAPTER THREE

LOCALITIES

Specimens were collected from Ankasa Resource Reserve in the Western Region (Plate 2A, B), from Kakum Forest Reserve near Cape Coast in the Central Region (Plates 1; 3 A, B), as well as from Kpong Head Pond at the fish landing site at Kpong, Marine Club on the Volta Lake at Akosombo and Boti falls (Plate 4 A) in the Eastern Region.

Ankasa Resource Reserve

The Ankasa Resource Reserve, located between latitude 5° 17'N and longitude 2° 35'W (Fig. 5), is situated in a wet evergreen forest (as defined by Hall & Swaine, 1981) in the Western Region of Ghana (Fig. 6). It is situated around the area of Ankasa River and has an area of 518.0 sq km. It was set aside as a forest reserve in 1934 but taken over by the Department of Wildlife and made a Resource Reserve in 1976.

The mean annual rainfall in this area usually exceeds 1750 mm, and can be more than 2000 mm in certain places. The forest is floristically very rich with a high diversity of species (Hall & Swaine, 1981). The forest canopy is low and trees rarely exceed 40 meters. The moist conditions of the wet evergreen forest support life forms which are absent or rare elsewhere.

Soils in this area are forest oxysols. Due to the high rainfall, they are severely leached with pH values within 3.8 to 4.3 (Hall & Swaine, 1981). Decomposition rates are high, leaf litter and humus are never abundant; the bulk of the plant nutrients at any time is probably held within the plants (Hall & Swaine, 1981). One (*N. insolita*) of the four species described here was caught at light on a bridge over the Ankasa River (Plate 3), a medium sized river (5-6 meters wide). Water current at the collecting site at the time of sampling was moderate and the

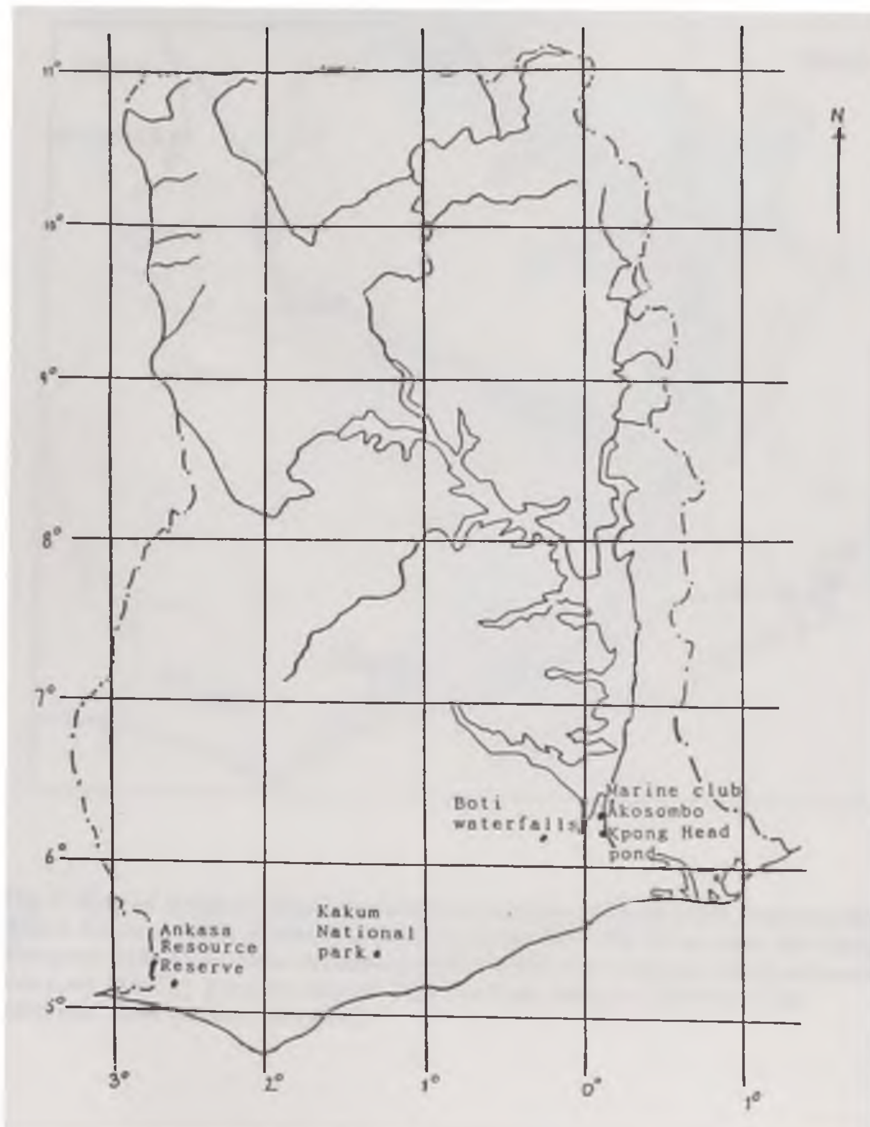

Fig. 5. Map of Ghana showing sampling sites.

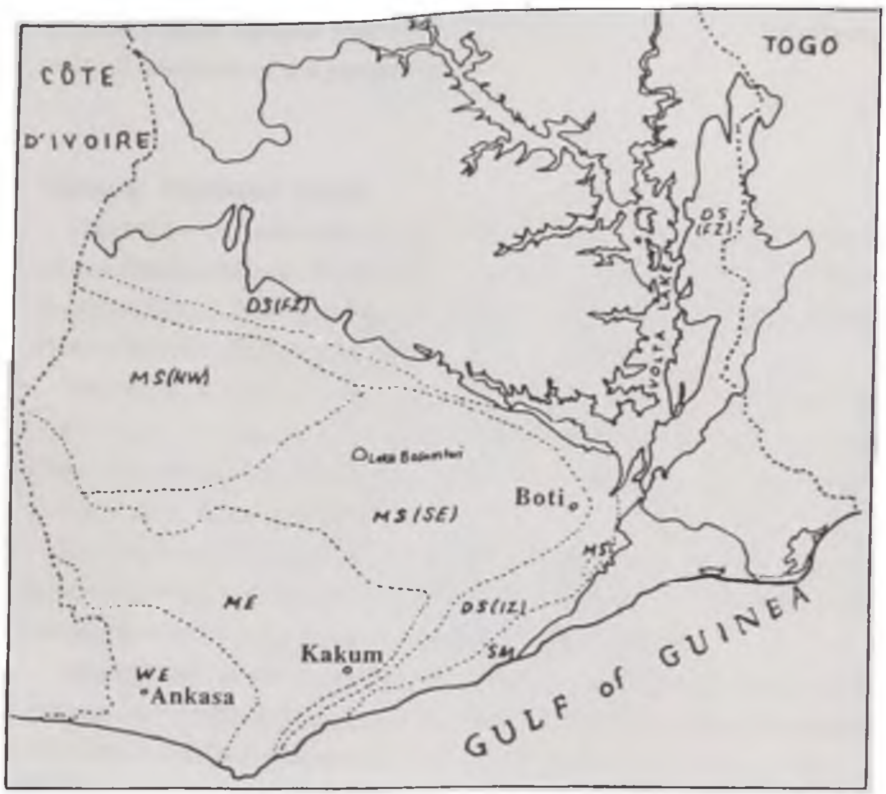

Fig. 6. Map of southern Ghana showing distribution of forest types (redrawn from Hall & Swaine, 1981). Forest-type abbreviations: WE=Wet Evergreen; ME=Moist Evergren; MS=Moist Semi-deciduous (NW=North-west subtype; SE=South-east subtype); DS=Dry Semi-deciduous (FZ=Fire Zone subtype; IZ=Inner Zone subtype); SM=Southern Marginal.

substrate mainly fine sand with some gravel and stones. The river runs through lowland rain forest of wet evergreen type.

Kakum National Park

Nilothauma tricaudata was obtained from a Malaise trap at Kakum National Park located between latitude 5^{o} 26'N and longitude 1^{o} 19'W (Fig. 5) in the Central Region of Ghana. It occupies an area of 212.4 sq km. The area became a Forest Reserve in 1931 and was designated as a National Park in 1991.

The Park is situated in a moist evergreen forest (Plates 1, 4, 5) on hills with many small streams draining into the Kakum River which is the source of water supply for Cape Coast Municipality. The water current of the streams is slow and the substrate is coarse sand, gravel and rocks (Plate1).

The annual rainfall within this zone varies between 1200 and 1800 mm. Soils in this area are forest oxysol-ochrosol intergrades which are poorer in nutrients as compared to the wet evergreen forest (Hall & Swaine, 1981).

Although not as rich as wet evergreen forests, it has a greater floristic diversity. The number of characteristic species is fewer. The tallest trees have an average height of 43 meters. Deciduous trees form only a small portion of the canopy (less than 20%).

Kpong Head Pond

The Kpong head pond is located between latitude 6^{o} 28'N and longitude 0^{o} 14' E in a savanna zone in the Eastern Region of Ghana. The head pond enclosure is completed by west and east dikes which are some 2300 and 3450 m long respectively. The Volta River at Kpong is some 600 m wide and at normal flow has an average depth of 3 m [Volta River Authority (V. R. A.)].

The sampling area is the fish landing site on the Volta River some 24 km downstream from the existing Akosombo dam and 80 km by road from Accra. Over the entire year the variation of the average daily temperature is only 3^{o} C to 6^{o} C. The mean annual rainfall is 1361 mm (V. R. A.).

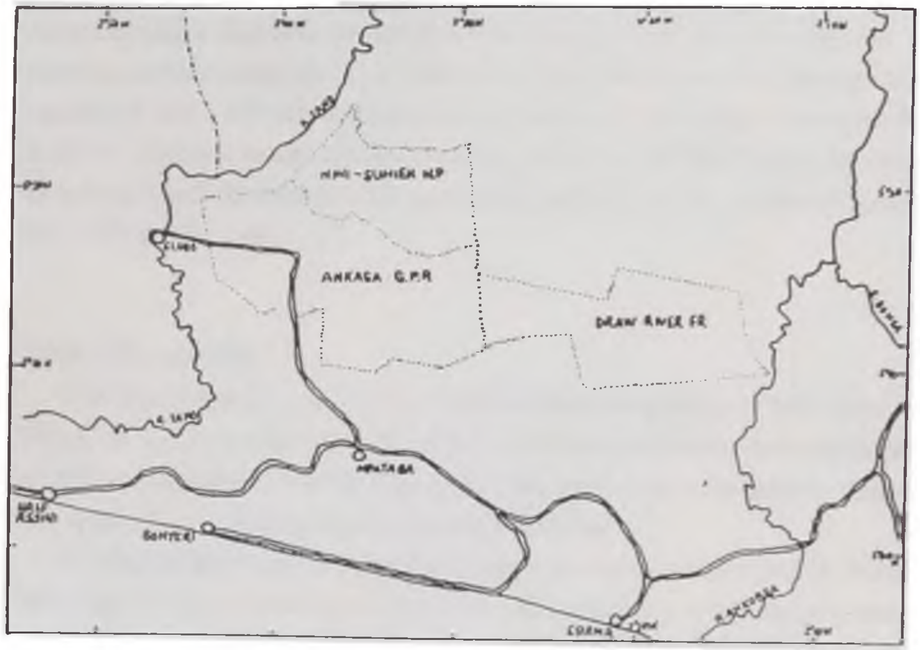

Fig. 7. Map of south-west Ghana showing Ankasa Resource Reserve and some other Forest Reserves. (Redrawn from Hall & Swaine, 1981.)

Marine Club Base

The Marine Club base is situated on Lake Volta at Akosombo. The Lake at Akosombo has a long term average flow of $1160 m^2/s$. The Akosombo dam and reservoir provide a high degree of regulation of this flow; the reservoir having a total capacity of $148 \times 10^9 m^3$. In surface area, the reservoir is the largest man-made lake in the world having an area at normal operation level of $8500 km^2$. The main dam is an earth and rock fill structure with a maximum height of 134 m (Quartey & Allen, Dec.1980 & Feb. 1981)

Boti Waterfalls

Nilothauma flabella was caught in a Malaise trap set up along the edge of the Boti River down the waterfall (Plate 4 A). Boti Waterfalls is located between latitude 6^o 12'N and longitude 0^o 14'W (Figs 5, 6). The forest reserve occupies an area of 1.3 sq km . It was declared as a forest reserve in 1969.

