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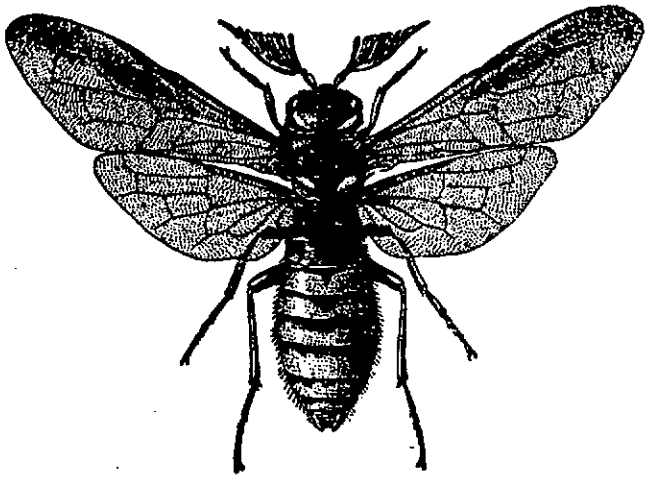
Megalodontidae (Insecta: Hymenoptera): a systematic revision and cladistic analysis



Thèse

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Révision systématique et analyse cladistique des Megalodontidae (insectes: hyménoptères)

de M. Neil Springate

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The taxonomy of the Palaearctic sawfly family Megalodontidae is revised. The family is represented by the single genus, *Megalodontes*, within which 31 species are considered valid. Five generic and 11 specific synonymies are established. 17 specific names are considered as species inquirendae and one generic and one specific name are considered to be nomina nuda. An analysis of morphological characters indicated that several used in previous classifications of the family are unreliable for this purpose or for that of the discussion of phylogenetic relationships. Characters derived from the mouthparts and male genitalia were found to be useful for the discrimination of species and the detection of phylogenetic relationships. Keys to males and females are presented, as is a cladogram indicating relationships between taxa. The biology and the biogeographical relationships are discussed briefly.

Keywords: Megalodontidae; *Megalodontes*; Hymenoptera; Pamphilioidea; systematic revision; cladistic analysis.

Introduction

There is ever-accruing evidence that floral and faunal, particularly phytophage, biodiversity is probably at its greatest in tropical rainforests and the canopies therein (e.g. Basset, 1993). Whilst this may be applicable as a general precept, there is substantial information which suggests that certain, less amenable, habitats have been colonised by a specialised but diverse flora. In tandem, this appears to have provided the stimulus for a diversification of an apparently equally specialised fauna of phytophages and their parasitoids. Examples of this kind of habitat are the Earth's arid and semi-arid zones. Within these zones there is a considerable diversity of specialised plant families, such as Rutaceae, Anacardiaceae and Zygophyllaceae, and their associated phytophages, for example members of the sap-sucking Psylloidea (Burckhardt and Lauterer, 1993).

Unlike the many biogeographic studies upon Gondwanan and Wallacean floral and faunal elements, the study of historical associations between arid and semi-arid areas has been all but ignored. The primary reason for this has not been a lack of interest, but the absence of a sound base for making comparisons between these areas.

Whilst many aspects of arid and semi-arid environments have been well documented (e.g. Soriano, 1978; Axelrod, 1979; Petrov, 1979a, 1979b; Walter, 1979), including many works on the floras and parts of the faunas, invertebrates, in particular insects, in xeric environments have received less attention. In part, this is due to a lack of basic information about their composition (e.g. West, 1983a, 1983b, 1983c). The roles of herbivorous insects in these ecosystems, especially as pollinators (e.g. Breckle, 1983) have not been documented as thoroughly as they have been for temperate and tropical forest, grassland and wetland habitats. Discussion of the composition of hymenopteran faunas, whilst correctly emphasising the pre-eminence of certain parasitoid families, ants, solitary, semi-social and social wasps and bees, usually maintain the misconception that the more ancient members of the Hymenoptera, i.e. the sawflies, are absent or are not adapted to xeric habitats (e.g. Crawford, 1981). This is incorrect, since members of six of the fifteen families are found in arid and semi-arid regions throughout the World and two of these, the Megalodontidae and Pergidae, appear to have become particularly well adapted to these biotopes.

The Symphyta or sawflies are the older of the two sub-orders of the Hymenoptera and, hence, are paraphyletic (Königsmann, 1976, 1977; Rasnitsyn, 1969, 1988). Thus they retain many of the primitive characters that have been lost or become modified in the more recent Apocrita (containing the parasitoid families and the more familiar bees, wasps and ants). The Symphyta are subdivided into six superfamilies and fourteen families. despite their significance in the evolution of the Hymenoptera (Malyshev, 1966) and their acknowledged economic importance as phytophages and xylophages (Gauld and Bolton, 1988), many aspects of their taxonomy, geographic distribution and habit remain unknown or, at best, poorly documented.