It is situated in a moist semi-deciduous south-east subtype forest (Hall & Swaine, 1981; Fig. 6). Trees in this type of forest are taller than in any other, heights often exceed 50 meters and sometimes 60 meters. The upper canopy which is discontinuous, is dominated by evergreen tree species. The understorey trees are sometimes gregarious (Hall & Swaine, 1981).

Annual rainfall within this forest type varies between 1200 and 1800 mm. The moderate rainfall leads to more depletion of soil nutrients than in forests with lower rainfall. The soil has pH between 5 and 6 (Hall & Swaine, 1981).

Mazumbai Forest Reserve

The Mazumbai Forest Reserve is located on the Kwagoroto Hill in West Usambara, North-east Tanzania. Several streams drain the moist, forest-covered hill. *Nilothauma loba* was caught in a Malaise trap along the Kaputu stream near Mazumbai Forest Reserve on the eastern side of Kwagoroto Hill (Andersen & Johanson, 1993). The stream is surrounded by nearly undisturbed evergreen montane forest (Plate 4 B). Altitude at the trapping site is 1770 m. The width of the stream at the collecting site is 1-2 m, the depth 2-4 cm. Water current is slow and substrate is fine sand and gravel. The water temperature measured varied between 14.6^{o} and 17.6^{o} with a pH of 5.9 (Andersen & Johanson, 1993).

Plate 2. Malaise trap in swampy wet evergreen forest at Ankasa Resource Reserve (Photo J. Kjærandsen.)

Plate 3. Light trap on a bridge over Ankasa River. Type locality for *Nilothauma insolita* sp. n. (Photo J. Kjærandsen.)

Plate 4. A stream in Kakum National Park.

Plate 5. Setting up a Malaise trap in the Kakum Forest.

Plate 6. Boti Waterfalls. Type locality of *Nilothauma flabella* sp. n. (Photo G. E. E. Søli.)

Plate 7. The Kaputu Stream, West Usambara, NE Tanzania. Type locality of *Nilothauma loba* sp. n. (Photo G. E. E. Søli.)

CHAPTER FOUR

RESULTS

Sampling

Four new species of *Nilothauma* were collected from Ankasa Resource Reserve of which one is described here, while one each was collected from Kakum National Park and Boti Falls. Among the larvae collected there was no *Nilothauma*.

Introduction to Systematic Part

The following presentation is in accordance with the rigid setup of modern works on chironomids (see for instance Sæther, 1990b).

The generic diagnostic characters and the generic diagnosis mainly follows Sæther, 1977; Pinder & Reiss, 1983; 1986; and Cranston *et al.*, 1989; Niitsuma 1991; and Sasa, 1993 with the addition of the characters of the four species described here and four additional new species collected in Ghana and to be described later.

The generic description is based upon examination of all available material of *Nilothauma* including undescribed species and Holarctic material.

Nilothauma Kieffer

Nilothauma Kieffer, 1921b: 270.
Kribioxenus Kieffer, 1921b: 270.

Type species: *Nilothauma pictipenne* Kieffer, 1921a, by subsequent monotypy (Kieffer 1921a: 37).

Diagnostic characters

The adult male of *Nilothauma* can be separated from all other genera of Chironomini except *Paranilothauma*, *Neelamia*, and some *Paratendipes* by the presence of 13 antennal segments, low to very low antennal ratio (less than 0.35), bare squama, high VR, anterior tibia with a long spur, combs of middle tibia with one spur and posterior tibia with two spurs. It differs from *Paranilothauma*, *Neelamia* and *Paratendipes* by the presence of at least one anal projection on tergite IX.

The pupa (Fig. 8) differs from other genera of Chironomini by having a thoracic horn consisting of 6 slender, equal-sized filaments; no cephalic tubercles or frontal warts; short and slender frontal setae; anal comb consisting of 1 main spur and 1 to several accessory spurs; and tergite VIII, in addition to a pair of very small anterolateral patches of shagreen, with central field of coarse shagreen.

The very small larva of *Nilothauma* (Fig. 9) is recognizable by the pale mental and mandibular teeth; characteristic mentum with median portion set off from the rest of the mentum and in contact with the anteriorly produced median ends of ventromental plates, median portion with 4 teeth, 2 small median teeth and 2 broad first lateral teeth; eyes touching; and segment 1 of the antenna shorter than the flagellum.

Generic diagnosis

IMAGINES

Small species, with wing length less than 2.5 mm. Body green to golden brown; legs golden brown to brown in some species, fore femur basally and apically with dark ring.

Head and antenna. Eyes bare with dorsomedial parallel-sided extension, almost in contact medially. Male antenna with 13 flagellomeres but last flagellomere very short, only about as long as the three penultimate combined, plume short, antenna female-like. Antennal ratio of male very low; usually less than 0.35. Female antenna with 6 flagellomeres. Frontal tubercles absent. Maxillary palp five segmented, with two long subapical sensilla clavata on third segment. Temporal setae uniserial, consisting of inner verticals, outer verticals and postorbitals.

Thorax. Antepronotal lobes much reduced and dorsally narrowed, occasionally with minute wart on each side of the median suture. Antepronotum usually not visible dorsally. Scutal tubercle absent, scutum not overreaching antepronotum. About 8-16 acrostichals present; 5-15 dorsocentrals widely spaced along scutum; 2-3 prealars; 2-3 scutellars.

Wing. Wing membrane without macrotrichia, finely granular, sometimes with a pattern of dark spots, anal lobe absent. Costa not extended beyond tip of R_{4+5}, ending before wing apex, proximally of M_{1+2}; R_{2+3} ends midway between apices of R_1 and R_{4+5}; Cu_1 strongly sinuate; FCu far distal to RM resulting in the VR being greater than 1.25. R, R_1 and R_{4+5} setose. Squama bare.

Legs. Apex of fore tibia with a narrow conical scale bearing a distinct, long, curved spur at most only slightly offset from the scale. Apical combs of mid and hind tibiae well separated; the former with one short spur and the latter with two short spurs. Mid tarsomere 1 with few (1-4) sensilla chaetica. Pseudospurs absent. Pulvilli very short or absent.

Abdomen. Abdominal tergites with few setae, with tendency for setal arrangement in transverse rows.

Hypopygium. Ninth tergite of male with distinct bands arranged along the anterior tergal margin and medially separated. Tergite IX with at least one anal projection. If more than one projection, the anterior projection is simple or divided and covered with stout, occasionally cleft setae; posterior projection simple and may be covered with setae. Apex of tergite IX usually with crowded group of short setae flanking base of anal point. Anal point present or absent; when present, usually broad and lancet-shaped and slightly bent ventrally. Superior volsella either broadly lobe shaped, densely microtrichiose and with few lateromedian setae, or narrow, free of microtrichia, distally with dense short setae, distolaterally often with long setae on wide tubercle and basolaterally with thin spine. Median volsella very short to moderately long; may be cleft with apical setae, with or without microtrichia and setae. Inferior volsella narrow, medially bent; often microtrichiose with few, very strong, apically plumose setae arising from tubercles which may be branched at the tips. Lateral sternapodeme usually acute angled medially and fused. Transverse sternapodeme absent. Gonostylus narrow, apically tapered to a point and distomedially with few, thin, long setae which may be split apically.

Female genitalia. Gonocoxapodeme VIII straight, ending on gonapophysis VIII. Gonapophysis VIII apparently simple or divided, but ventrolateral lobe vestigial and hidden underneath dorsomesal lobe. Dorsomesal lobe broad, and rounded or straight caudally. Apodeme lobe very weak, perhaps occasionally absent. Tergite IX normal. Gonocoxite IX bare or at most with a few setae. Coxosternapodeme nearly straight. Segment X without setae. Postgenital plate relatively large, triangular. Cerci of moderate size.

Seminal capsules relatively small, oval with distinct cylindrical neck. Spermathecal ducts straight, conspicuously wide.

IMMATURES

As in Pinder & Reiss (1983, 1986). The pupa and larva are illustrated in Figs 8 and 9 respectively.

Generic description

IMAGO

Total length 1.45-4.28 mm. Wing length 0.76-2.40 mm. Total length /wing length 1.69-2.34. Wing length /length of profemur 2.08-2.32.

Head. Antennal ratio (AR) 0.14-0.33. Flagellum with 13 flagellomeres. Temporal setae 6-12.

Thorax. Dorsocentrals 5-16. Acrostichals 8-18 biserial, 2-3 prealars, 2-3 scutellars.

Wing. VR 1.29-1.59. Brachiolum with 0-2 setae. R with 6-13 setae, R_1 with 2-13 setae and R_{4+5} with 2-17 setae.

Legs. LR_1 1.16-1.66, LR_2 0.49-0.70, LR_3 0.49-0.64.

Hypopygium. Number and variation of projections as well as volsellae vary specifically.

IMMATURES

Not examined.

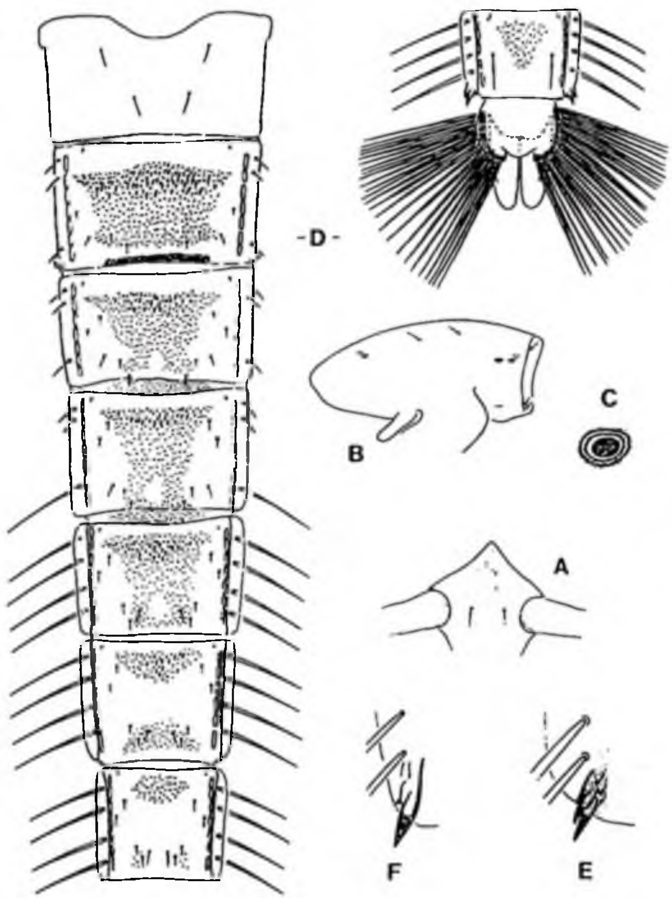

Fig. 8. *Nilothauma*, pupae.—A. Frontal apotome.—B. Thorax.—C. Basal ring.—D. Tergites.—E, F. Anal comb.—A-E. *Nilothauma* sp.; F. *N. brayi* (Goetghebuer). (From Pinder & Reiss, 1986 fig.10.47.)

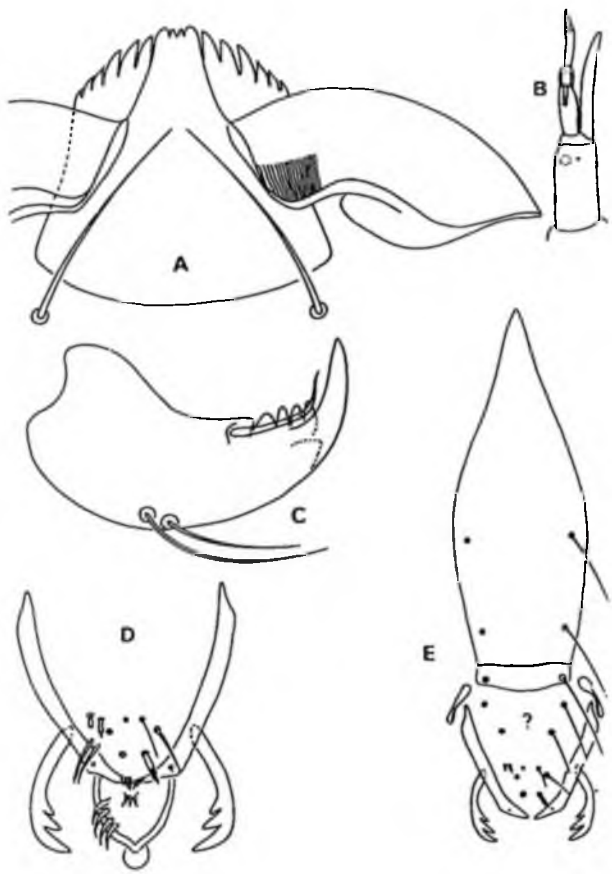

Fig. 9. *Nilothauma brayi* (Goetghebuer), larva. —A. Mentum.—B. Antenna.—C. Mandible.—D. Labro-epipharyngeal region.—E. Dorsal sclerites of head. (From Pinder & Reiss 1983, fig.10.47.)

Systematics

Previously described species

The genus *Nilothauma* Kieffer, 1921, belonging to the tribe Chironomini of subfamily Chironominae presently contain twelve described species in the world. Six are Palaearctic, three Nearctic, two Neotropical and one Afrotropical.

Palaearctic species:

brayi (Goetghebuer, 1921: 173 as *Chironomus*). Europe, Japan.
hibaratertia Sasa, 1993: 73. Japan.
hibaraquarta Sasa, 1993: 74. Japan.
japonicum Niitsuma, 1985: 230. Japan.
jintuprima (Sasa 1990: 32, as *Kribioxenus* comb. n.) Japan.
nojirimaculata Sasa 1991: 86. Japan.

Nearctic species:

babiyi (Rempel, 1937: 274 as *Chironomus*). Canada, USA.
bicorne (Townes, 1945: 35 as *Kribioxenus*). South Carolina.
mirabile (Townes, 1945: 35 as *Kribioxenus*). New York.

Neotropical species:

aleta Roback 1960:101 [= *Paratendipes aleta* (Roback) *nomen dubium*, comb. n.] Peru.
duena Roback 1960: 101 [= *Paratendipes duena* (Roback) *nomen dubium* comb. n.] Peru.

Afrotropical species:

pictipenne Kieffer, 1921a: 37. Sudan, Chad.

As indicated above, two previously described species here are regarded as not belonging to *Nilothauma* since according to the descriptions they lack any projection on tergite IX. They almost certainly belong to *Paratendipes* differing from other species of that genus only in having a low antennal ratio. However, the type material is lost and the species must be regarded as *nomina dubia*.

Phylogeny

The genera *Nilothauma*, *Paranilothauma*, and *Neelamia* apparently form a clearly delimited monophyletic unit characterized by having wing membrane and squama bare, antenna with 13 flagellomeres, AR lower than 0.40, fore tibia with long tapered scale, mid tibia with one spur only, minute pulvilli, median volsella small to absent, and transverse sternapodeme lacking.

The genera *Paratendipes*, *Baerdius* Reiss et Sublette, *Omisus* Townes, *Zavreliella* Kieffer, *Stelochomyia* Reiss, *Lauterborniella* Thienemann et Bause, *Pagastiella* Brundin, and *Polypedilum* Kieffer are related to the *Nilothauma* group of genera as shown by the combination of a long apical spine on the fore tibial scale and 13 flagellomeres, but all have a distinct, often plate-like, transverse sternapodeme, sometimes with oral projections. The squama is bare also in *Baerdius*, *Zavreliella*, *Stelochomyia*, *Lauterborniella*, some *Pagastiella*, and some *Paratendipes*. The antennal ratio is lower than 0.4 only in some *Paratendipes* previously placed in *Nilothauma*. The mid tibia carries one spur only in all the above mentioned genera except in most *Pagastiella* and some *Paratendipes*. The pulvilli are minute in *Paratendipes* only, small to large in the other genera. A median volsella is present in *Paratendipes* only.

The genera *Nilothauma*, *Paratendipes*, *Zavreliella*, *Stelochomyia*, and *Polypedilum* all have some or all species with a pattern of dark spots on the wings and all have at least some species with more or less distinctly ringed tibiae.

The pupae of *Nilothauma, Paranilothauma* and *Paratendipes* all have a thoracic horn with about 6-12 equal-sized filamentous branches (the pupa of *Neelamia* is unknown). Cephalic tubercles and frontal warts are absent except in some *Paratendipes*. Tergite I is bare, T II-VI with extensive and distinct shagreen, T VII and VIII with anterior shagreen in all three genera. Tergite VIII and sternite VIII both have a large central patch of spines in *Paranilothauma* and *Nilothauma*. The row of caudal hooklets on tergite II is continuous, occupying central 1/3 - 2/3. Conjunctives III/IV and IV/V always have a continuous band of shagreen extending onto preceding segment. Segments VI-VIII (V- VIII in *Paranilothauma* and *Nilothauma*) each have 4 taeniate L setae. The caudolateral comb of segment VIII consists of 1-3 larger teeth and 0-5 smaller basal teeth.The anal lobe carries 1 long dorsal subapical seta. The male genital sac extends beyond the anal lobe by 1/2 to its full length.

The larvae are known from only two species of *Nilothauma* and a few *Paratendipes*. These larvae resemble each other in having a mentum with small median teeth. However, the antennae apparently are quite different. *Paratendipes* has a six-segmented antenna with Lauterborn organs on segments 2 and 3, while *Nilothauma* has a 5-segmented antenna with very small Lauterborn organs opposite on segment 2.

Except for the larval characters it will be clear from the above that *Paratendipes* is the most likely sister group of the *Nilothauma* group of genera.

The following attempt to delineate the cladogenesis of the sufficiently known species groups can only be regarded as tentative because of the lack of associated material for many species. Nevertheless, in order to obtain at least a preliminary picture of phylogenetic relationships and to pinpoint future areas of investigations, a tentative scheme of argumentation is desirable (Fig.10). In the figure, trends showing the same directions are grouped. The trends are polarized using series of nested sets in relevant outgroups at each level of analysis, (see for instance Sæther 1983, 1986, 1990a, c). All characters included in the data matrix are judged according to their absence or presence and distribution in outgroups.

The following trends are used (a = apomorphous, p = plesiomorphous):

Trend 1. Anal point absent or when present reduced (parallelism in *hibaratertia* - *mirabile* group) (a); anal point present and not reduced (p).

Trends 2. Anal point absent or when present broad-shaped (a); narrow (p).

— Anterior projection absent or when present long and deeply divided with apical setae (a); absent, short or long, when long undivided and without apical setae (p). (When only one projection is present, this is regarded as the anterior projection).

Trends 3. Anterior projection absent, or when present apical setae fan-like with apical split (a); fan-like without apical split (p).

— Transverse sternapodeme triangular with long median projection (a); well developed with oral projections (p).

Trend 4. Setae at apex of anterior projection thickened at apex, forming fan-shaped groups (a); setae not thickened at apex, with or without fan-shaped groups (p).

Trends 5. Anterior projection absent, or when present apical setae fan-like (a); not fan-like (p).

— Anal point absent or when present broadly lanceolate with transparent margins and with median ridge (a); not broadly lanceolate and without transparent margins and median ridge (p).

— Posterior (or third) projection absent, or when present apically truncate (a); apically rounded, nearly semi-circular or slightly pointed (p).

Trends 6. The placement of *loba* is ambiguous.

— Dorsocentrals 10 or more with acrostical more than 12 (a); 10 or fewer dorsocentrals, 12 or few acrostichals (p).

Trend 7. Median (or second) projection absent, or when present with an apical lobe (a); projection without apical lobe (p).

Trend 8. Wings with a pattern of 5 dark spots (a); without 5 dark spots (p).

Trend 9. Superior volsella somewhat Y-shaped with 5 apical setae (a); not Y-shaped and without apical setae (p).

Trend 10. Median (or second) projection absent, or when present bare (except at base) (a); with microtrichia (p).

Trend 11. Superior volsella apparently bifid at apex (a); single (p).

Trends 12. Median (or second) projection absent, or when present triangular, broad based with pointed apex (a); parallel-sided without conspicuously broad base (p).

— Wing almost semi-circular (a); wing normal shape (p).

Trends 13. Wings with a pattern of dark spots or bands (a); without a pattern of dark spots or bands (p).

— Anterior projection absent, or when present long and deeply divided (a); short or long undivided (p).

Trend 14. Anterior projection absent, or when present completely or nearly completely divided, broader than long (a); divided or undivided, when divided longer than broad (p).

Trend 15. Anterior projection absent, or when present divided (a); undivided (p).

Trend 16. Inferior volsella conspicuously narrow (a), not conspicuously narrow (p).

Trend 17. Tergite IX with 2-3 projections (a), without projection (p).

Trend 18. Anal point absent, or when present parallel-sided (secondarily broadened in an undescribed new species) (a), narrow and tapering (p).

Trends 19. Tergite IX with at least an anal projection (a); without anal projection (p).

— Frontal tubercles absent (a); frontal tubercles present (p).

Trend 20. Antepronotal lobes with medial projection (a); without (p).

Trend 21. Antepronotal lobes widely separated (a); at most slightly reduced, with at least an indication of medial projection (p).

Trend 22. R_1 bare (a); with more than 10 setae (p).

Trends 23. Median volsella small, reduced, vestigial or absent (a); well developed (p).

— Transverse sternapodeme absent or weakly developed without oral projections (a); well developed with oral projections (p).

Trend 24. Inferior volsella curved with sensilla chaetica at apex (a); curved without sensilla chaeticae at apex (p).

Trends 25. Wing membrane bare (a); with setae (p).

— Anal lobe absent or weakly developed (a); anal lobe well developed (p).

— Apex of fore tibia with a spur (a); without a spur (p).

— Squama bare (a); squama setose (p).

— AR lower than 0.4 (a); higher than 0.4 (p).

— Median volsella small to absent (a); well developed (p).

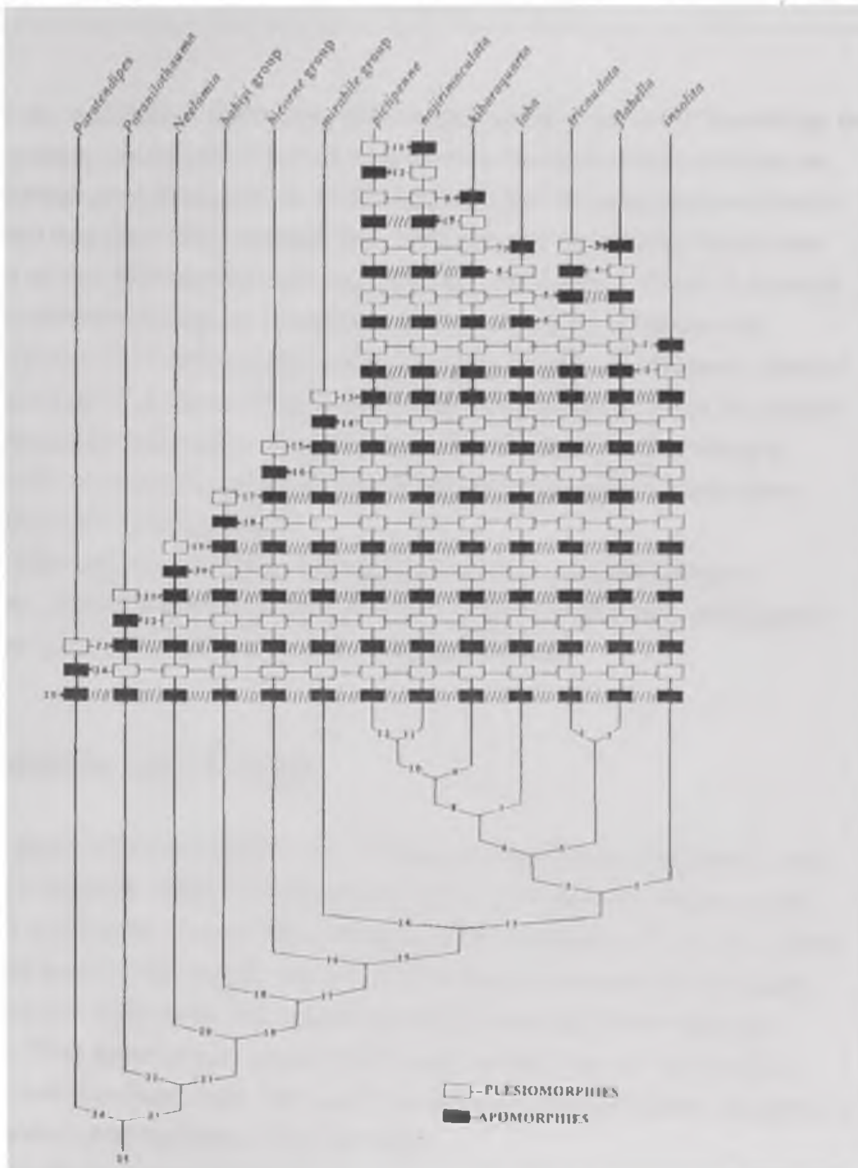

Fig. 10. Scheme of argumentation delineating the cladogenesis of the *Nilothauma pictipenne* group; other groups of *Nilothauma;* the genera *Nilothauma, Neelamia, Paranilothauma*; and *Paratendipes* by means of trends 1-25.