An example of these virtually unknown aspects concerns the relatively primitive family, Megalodontidae. It and the related Pamphiliidae are placed in the superfamily Pamphilioidea (or Megalodontoidea according to some authors) and both families are thought to date from the Middle Jurassic period (Rasnitsyn, 1988). The taxonomy and systematics of this family have been compiled, fragmentarily, over the last 200 years and several revisions have been made during this period, the most recent in 1935. Examination of the species' descriptions, their placement in dichotomous keys and the cursory, seemingly haphazard and highly tentative discussions of their relationships indicate that a thorough revision and re-analysis are necessary. Eight generic names, five of which are in current use (some treated as sub-generic, dependent upon author) and 74 specific names exist, of which about 45 have been considered as valid. Megalodontidae are Palaearctic in distribution, between the latitudes 27° and 54° N. Thus, the Megalodontidae represent a relatively small taxon with a wide distribution and these, coupled with their host-plant associations with Rutaceae and Apiaceae (with the exception of species of Tenthredinidae, unique within Hymenoptera) within arid, semi-arid or

locally xeric habitats, suggest strongly, that the family is an ideal subject for biogeographical analysis using contemporary techniques.

Taxonomic History

The first described member of the family, *Tenthredo cephalotes*, was described by Fabricius (1781) and, later, placed in a new genus *Megalodontes*, described by Latreille (1802). Dalla Torre's (1894) catalogue cites species referable to Megalodontidae which had been listed under *Tenthredo* (without designation of specific names) in three works by Schaeffer between 1766 and 1768. Unfortunately, these and the relevant material were unavailable for examination. Later, and with the knowledge of Latreille's description of *Megalodontes*, Fabricius (1804) erected the genus *Tarpa* and placed *cephalotes* and a new species, *plagiocephalus*, within it. This was to set a precedent for more than ninety years, since all but one of the species described before Konow's (1897) revision were placed within this genus, thus suggesting that the works of Fabricius were more widely accepted by other naturalists. Latreille (1810) placed both species within *Megalodontes*.

The first synopsis of megalodontid species, was that of Klug (1824) who described seven new species, 3 of which are here considered valid. Although his treatise was limited in its scope, since it included nine species only, Klug was probably the first symphytologist to realise the extremely widespread distribution of, what was then, a relatively small genus. His material is still available for examination, compensating for his unillustrated, but detailed descriptions. His citation of some type localities, particularly the confusion of Tauria (in Crimea) with Dauria (Chitinskaya Oblast, east of Lake Baikal, Russia) (possibly as a result of misunderstanding the localities of Pallas' expedition to Russia) and that of Germany for *flavicornis*, is debatable. The lack of contact between entomologists of this period is illustrated by the non-inclusion of six species described by Germar (1817), Leach (1817) and Lepeletier (1823) (four of which are now considered to be valid), although Klug's work may well have been in press before the last named was published. The unavailability of Germar's work to Klug appears bizarre, since the two were contemporaries, working in Halle and Berlin respectively, although it appears that Germar was reluctant to describe new species since he cited Ullrich as their author. Leach's citation of material and their British distribution, in the vast Zoological Miscellany, is to be doubted, since it was discovered that much continental material was mixed with British (Perkins, 1923, 1928; see also Benson, 1943).

Brullé (1846), Eversmann (1847) and Lucas (1848) each described a single species, 2 of which are here recognised as valid. The next comprehensive review of species was that of Zaddach (1865), in collaboration with C.G.A.Brischke who discussed sixteen, including three new, species. They worked in Königsberg and Danzig respectively and, although much of the valuable collections in both were destroyed in

1944-45, their descriptions may easily be interpreted. Two of their species are considered as synonyms and the third is placed in species inquirendae due to the unavailability of material. Erroneously, their synopsis included a Nearctic species of Pamphiliidae, *Tarpa scripta*, described by Say in 1824. Horn et al. (1990) state that Brischke's collection was divided between the zoological museums in Danzig and Königsberg and a third part in the Zoological Cabinet of the University of Kharkhov. Kharkhov was twice obliterated in 1942 and 1943 and attempts to locate any Megalodontidae within its university have proven unsuccessful (Taeger, pers. comm.).