The above analysis is incomplete, particularly because of the lack of knowledge on the immatures and females as well as uncertainty in basing evaluation of trends on insufficiently good descriptions from the literature. The different groups are clearly delimited and undoubtedly monophyletic, but the mutual relationship between the species may be different from that suggested here. For instance, Trend 11, absence of microtrichia on median (or second) projection, used to link *pictipenne* and *nojirimaculata* is a highly uncertain character as it is based on insufficiently detailed drawings from the literature. The *bicorne* group kept together by Trend 16, inferior volsella conspicuously narrow, is also an uncertain character as it is difficult to differentiate between conspicuously narrow and not being conspicuously narrow from drawings of the literature.

The *babiyi* group is clearly the most plesiomorphic based on the imagines. However, when more of the immatures become known the result of a phylogenetic analyses may well be different from the one presented here.

Distribution and Ecology

The genus is widely distributed in the Holarctic, Sino-Indian, Afrotropical, and Australian regions. Of the described species, *N. brayi*, occurs both in Europe and Japan; 3 are Nearctic, 4 are confined to Japan, one Afrotropical and the larvae of the genus are known from western Australia. All the four new species of *Nilothauma* described here are from the Afrotropical region and were caught near rivers or streams. Their immatures are unknown. Similarly, most of the already described species have been caught near lakes and rivers indicating that most likely the genus is truly aquatic, occuring both in rivers and lakes.

The immature stages of the genus are found in the littoral and sublittoral sediments of standing and flowing waters (Cranston *et al.*, 1989). According to Brundin (1949), the larvae can be found in mud at the bottom of the lower littoral zone of Lake Innaren between depths of 4 to 19 m, but were most common at a depth of 4-5

m. The relative density was never higher than 0.6 % at any depth. Goetghebuer (1936) regarded the species as rheophilous in the Ardennes. Material from Sweden shows that *Nilothauma* regularly inhabits lakes. In Småland the larvae have up to now been found in oligo- and mesohumic lakes only. The imagines emerge in July and August. At least one of the species of *Nilothauma* is among the most acid-sensitive taxa disappearing when the pH was artificially lowered below pH 6.0. When the pH was returned to 7.4, the composition and the density of the community of the different species changed rapidly; with the acid-sensitive *Nilothauma* reinvading quickly (Griffiths, 1992).

Key to male imagines of the *Nilothauma pictipenne* group

1. Tergite IX with 2-3 anal projections; anterior projection deeply divided, longer than broad. Wings with a pattern of dark spots or bands 2

—Tergite IX with one anal projection, or when with 2-3 then anterior projection undivided, broader than long. Wings without a pattern of dark spots or band .... other groups of *Nilothauma*

2. Anterior projection with setae not concentrated to apex. Second projection triangular, broad based with truncate apex bearing 6 setae. Anal point absent or secondarily reduced. Wings with 2 dark spots ....*Nilothauma insolita* sp. n.

— Anterior projection with apical setae.Second projection may be triangular and broad based, but without a truncate apex. Anal point present and broad. Wings with 3-5 dark spots.. 3

3. Wings with 5 dark spots or bands 4

— Wings with 3 or 4 dark spots or bands 6

4. Median projection with microtrichia. Superior volsella with broad base bearing microtrichia, 4 apical setae and a sickle-shaped posterior portion with one seta.

Tergite IX with 3 anal projections........... *Nilothauma hibaraquarta* Sasa, 1993

— Median projection without microtrichia (except at base)............................ 5

5. Median (or second) projection apically rounded. Superior volsella long with microtrichia and short, apical setae. Inferior volsella slender, curved and bearing 8-10 short recurved setae .... *Nilothauma nojirimaculata* Sasa, 1991

— Median (or second) projection triangular and apically pointed. Wing almost semi-circular. Median volsella with one apical seta. Anal point very broadly lanceolate with transparent margins and with microtrichia .... *Nilothauma pictipenne* Kieffer, 1921

6. Anal point broadly lanceolate with transparent margins. Anterior projection with long apical setae. Median (or second) projection triangular with apical lobe. Wings with 3 dark spots ....*Nilothauma loba* sp. n.

— Anal point broadly lanceolate with transparent margins and median ridge. Anterior projection with fan-like apical setae 7

7. Fan-like apical setae branched at tips. Wings with a pattern of 4 dark spots....... ....*Nilothauma flabella* sp. n.

— Fan-like apical setae not branched at tips. Wings with a pattern of 3 dark spots or bands .... *Nilothauma tricaudata* sp. n.

Description of species

The described species in the genus fall into four distinct groups based primarily on adult characters. The species groups are the *babiyi*, the *bicorne*, the *mirabile* and the *pictipenne* groups.

babiyi group

Anal tergite of male imagines with one projection only. Wings without a pattern of dark spots or bands. Anal point mostly narrow and parallel-sided, occasionally slightly broadened in the middle. This group includes *N. babiyi* from North America, *N. jintuprima* and *N. japonicum* from Japan. In addition there are two new undescribed species from Ghana.

bicorne group

Anal tergite of male with 2-3 projections, with anterior projection undivided. Inferior volsella narrow. Wings without a pattern of dark spots. This group includes *N. bicorne* from North America, *N. brayi* from Europe and Japan as well as a new species from Zaire and one new species from Ghana.

mirabile group

Anal tergite with 2-3 projections; anterior projection divided, broader than long. Anal point occasionally reduced. Wings without a pattern of dark spots. This group includes *N. mirabile* from North America and *N. hibaratertia* from Japan.

pictipenne group

Anal tergite with 2-3 projections; anterior projection deeply divided, much longer than broad. Anal point very broad, lanceolate with transparent margins. Wings with a pattern of 2-5 dark spots or bands. The group consists of the Afrotropical *N. pictipenne* redescribed here; *N. nojirimaculata* and *N. hibaraquata* from Japan plus three new species from Ghana and one new species from Tanzania described here.

Nilothauma pictipenne Kieffer
(Figs 11, 12)

Nilothauma pictipenne Kieffer, 1921a: 270.

Diagnostic characters: The male imagines differ from other members of the genus in having an almost semi-cicular shaped wing with a pattern of 5 dark spots and from other members of the *pictipenne* group in having a median projection which is apically pointed and having a bare superior volsella.

Material examined: SUDAN, Khartoum, at light, 4 ♂, 2 ♀, x 1957, D. J. Lewis, B. M. 1953-679 (BMNH).

Description

Male imago (n = 4, except when otherwise stated).

Total length 1.81-2.30, 1.94 mm. Wing length 0.78-1.0, 0.85 mm. Total length / wing length 2.19-2.34, 2.28. Wing length / length of profemur 2.08-2.19, 2.13. Colouration: Pale with brown vittae, brown postnotum, brown anepisternum II and lower part of preepisternum brown. Legs pale yellow, femora with a subapical brown band, anterior tibia dark on apical half or third.

Head (Fig. 11 A). AR 0.20(1). Thirteenth flagellomere 84 µm long. Temporal setae 10 (1), in single row; including 2 inner verticals, 5 outer verticals, and 3 postorbitals. Clypeus with 9-16 setae. Tentorium 80-104, 91 µm long; 12-14 µm, 13 µm wide at sieve pore; and 6-10, 8 µm wide at posterior tentorial pit. Stipes 92-118, 103 µm long; 6-22, 13 µm wide. Palp segment lengths (in µm, n= 3): 28-32, 20-26, 60-72, 76-108, 108-124. Third palpal segment with 2 sensilla clavata, longest 12-23 µm (3). Fifth palpal segment/ third palpal segment 1.72-1.90 (3).

Thorax (Fig. 11 B). Dorsocentrals 11-16 (3), in single row; acrostichals 14-16 (3), in double row on front portion of scutum; prealars 2. Scutellum with 2 setae.

Wing (Fig. 11 C). VR 1.48-1.57, 1.51. Brachiolum with 1-2 setae; R with 9-12, 10 setae; R_1 with 3-5, 4; and R_{4+5} with 9-10 setae including pair at apex in some

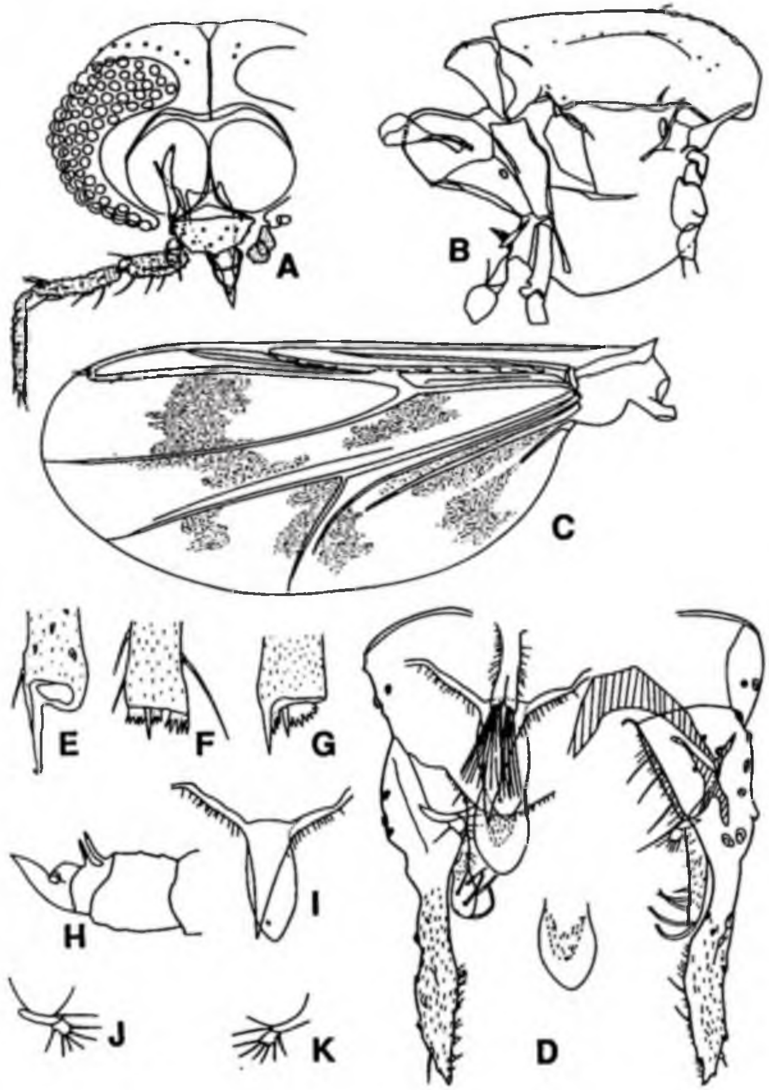

Fig. 11. *Nilothauma pictipenne* Kieffer, male imago. —A. Head. —B. Thorax. —C. Wing. — D. Hypopygium, dorsal view to the left, ventral view and apodemes to the right, anal point below. —E-G. Apices of front, middle and hind tibiae. —H. Hypopygium, lateral view. —I. Median and posterior projections of tergite IX. —J, K. Superior and median volsellae, dorsal (J) and ventral (K) views.

specimens. Remaining veins bare. Wing almost semi-circular shaped. Wing membrane brownish with 5 dark spots.

Legs (Figs 11 E-G). Spur of front tibia 34-36 µm (3) long including a scale each of 16-18 µm long; spur of middle tibia 16-22, 20 µm long; hind tibia with two spurs 18-22, 20 µm and 20-24, 22 µm long. Combs of middle tibia 10-14, 13 µm long; of hind tibia 12-20, 16 µm long. Width at apex of front tibia 29-37 µm (3); of middle tibia 31-39 µm (3); of hind tibia 35-41, 38 µm. Sensilla chaetica 2 at 0.61 and 0.84 (1) of ta_1 of middle leg. Leg lengths and proportions as in Table 2.

Table 2. Lengths (in µm) and proportions of legs (n=3 for p_1, n=2 for ta_1-ta_2 for p_2, p_3 and n=1 for ta_3-ta_5 for p_2, p_3) of male imago of *Nilothauma pictipenne* Kieffer.

	fe	ti	ta_1	ta_2	ta_3
p_1	356-463, 405	272-284, 277			
p_2	353-453, 388	263-288, 274	166-200	69-88	66
p_3	388-475, 416	400-481, 423	225-284	100-138	125

	ta_4	ta_5	LR	BV	SV	BR
p_1						
p_2	56	50	0.60-0.70	3.63	3.70-3.89	2.89-3.00
p_3	72	47	0.56-0.59	3.25	3.36-3.50	3.67-3.70

Hypopygium (Figs 11 D, H-K). Tergite IX with 3 projections. Anterior projection 33-37 µm (3) long excluding apical setae; 8-16 µm (3) wide at base, with split into two lobes at 0.43-0.59 (3) of length. Each lobe 14-21 µm (3) long excluding setae, 4 µm (3) wide at base, with apical setae 31-39 µm (3) long. Median (or second) projection 35-41 µm (3) long, 18-21 µm (3) wide at base; tapering to 4-6 µm (3) at apex. Posterior (or third) projection 14-29 µm (3) long, 16-21 µm (3) wide at base and apically rounded. The posterior projection is basally fused to the base of the median projection. Anal point very broadly lanceolate with transparent margins and microtrichia, 18-33 µm (3) long, 16-18 µm (3) wide at base, 18-23 µm (3) wide medially and apically rounded. Posterior margin of tergite IX with hair-like setae. Laterosternite IX with 2 strong setae. Phallapodeme 39-53 µm (3) long.

Sternapodeme thickened anterioly. Gonocoxite 57-76 μm (3) long with 4 setae along inner margin. Gonostylus 45-76 μm (3) long. Superior volsella 8-10 μm (3) long with more than 5 apical spines. Median volsella small, 4-6 μm (3) long and apically pointed with one seta. Inferior volsella 33-41 μm (3) long with 5-6 apical setae some of which are branched at the tips. Inferior volsella with microtrichia, superior and median volsellae without microtrichia. HR 0.97-1.27, 1.11; HV 2.40-2.76, 2.54 (3).

Female imago (n=2, except when otherwise stated)

Total length 1.50-1.67 mm. Wing length 0.91-0.99 mm. Total length / wing length 1.65-1.69. Wing length / length of profemur 2.48-2.93. Colouration: As in male.

Head (Fig. 12 A). AR 0.39 (1). Length (in μm) of flagellomeres 26, 26, 32, 34, 26, 56. Temporal setae 9 (1), in single row; including 2 inner verticals, 5 outer verticals, and 2 postorbitals. Clypeus with 16-17 setae. Tentorium 70-80 μm long, 8 μm wide at sieve pore and 6 μm wide at posterior tentorial pit. Stipes 90-96 μm long, 8-18 μm wide. Palp segment lengths (in μm): 24-28, 20, 52 (1), 80 (1), 112 (1). Third palpal segment with 2 sensilla clavata, longest 10-12 μm long.Fifth palpal segment/ third palpal segment 2.15 (1).

Thorax (Fig. 12 B). Dorsocentrals 9-10 in single row, acrostichals 10-16 in two rows, prealars 2 . Scutellum with 2 setae.

Wing (Fig. 12 C). VR 1.44-1.46. Brachiolum with 1 seta (1). R with 11 setae, R_1 with 4 setae and R_{4+5} with 10-15 setae including a pair at the tip, remaining veins bare. Wing almost semi-cicular shaped. Wing membrane brownish with 5 dark spots.

Legs. Spur of front tibia 34 μm (1) long, including 14 μm long scale; spur of middle tibia 22-25 μm long; hind tibia with two spurs about 18-22 and 24 μm long. Combs of middle tibia 14-16 μm long; of hind tibia 14-16 μm long. Width at apex of front tibia 30-32 μm, of middle tibia 34 μm, of hind tibia 36-40 μm. Sensilla chaetica 2 at 0.68 and 0.82 of ta_1 of middle leg. Leg lengths and proportions as in

Table 3.

Table 3. Lengths (in µm) and proportions of legs of female imago of *Nilothauma pictipenne* Kieffer.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	313-400	238-250									
p_2	344-375	263-297	156-163	68-75	56-63	41(1)	38(1)	0.55-0.60	3.75 (1)	3.88-4. 13	2.33 (1)
p_3	366-403	384-441	231-238	106-122	94-116	56-66	47-53	0.54-0.60	3.03-3.24	3.24-3.54	2.40 (1)

Abdomen. Number of setae on tergite I-VIII as: 20-22, 18-20, 10-16, 8-19, 9-20, 9-17, 11-13, 7-11. Number of setae on sternites I-VIII as: 0, 2, 4-7, 1-2, 3-4, 5-13, 11, 13-22.

Genitalia (Figs 12 D-H). Tergite IX with 17-19 setae. Gonocoxite IX with 0-1 seta. Cercus 64-70 µm long. Gonapophysis VIII apparently with vestigial ventrolateral lobe consisting of a few longer microtrichiae and hidden underneath dorsomesal lobe. Apparent apodeme lobe vestigial. Seminal capsule 47-53 µm long including 10-12 µm long neck, about 33-45 µm wide. Notum 76-96 µm long.

Remarks

The species is the same as redescribed by Freeman (1957) except that tergite IX has 3 anal projections; the third projection being more or less fused to the base of the second projection. The inferior volsella has 5-6 apical setae some of which are branched at the tips.

Ecology and distribution

The immatures are unknown. The species is known from Sudan, Chad, (Kieffer, 1921a) and the lower Orange River in South Africa (Dr. A. D. Harrison pers. comm.)

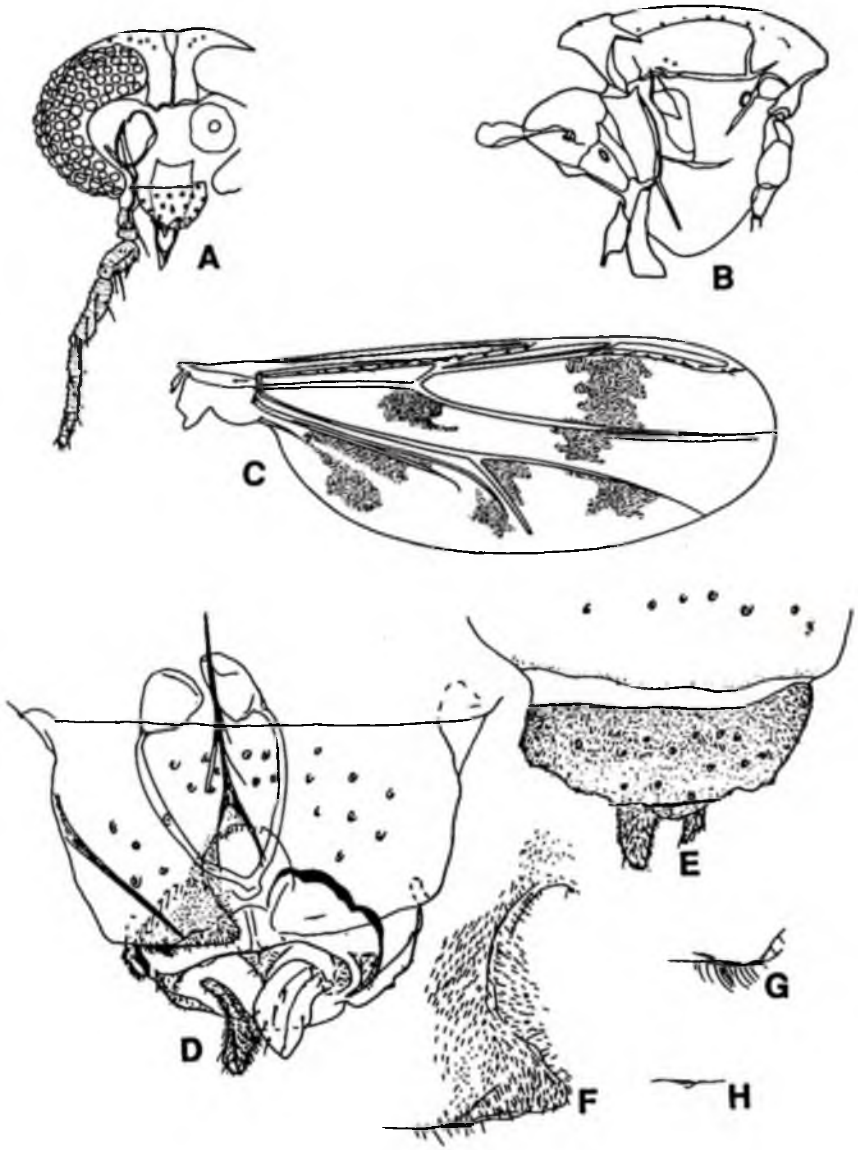

Fig. 12. *Nilothauma pictipenne* Kieffer, female imago. —A. Head. —B. Thorax. —C. Wing.—D. Genitalia, ventral view. —E. Genitalia dorsal view. —F. Dorsomedian lobe of gonapophysis VIII. — G. Ventrolateral lobe of gonapophysis VIII. —H. Apodeme lobe of gonapophyses IX.

Nilothauma loba sp. n.

(Fig. 13)

Type locality: Tanzania, Tanga Region, W. Usambara Mts, Mazumbai.

Type material: Holotype ♂, TANZANIA: Western Usambara Mts, Mazumbai, Malaise trap, 29 XI 1990, ZMB's Tanzania Exp. (ZMBN).

Diagnostic characters: The adult male can be separated from all other species in having a posterior projection which is triangular but rounded at the apex with an apical lobe. The presence of a pattern of 3 dark spots on the wing will also separate the species from other members of the *pictipenne* group except *tricaudata* (described below). It differs from the above species in not having fan-like apical setae at the anterior projection.

Etymology: From the Latin word *lobus*, meaning lobe, referring to the apical lobe of the posterior (or second) projection.

Description

Male imago (n = 1)

Total length 1.79 mm. Wing length 1.06 mm. Total length / wing length 1.69. Wing length / length of profemur 2.32. Colouration: Pale with vittae, postnotum, median anepisternum II and lower part of preepisternum brown.

Head (Fig. 13 A). AR 0.20. Thirteenth flagellomere 91 µm long. Temporal setae 9, in single row; including 1 inner vertical, 5 outer verticals, and 3 postorbitals. Clypeus with 16 setae. Tentorium 86 µm long, 16 µm wide at sieve pore and 8 µm wide at posterior tentorial pit. Stipes 88 µm long, 12 µm wide. Palp segment lengths (in µm): 32, 24, 50, 100, 116. Third palpal segment with 2 subapical sensilla clavata, longest 20 µm long. Fifth palpal segment/ third palpal segment 2.32.

Thorax (Fig. 13 B). Dorsocentrals 8 in single row, acrostichals about 16 in two rows, prealars 2. Scutellum with 2 setae.

Wing (Fig. 13 C). VR 1.51. Brachiolum with 1 seta; R with 12 setae; R_1 with 7; and R_{4+5} with 17 setae, including a pair at tip; remaining veins bare. Wing membrane brownish with 3 dark spots.

Legs (Figs 13 E-G). Spur of front tibia 50 µm long, including a scale of 26 µm long; of middle tibia 28 µm long; hind tibia with two spurs 24 and 30 µm long. Combs of middle tibia 16 µm long, of hind tibia 16 µm long. Width at apex of front tibia 34 µm, of middle tibia 36 µm, of hind tibia 38 µm. Leg lengths and proportions as in Table 4.

Table 4. Lengths (in µm) and proportions of legs of *Nilothauma loba* sp. n.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	456	331		-							
p_2	416	328				-	-				
p_3	506	475	253	131	128	84	56	0.53	3.09	3.88	2.91

Hypopygium (Figs 13 D, H-J). Tergite IX with 2 anal projections. Anterior projection arises from anterior tergal band, 49 µm long to base of long apical setae; 25 µm wide at base; split into two lobes at 0.47 of length. Each lobe 25 µm long to base of setae, 8 µm wide at base of split, narrowing to 4 µm wide at apex. Length of setae 23 µm. Posterior projection 27 µm from base of anterior projection, 37 µm long, 27 µm wide at base and 25 µm in middle. Posterior projection triangular shaped with an apical lobe 18 µm long, 6 µm wide in middle and rounded at apex. Anal point very broadly lanceolate with transparent margins; 33 µm long, 25 µm wide at base, 29 µm wide in middle and rounded at apex. Laterosternite IX with 3 strong setae. Phallapodeme 46 µm long. Sternapodeme is V-shaped with a short median projection. Gonocoxite 76 µm long with 4 setae along inner margin. Gonostylus 104 µm long with apical seta. Superior volsella 24 µm long with 3-5 apical setae. Median volsella small, 14 µm long with 3 or more apical setae. Inferior volsella 54 µm long with 5 apical setae which are branched at the tips. Inferior volsella with microtrichia, superior and median volsellae without microtrichia. HR 0.90 ; HV 2.13.