Freymuth (1870), working upon the Central Asian fauna, described *nitens*, *skorniakowii*, and *eversmanni*; the last included within the key to species only. Stein (1876) contributed two new species, but his descriptions were difficult to interpret, judging from the number of authors who, erroneously, ascribed material of *phaenicius* Lepeletier to his species *loewii*, resulting from Konow's redescription. Mocsáry (1877, 1881) described four new species, two of which are here considered valid.

André (1879-1882) presented a key and brief descriptions of twenty-four, including two new, species. A third, *lamellata*, from Turkestan (André, 1881a) was described and published separately. despite the cumbersome nature of his key and the lack of suitable illustrations (only *speciosa* Mocsáry = *flabellicornis* Germar is shown), the work was a most significant development in the study of Megalodontidae. All but three taxa (those of Freymuth) are accounted for. André separated species on the smallest of differences in colour and numbers of antennal segments. For example, in the initial couplet, *speciosa* is separated from all other species by its unique possession of red markings on the head and thorax.

Kirby (1882) synonymised *Tarpa* with *Megalodontes* and listed twenty-eight species. The Hymenoptera list was widely circulated and the significance of this synonymy was profound, since only six species were subsequently described, by Jakovlev (1888, 1892), Mocsáry (1891) and Konow (1894), within *Tarpa*. Mocsáry had already described *Megalodontes anatolicus* in 1883 and, thus, his subsequent description of *Tarpa jucunda* and *multicincta*, with *Megalodontes* as a subgenus is nomenclaturally strange. All of the available nomenclatural information was collated in the Hymenopterorum Catalogus (Dalla Torre, 1894) which lists thirty two species and all known references.

Until the end of the nineteenth century, the systematic position of *Megalodontes* received little attention. In nearly all the catalogues and keys, they were placed near *Pamphilius* (or its synonym *Lyda*), thus indicating the systematic proximity of both taxa. In turn, both were included within either the tribe "Lydidae" (e.g. André, 1879) or the subfamilies "Lydina" (e.g. Kirby, 1882) or Pamphiliinae (e.g. Dalla Torre, 1894) and incorporated into a large and diverse Tenthredinidae. Konow (1897) erected a new subtribe "Megalodontides" and separated it from "Lydides" on the bases of the absence of

the subcostal vein and the undivided second tergum in the former. He divided the genus into two subgenera (*Megalodontes* s. str. and *Rhipidioceros*) on the bases of the relative lengths of the third and fourth antennal segments and the relative lengths of the flabella of the third, in comparison with that of the fourth. In the same study Konow erected two new genera (*Melanopus* and *Tristactus*) and described four new species. Konow retained the concept of "Megalodontides" within the tribe Lydini of the subfamily "Lyditae", this in turn within Tenthredinidae. Unlike his predecessors, Konow was less reliant upon subtle colour differences for the distinction of species, placing far greater emphasis upon differences in antennal morphology, supported by differences in microsculpture. His key to species and all of his subsequent descriptions of Megalodontidae were unillustrated but his detailed descriptions and the availability of his material make the interpretation of his species a relatively easy matter. However, the validity of some of his specimens labelled as types must be questioned, since it appears that several were subsequently labelled as such and not selected by Konow himself (Taeger, pers. comm.). Of the fifteen megalodontid species described by Konow between 1894 and 1906, 4 are considered as valid. Ashmead (1898) standardised the endings of Hymenoptera suprageneric names, Megalodontides thus becoming Megalodontinae. The formal elevation to family status was made by MacGillivray (1906) in his study of wing morphology. Rohwer (1911b) included Pamphiliinae as a subfamily of Megalodontidae, within a superfamily Megalodontoidea, which included Xyelidae and Cephidae on the bases of their straight or nearly straight posterior margin of the pronotum, their short mesonota and the absence of the proepimeron.

For more than the next thirty years isolated descriptions of species were made (Enslin, 1913; Rohwer, 1925; Zhelochovtsev, 1927; Takeuchi, 1927; Dovnar-Zapolskij, 1930) and only three of these are considered valid. Pic (1915) erected the subgenus *Forficulotarpa* for *levaillantii* Lucas, although this name remained unused until listed in abe and Smith (1991).

Gussakovskij's (1935) revision preferred to retain megalodontids as a subfamily of Pamphiliidae. He presented a key to, and detailed descriptions of, 42 (including three new) species and one subspecies and placed many species in synonymy. Gussakovskij's was the first taxonomic revision based upon access to far greater quantities of material than had been available to others. His key is functional but rather laborious for the identification of some common western Palaearctic species. Like many of his predecessors and contemporaries, he was heavily reliant upon subtle differences in colour and numbers and relative lengths of antennal segments for his diagnoses of species. Unfortunately, the key and descriptions were unillustrated, with the exceptions of *skorniakowii* and *fabricii* (his illustration of the former appearing on the title page). It appears that some species were included which he had not examined, notably his following of Konow's incorrect placement of *levaillantii* as a synonym of *bucephalus*. A

strange lapsus was the description of *xanthocerus*, for one male and three females specimens without locality data, which he believed to have come from Algeria or southern France. These minor caveats apart, Gussakovskij's study, included within the framework of two substantial tomes of the Fauna USSR (Chalastrogastra, Parts 1 & 2), represented the largest single contribution to the taxonomy of Megalodontidae.