Remarks

This species appears to be close to *N. pictipenne* in the anterior projection having a split at 0.47 of the length with long apical setae; having a broad, lanceolate anal point with transparent margins; an AR of 0.20; a triangular and broad-based

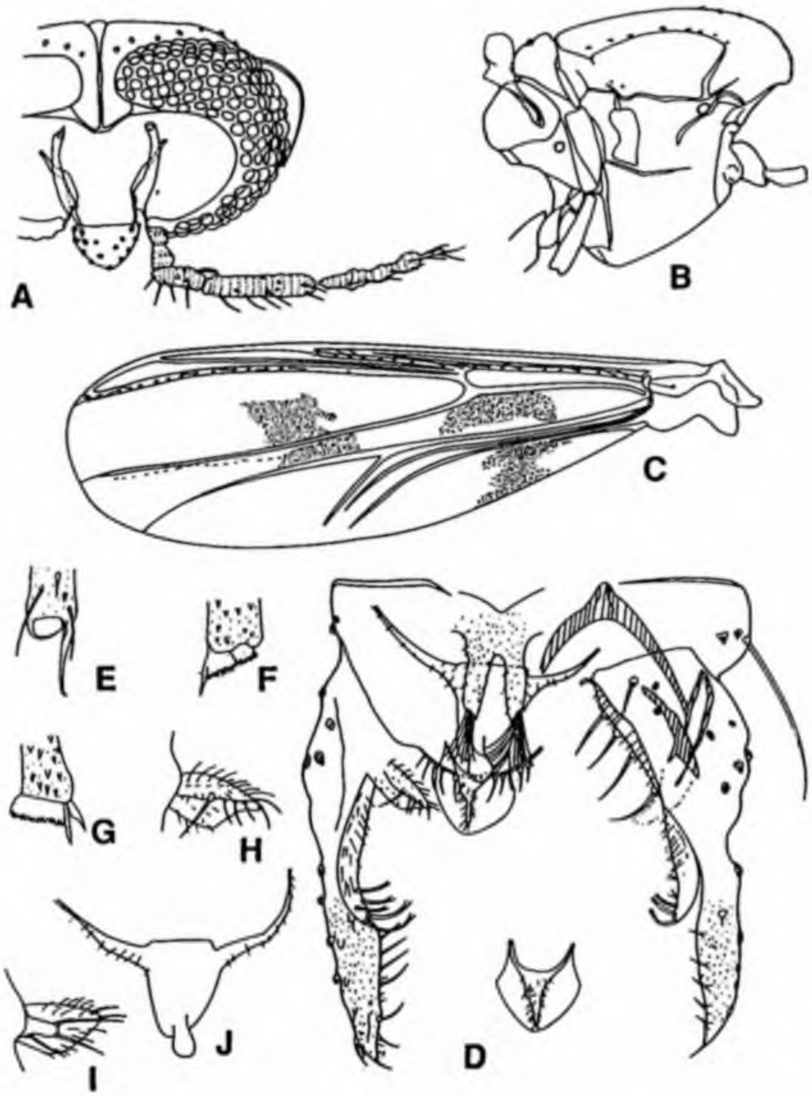

Fig. 13. *Nilothauma loba* sp. n. , male imago. — A. Head. —B. Thorax. —C. Wing. —D. Hypopygium, dorsal view to the left, ventral view and apodemes to the right, anal point below. —E-G. Apices of front, middle and hind tibiae. —H, I. Superior and median volsellae, dorsal (H) and ventral (I) views.—J. Posterior projection of tergite IX.

posterior projection; and wings with a pattern of dark spots. However, the shape of sternapodeme and median volsellae as well as the number of dark spots differ significantly from those of *N. pictipenne*. Also the apex of the posterior projection of this species is rounded with an apical lobe and the wings have a pattern of 3 dark spots.

Distribution

The species is known from the type locality in Tanzania. The specimen was obtained from a Malaise trap at Station 1 along the Kaputu stream near Mazumbai Forest Reserve.

The biology and immature stages are unknown.

Nilothauma tricaudata sp. n.

(Fig. 14)

Type locality: Ghana, Central Region, Kakum Forest Reserve.

Type material: Holotype ♂, GHANA: Central Region, Kakum Forest Reserve, 8-18 XI, 1994, Malaise trap, NUFU Project (ZMBN).

Diagnostic characters: The presence of an anterior projection with fan-like apical setae, truncate apex of the posterior projection and broad, lanceolate anal point with transparent margins and median ridge will separate the species from all members of the genus except *flabella* (described below). It differs from *flabella* in having wings with a pattern of 3 dark spots and triangular, V-shaped sternapodeme with a short median elongation.

Etymology: From the Latin *tri*, three, and *cauda*, tail, referring to the three anal projections.

Description

Male imago (n = 1)

Total length 1.45 mm. Wing length 0.76 mm. Total length / wing length 1.91 Wing length / length of profemur 2.08. Colouration: thorax dark brown with yellowish brown vittae, metanotum, median anepisternum II and lower part of preepisternum. Front femora dark at basal third and apical third, mid and hind femora darker at apical third. Abdomen brown with gonocoxite and gonostylus pale.

Head (Fig. 14 A). AR 0.20. Thirteenth flagellomere 79 µm long. Temporal setae 8, in single row; including 2 inner verticals, 2 outer verticals, and 4 postorbitals.

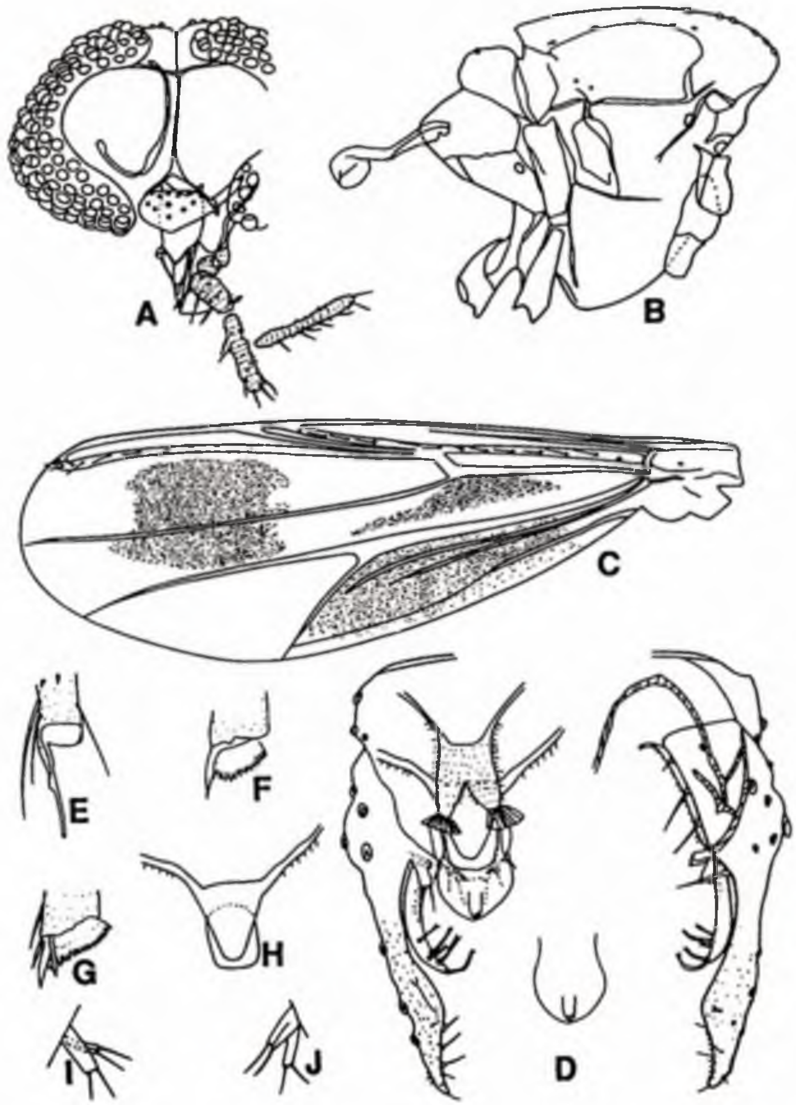

Fig. 14. *Nilothauma tricaudata* sp. n., male imago.—A. Head.—B. Thorax.—C. Wing.—D. Hypopygium, dorsal view to the left, ventral view and apodemes to the right, anal point below. —E-G. Apices of front, middle and hind tibiae.—H. Median and posterior projections of tergite IX. —I, J. Superior and median volsellae, dorsal (I) and ventral (J) views.

Clypeus with 12 setae. Tentorium about 50 μm long, 14 μm wide at sieve pore and 10 μm wide at posterior tentorial pit. Stipes 70 μm long, 6 μm wide. Palp segment, lengths (in μm): 18, 18, 44, 78, 96. Third palpal segment with 2 sensilla clavata, longest 10 μm. Fifth palpal segment / third palpal segment 2.18.

Thorax (Fig. 14 B). Dorsocentrals 5 in single row, acrostichals 12 in two rows on front portion of scutum, prealars 2. Scutellum with 2 setae.

Wing (Fig. 14 C). VR 1.54. Brachiolum without setae, R with 9 setae, R_1 with 4 and R_{4+5} with 9 setae, remaining veins bare. Wing membrane brownish with 3 dark spots.

Legs (Figs 14 E-G). Spur of front tibia 54 μm long including scale of 20 μm, spur of middle tibia 32 μm long, hind tibia with two spurs 26 and 30 μm long. Combs of middle tibia 18 μm long, of hind tibia 18 μm long. Width at apex of front tibia 28 μm, of middle tibia 30 μm, of hind tibia 34 μm. Sensilla chaetica 1 at 0.76 of ta_1 of middle leg. Leg lengths and proportions as in Table 5.

Table 5. Lengths (in μm) and proportions of legs of *Nilothauma tricaudata* sp. n.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	366	219	-								
p_2	353	244	119	50	41	25	22	0.49	5.20	5.03	4.38
p_3	375	353	175	94	100	66	44	0.50	2.98	4.16	4.11

Hypopygium (Figs 14 D, H-J). Tergite IX with 3 anal projections. Anterior projection arises at 33 μm from anterior tergal band. Projection 23 μm long excluding fan-shaped setae at apex, 18 μm wide at base; split into two lobes at 0.34 of length; each lobe 12 μm long to base of setae, 8 μm wide at base of split, narrowing to 6 μm wide at apex. Apical setae 8 μm long, 12-14 μm wide at apex. Median projection triangular, broad based; 10 μm from base of anterior projection, 23 μm long, 21 μm wide at base and 16 μm wide at apex. Posterior projection 10 μm from base of median projection 14 μm long from apex of setae of anterior projection, 21 μm wide at base and truncate at apex. Anal point broadly lanceolate with transparent margins and median ridge; 31 μm long from apex of setae of anterior projection, 33 μm wide at base and rounded apically. Posterior margin of tergite IX with 6 setae. Laterosternite IX with 2 strong setae. Phallapodeme 29 μm long. Sternapodeme V-shaped with a short median projection. Gonocoxite 59 μm long with 4 setae along inner margin. Gonostylus 66 μm long with apical seta. Superior volsella 12 μm long with two apical spines. Median volsella 8 μm long, split into two lobes at apex; each lobe with an apical spine. Inferior volsella 39 μm long, with 5 apically cleft setae. Seta at apex of volsella strongly curved inwards. Inferior volsella with microtrichia, superior and median volsellae without microtrichia. HR 0.91, HV 2.21.

Remarks

This species is close to *N. flabella* described below in having anterior projection with fan-like apical setae, broad, lanceolate anal point with transparent margins and median ridge. There are, however, sufficient differences in the number of dark spots on the wings, and in the shape of the sternapodeme in order to regard them as separate species.

Distribution

The species is known only from the type locality in Ghana. The specimen was obtained from a Malaise trap set up along the banks of a slow flowing stream in the Kakum National Park.

The biology and immature stages are unknown.

Nilothauma flabella sp. n.

(Fig. 15).

Type locality: Ghana, Eastern Region, Boti Falls.

Type material: Holotype ♂, GHANA: Eastern Region, Boti falls, 14 X, 1994. Light trap. NUFU project (ZMBN).

Diagnostic characters: The anterior projection with fan-like apical setae, truncate apex of the posterior projection and broad, lanceolate anal point with transparent margins and median ridge will separate the species from all other species except *tricaudata*. It differs, however, from *tricaudata* in having the fan-like apical setae branched at the tips, wings with a pattern of 4 dark spots and triangular sternapodeme with median projection.

Etymology: From the Latin word *flabellum*, meaning fan, referring to the fan-shaped setae at the apex of the anterior anal projection.

Description

Male imago (n = 1)

Total length 1.53 mm. Wing length 0.77 mm. Total length / wing length 1.99. Wing length / length of profemur 2.14. Colouration: Thorax with brown vittae, metanotum, and lower part of preepisternum. Front femora dark at basal third and apical third, mid and hind femora dark at apical third. Tibiae with indication of dark basal and apical rings.

Head (Fig. 15 A). AR 0.22. Thirteenth flagellomere 88 µm long. Temporal setae 6, in single row; including 2 inner verticals, 2 outer verticals, and 2 postorbitals. Clypeus with 12 setae. Tentorium 70 µm long, 12 µm wide at sieve pore and 8 µm wide at posterior tentorial pit. Stipes 86 µm long, 12 µm wide. Palp segment lengths (in µm): 24, 20, 50, 82, 110. Third palpal segment with 2 subapical sensilla clavata, longest 12 µm. Fifth palpal segment / third palpal segment 2.2.

Thorax (Fig. 15 B). Dorsocentrals 5 uniserial, acrostichals 10 biserial, on front portion of scutum, prealars 2. Scutellum with 2 setae.

Wing (Fig. 15 C). VR 1.53. Brachiolum with 1 seta; R_1 with 4 setae; R_{4+5} with 9 setae, including apical pair; remaining veins bare. Wing membrane brownish with 4 dark spots.

Legs (Figs 15 E-G). Spur of front tibia 44 µm long, including scale of 24 µm long; spur of middle tibia 26 µm long, hind tibia with two spurs of 24 and 28 µm long. Combs of middle tibia 14 µm long, of hind tibia 16 µm long. Width at apex of front tibia 28 µm, of middle tibia 31 µm, of hind tibia 32 µm. Sensilla chaetica 1 at 0.64 of ta_1 of middle leg. Leg lengths and proportions as in Table 6.

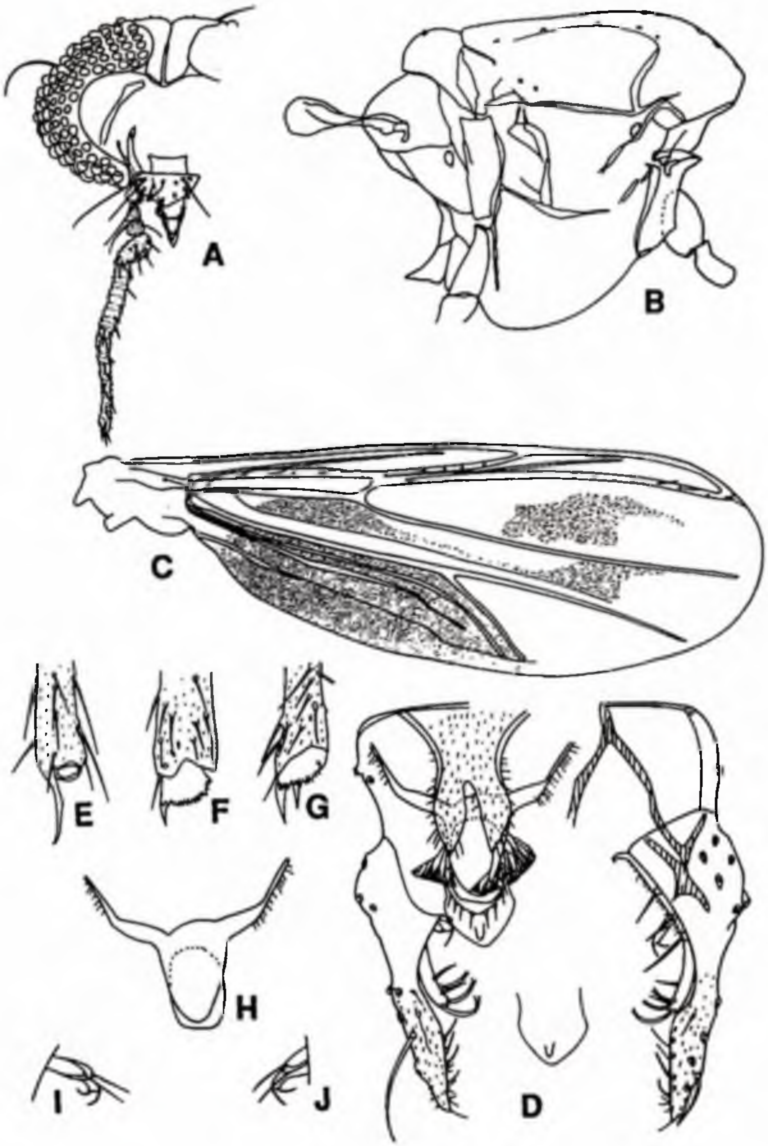

Fig. 15. *Nilothauma flabella* sp. n., male imago. —A. Head.—B. Thorax. —C. Wing.—D. Hypopygium, dorsal view to the left, ventral view and apodemes to the right, anal point below. —E-G. Apices of front, middle and hind tibiae. —H. Median and posterior eprojections of tergite IX. — I, J. Superior and median volsellae, dorsal (I) and ventral (J) views.

Table 6. Lengths (in µm) and proportions of legs of *Nilothauma flabella* sp. n.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	359	250	359	144	113	88	53	1.44	2.44	1.70	
p_2	353	256	125	53	41	28.	25	0.49	5. 00	4. 88	
p_3	384	359	178	97	100	66	47	0.50	2.98	4. 18	

Hypopygium (Figs 15 D, H-J). Tergite IX with 3 anal projections. Anterior projection arises from anterior tergal band, 59 µm long to base of setae, 47 µm wide at base, with split at 0.48 of length into two lobes; each lobe 29 µm long excluding length of apical setae, 10 µm wide at base and 6 µm wide at apex. Width of anterior projection before split 25 µm. Each lobe bears apical fan shaped, 16 µm long setae branched at the tips. Median projection 33 µm from base of anterior projection; 37 µm long, 16 µm wide at base, 12 µm wide at apex. Median projection triangular shaped, broad based, with bluntly rounded apex. Posterior projection 21 µm long from apex of setae of anterior projection, 25 µm wide at base and apically truncate. Anal point broadly lanceolate with transparent margins and median ridge; 25 µm long, 25 µm wide at base and apically rounded. Laterosternite IX with 2 strong setae. Phallapodeme 41 µm long. Sternapodeme triangular with a long median projection. Gonocoxite 53 µm long with 3 setae along inner margin. Gonostylus 64 µm long, with an apical seta. Superior volsella 10 µm long, with two apical spines. Median volsella 4 µm long, split into two lobes apically, each with an apical spine. Superior and median volsellae without microtrichia. Inferior volsella 35 µm long with 5 setae, some apically cleft. Inferior volsella apparently without microtrichia. HR 0.84, HV 2.41.

Remarks

Except for the number of dark spots on the wings, the shape of the sternapodeme and the branching of the anterior projection fan-like apical setae at the tips, this species could conceivably be conspecific with *N. tricaudata*. However, the differences are quite significant to describe them as separate species. Furthermore, the two species were collected from different localities.

Distribution

The species is known from the type locality in Ghana. The specimen was caught in a Malaise trap along the banks of The Boti River below the water fall.

The biology and immature stages are unkown.

Nilothauma insolita sp. n.

(Fig. 16)

Type locality: Ghana: Western Region, Ankasa Resource Reserve.

Type material: Holotype ♂, GHANA: Western Region, Ankasa Resource Reserve, 10-12 XII, 1993, at light, NUFU Project (ZMBN).

Diagnostic characters: The adult male differs from other members of the group in anal point being absent or secondarily reduced, anterior projection deeply divided but with setae not concentrated to the apex, second projection triangular, broad based, with truncate apex bearing setae and wings with 2 dark bands.

Etymology: From the Latin word *insolitus,* meaning odd referring to the strange nature of the species in not having an anal point.

Description

Male imago (n = 1)

Total length 1.71 mm. Wing length 0.79 mm. Total length / wing length 2.16. Wing length / length of profemur 2.11. Colouration: thorax pale brown with blackish vittae metanotum and median anepisternum with black spot. Abdomen brown with hypopygium pale. Legs pale.

Head (Fig. 16 A). AR 0.20. Thirteenth flagellomere 81 µm long. Temporal setae 7, in single row; including 2 inner verticals, 2 outer verticals, and 3 postorbitals. Clypeus with 13 setae. Tentorium about 52 µm long, 12 µm wide at sieve pore and

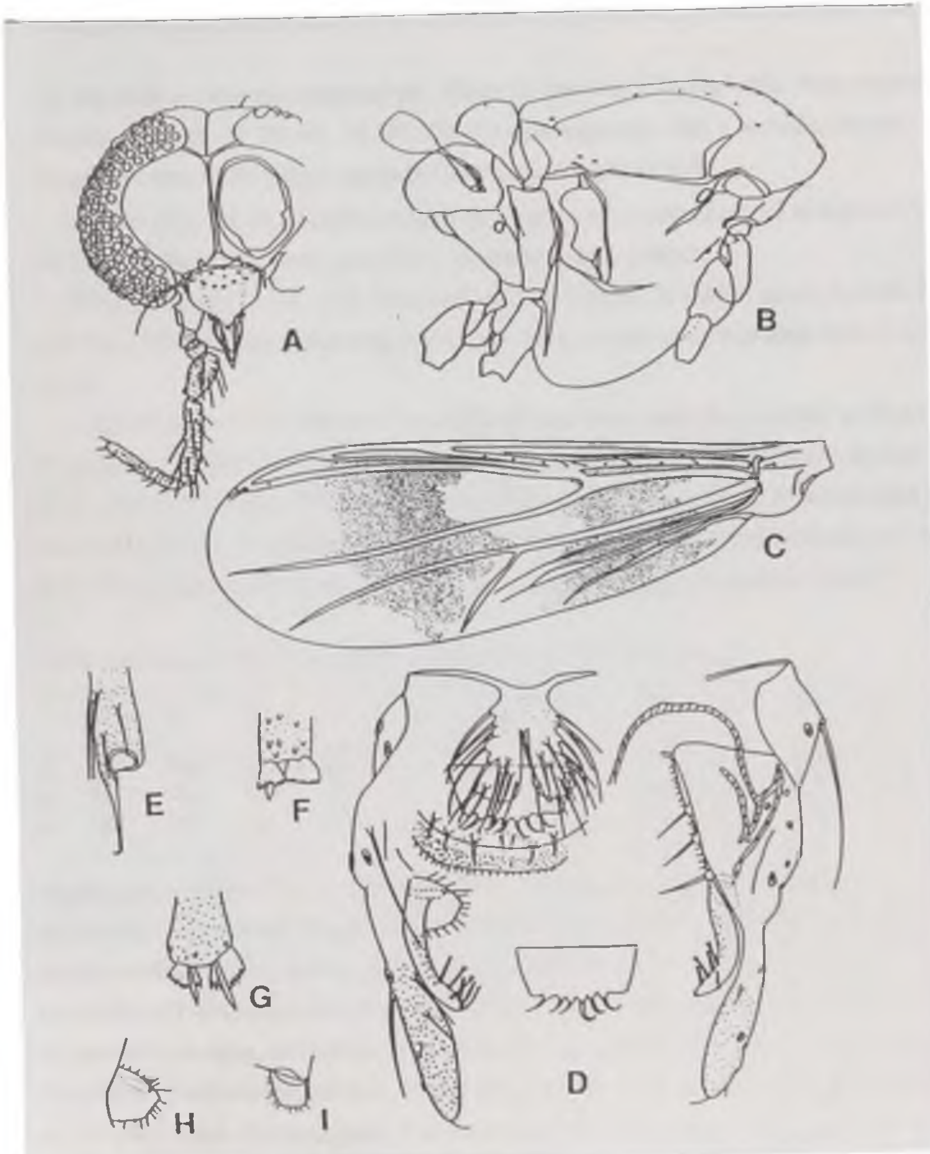

Fig. 16. *Nilothauma insolita* sp. n., male imago. —A. Head. —B. Thorax. —C. Wing. —D. Hypopygium, dorsal view to the left, ventral view and apodemes to the right, posterior projection of tergite IX below. —E-G. Apices of front, middle and hind tibiae. —H, I. Superior and median volsellae, dorsal (H) and ventral (I) views.

10 µm wide at posterior tentorial pit. Stipes 55 µm long, 12 µm wide. Palp segment lengths (in µm): 18, 20, 48, 86, 90. Third palpal segment with 2 sensilla clavata, longest 16 µm. Fifth palpal segment /third palpal segment 1.88.

Thorax (Fig. 16 B). Dorsocentrals 9 in single row, acrostichals 12 in two rows on front portion of scutum, prealars 2. Scutellum with 2 setae.

Wing (Fig. 16 C). VR 1.45. Brachiolum with 2 setae. R with 6 setae, R_1 with 2 and R_{4+5} with 2 setae, remaining veins bare. Wing membrane brownish with 2 dark bands.

Legs (Figs 16 E-G). Spur of front tibia 50 µm long, including a scale of 20 µm long spur, of middle tibia 28 µm long, hind tibia with two spurs of 22 and 26 µm long. Combs of middle tibia 18 µm long, of hind tibia 16 µm long. Width at apex of front tibia 28 µm, of middle tibia 30 µm, of hind tibia 32 µm. Sensilla chaetica 1 at 0.77 of first tarsomere of middle leg. Leg lengths and proportions as in Table 7.

Table 7. Lengths (in µm) and proportions of legs *Nilothauma insolita* sp. n.

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	375	244	375	141	106	72	56	1.54	2.65	1.65	5.8
p_2	344	244	131	56	41	25	25	0.54	4.89	4.48	5.0
p_3	366	347	172	103	91	69	53	0.50	2.80	4.15	5.4

Hypopygium (Figs 16 D, H, I). Tergite IX with 3 anal projections. Anterior projection 37 µm long, 18 µm wide at base, setose, split into two lobes at 0.27 of length; each lobe 27 µm long, 10 µm at base and 12 µm wide at apex. Median projection 23 µm from base of anterior projection, 18 µm long, 37 µm wide at base, 31 µm wide at apex, with short, stout apical setae. Posterior projection 51 µm long from base of anterior projection, 16 µm long, 39 µm wide at base, apically rounded with 7 stout setae. No anal point. Laterosternite IX with 2 setae. Phallapodeme 29 µm long. Sternapodeme not thickened and anteriorly rounded. Gonocoxite 64 µm long, with 3 setae along inner margin. Gonostylus 86 µm long ending bluntly at apex with a seta. Superior volsella 12 µm long with brush-like hairs along margins. Median volsella 4 µm long, with apical spine. Inferior volsella 43 µm long, curved and bearing 6 apical setae which are split at tips. Inferior volsella with microtrichia, superior and median volsellae without microtrichia. HR 0.74, HV 1.99.

Remarks

This species is quite unusual as a member of the genus in lacking an anal point. However, the wings have a pattern of 2 dark spots, the anterior projection is deeply divided and longer than broad, i. e. as members of the *pictipenne* group but without apical setae. More material of the species is needed for further evaluation.

Distribution

The species is known from Ankasa Resource Reserve in the Western Region of Ghana. The specimen was collected at light on a bridge over the Ankasa River.

The biology and immature stages are unkown.

CHAPTER FIVE

DISCUSSION

Zoogeography

Despite the fact that the phylogeny of the *Nilothauma* group of genera (*Nilothauma*, *Neelamia* and *Paranilothauma*) may not be fully solved, it is possible to draw some conclusions about the place of origin of the genera and the zoogeographical distribution and likely dispersals.

Past distribution processes combined with evolution have led to present day distribution patterns of insect species (Williams & Feltmate, 1992). For convenience, and the furtherance of zoological research, Bănărescu (1992) has delimited the following accepted eight zoogeographical regions for the entire freshwater fauna, the first two being subdivided:

(1). **The Holarctic Region** comprising the Eastern, Western and Arctic North America, as well as the Mexican subregions, the Euro-Mediterranean, the Siberian, Baikal and Mongolian subregions.

(2). **The Sino-Indian Region** made up of East Asia, High Asia, South Asia or Indo-Malaysian subregions and Western Asia representing an intermediary area between the Holarctic and Sino-Indian regions.

(3). **The Afrotropical Region.**

(4). **The Malagasy Region.**

(5). **The Neotropical** or **South American Region** consisting of Central America and the Antilles being an intermediary area between this and the Holarctic region.

(6). **The Australian region.**

(7). **The New Zealand Region.**

(8). **The Indo-West Pacific Region**, as "Indo-West Pacific peripheral areas", alongside the circum-Antarctic islands.

The phyletic relationships among the species of *Nilothauma* and the genera *Nilothauma*, *Neelamia*, *Paranilothauma* and *Paratendipes* are as depicted in the cladogram shown in Fig. 10. Substitution of the names of species and genera with their respective areas of endemism gives an area cladogram (Fig. 17). The presence of the larvae of *Nilothauma* in Western Australia (Cranston *et al.*, 1989) shows that the *Nilothauma* group of genera appears to be present in five of the eight zoogeographical regions, hence is of cosmopolitan distribution and certainly of Pangaeic origin (Laurasia and Gondwana combined).

Paratendipes is cosmopolitan in distribution as it is found in all the three super-regions (Megagaea, Neogaea and Notogaea) accepted in classical zoogeography. The Neotropical group of genera (*Neelamia* and *Paranilothauma)* appears to have split off very early with the fragmentation of Pangaea.

The species of *Nilothauma* treated here are of Megagaeic lineages and are confined to the Holarctic, Sino-Indian, Afrotropical and Australian zoogeographical regions for freshwater fauna.

The *babiyi* group is made up of 2 Afrotropical, 1 Holarctic and 1 Sino-Indian species. *N. babiyi*, and *N. japonicum* limited to North America (Holarctic region) and Japan (Sino-Indian region) apparently are sister species. Two as yet undescribed apparent sister species are exclusively Afrotropical and from the same locality in Ghana, indicating that some speciation also may have taken place more recently or perhaps sympatrically. The group apparently first speciated with the fragmentation of Megagaea.

In the *bicorne* group, *N. bicorne* and *N.* brayi occur in the Holarctic region, while there are two as yet undescribed Afrotropical species. However, *N. brayi* has also been described from Japan in the Sino-Indian zoogeographical region by Sasa (1985). This group is also of a Megagaeic lineage. However, dispersal to some extent has probably taken place. Arguments have been advanced that most dispersals of freshwater fauna between East Asia and Europe took place by a northern, Siberian route; that only certain lineages of rheophilic aquatic insects dispersed by a southern central Asian route. Whether dispersal of the species is by a Siberian or by a Southern Central Asian route, the

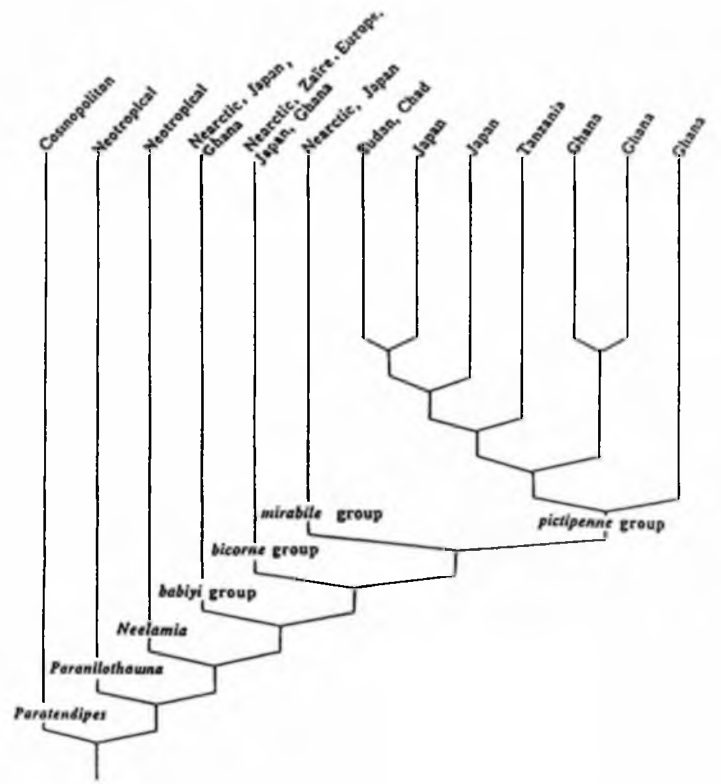

Fig. 17. Area cladogram showing the geographical distribution of the different species of the *Nilothauma pictipenne* group and other groups of *Nilothauma* Kieffer.

presence of the species of *Nilothauma* in North America, Europe, and East Asia shows Holarctic / East Asian disjunctions.

The group delineated by trend 14 in the synapomorphic diagram (Fig. 10) consisting of *N. mirabile* and *N.hibaratertia* present in North America and Japan respectively, shows a Holarctic and East Asian distribution pattern. East Asia has been constantly connected with South-eastern Asia and Siberia, and almost constantly with North America since the Oligocene period as well as with Europe (via Siberia) and India. Large scale faunal exchanges was possible with all these areas.

The *pictipenne* group is made up of 2 species (*N. nojirimaculata* and *N. hibaraquarta*) from the Sino-Indian region and 5 species (*N. pictipenne, N. loba, N. tricaudata, N. flabella* and *N. insolita*) from the Afrotropical Region. The absence of the *Nilothauma* group of genera from Malagasy region which belonged to the Afro-Indian fragment of Gondwanaland and from Western Asia which links Africa with Asia is a possible indication that the ranges of the Megagaeic lineages are disjunct. The other possibility and more likely reason is that the area as a whole has barely been investigated.

Several previous biogeographic analyses of other taxa show a clear relationship between Africa and the Indopacific, with African taxa basal to those occurring further east (for instance Schuh & Stonedahl, 1986; Schuh, 1991; Coscarón & Morrone, 1995, for Heteroptera; and Grehan, 1991 for Lepidoptera). Most of these taxa can be hypothesized to be tropical Gondwanian elements, with minor subsequent dispersal to the Palaearctic (and/or the Nearctic). In the present case there are multiple sister group relationships between and within the groups strengthening this generalized track. The lack of species in Southeast Asia almost certainly is a result of lack of investigations rather than absence of the genus.

To summarize, the phyletic interrelationship of the *Nilothauma* group of genera suggests the early splitting of their common ancestor into the Neotropical group (namely *Neelamia* and *Paranilothauma*) and the Megagaeic lineage group during the fragmentation of the super-continent Pangaea. The Megagaeic lineage group made up of *Nilothauma* species with further fragmentation and possible dispersal into the

Holarctic, Sino-India, Afrotropical and Australian regions.

Future plans

The present thesis describes four new species and redescribes one Afrotropical species. The phylogenetic treatment of the genus *Nilothauma* is incomplete since not all known species of the pictipenne group are redescribed, although they are included in the key; the other species groups are treated as monophyletic; very few immatures presently are known; the closely related genus *Paratendipes* may be heterogeneous and certainly it is necessary to re-examine some of its species in order to re-evaluate some of the postulated trends within *Nilothauma*; and there are certainly several more species to be found particularly in the material from the Afrotropical region. Specimens of *Nilothauma* are never abundant in any one locality. Most finds consist of one or a few specimens. It thus may be difficult also to find the immatures and do rearings. Such rearings may, however, be indispensable for a more complete phylogenetic treatment. On the other hand, the male hypopygium of *Nilothauma* possesses many potential apomorphies and the difficulties here have not been the lack of characters, but the lack of knowledge of extralimital species. The Nearctic and Western Palaearctic species are practically undescribed except for drawings and colourations, while the Japanese species are relatively well described but the drawings are not clear enough.

The genus *Nilothauma* as a whole and its different species very likely may be of indicator value, as genera and species never occurring in high densities often include members of indicator communities. The distribution of *N. brayi* indicate that this species is typical of the littoral zone of medium oligotrophic lakes and unpolluted streams (Brundin, 1949).

It is my intention in future studies to redescribe the remaining species of the genus if available, to re-examine the species of *Neelamia* and *Paranilothauma*, to study new material, and to attempt to rear as many species as possible.

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