Subsequent to the publication of Klima's (1937) catalogue of species (which, like Gussakovskij's revision, retained Megalodontinae within Pamphiliidae), interest in the family appears to have waned considerably and mention was restricted to listings and keys within national faunas (e.g. Moczar & Zombori, 1975; Chevin, 1987) or isolated species descriptions (Zombori, 1971; Togashi, 1973, Chevin, 1985). The discovery of a new species from the Maghreb prompted Chevin (1985) to erect a new genus *Tristactoides*, which he compared with the Levantine *Tristactus judaicus*, the Algerian *luteiventris* and the Iberian *bucephalus*. He distinguished the new species, *lacourti*, from these three on the bases of its colour pattern and form of antennal flabellae.

It was found that Megalodontidae of Symphyta is a homonym of the same name within the fossil Bivalvia, the latter based upon the fossil genus *Megalodon* Sowerby, 1827. A case has been submitted to the International Commission on Zoological Nomenclature (Springate, 1994) for the sawfly family name to be emended.

Materials and methods

Collecting and preserving Megalodontidae

Megalodontids have been taken by hand-netting, using a ring-net, whilst sweeping from and around their host plants or from species of Euphorbiaceae, Apiaceae, Ranunculaceae and Asteraceae. Hand-netting remains a favoured technique for symphytologists, requiring only the transfer of captured material to a killing-jar or a tube of 70 - 95% ethanol. The lower strength of alcohol is preferable as it reduces the tendency to dehydration and, hence, collapse of the sclerites, particularly those of the abdomen. Static trapping, such as the use of Malaise- and yellow-pan-traps, has proven particularly effective for many groups of Hymenoptera. Yet, whilst this remains true for most families of Symphyta, megalodontids are taken rarely.

Pschorn-Walcher's (1990) detailed account of the biology of *klugii* suggests transferring collected final instar larvae to a flowerpot, filled with sand at the base and with peat in the upper half, and leaving the imagines to emerge the following year, as a method of rearing megalodontids.

All collected material of adults was pinned whilst fresh and the mouthparts of both sexes and the male genitalia were exposed, although the latter were often dissected, in order to reveal some of the smaller structures, particularly the digitus and cuspis. Examination of older material, particularly that killed in cyanide, presented far more of a problem, since it is almost impossible to dissect, even after placing the specimen for

several days in a relaxing box, without risking it serious damage. These specimens were treated with pepsin or with Barber's solution.

A temporary card-mount may be used for the examination of some of the gross morphology of the genitalia. The majority of the illustrations of male genitalia included herein have been made after clearing the genitalia in 5% potassium hydroxide solution and preparing a temporary slide-mount in glycerine. Once cleared, the male genitalic capsule has a tendency to collapse on a permanent card-mount and its storage in a stoppered and labelled vial of gelatine is an alternative.

Dissection and examination of the female genitalia should be attempted with fresh material only. Fresh material from the Geneva Basin required the dissection of the entire female genitalic capsule in order to investigate the forms of the ovipositor, valvulae and valvifers. All of these are powerfully attached to the seventh sterna and to each other by membranes. Dissection of this capsule in older material (see above) may result in its fragmentation and the destruction of the surrounding sclerites. The amputation of the saws after the lateral crushing of the abdomen is not recommended.

Field work in the Geneva Basin, Switzerland, suggested that visiting sites containing known host plants and subsequent observation of adult food-plants is the most effective method of collecting relatively large numbers of megalodontids. Sweeping from the flowers of *Ranunculus repens* and *Tripleurospermun inodorum* (Ranunculaceae and Asteraceae, respectively) at two sites, one a dry prairie at Courtille (elevation 400m) and the other the borders of a wheatfield at Chânières (400m) in June and July, 1993 and June 1994, more than 110 males and females of *cephalotes* Fabricius were taken, possibly the largest single population of a member of Megalodontidae.

Abbreviations

The following abbreviations, following Arnett *et al.* (1986), for museums and other repositories of specimens are used in the text:

BMNH, Natural History Museum, London;

DEIC, Deutsches Entomologisches Institut, Eberswalde;

FUUN, Fukui University, Japan;

HNHM, Hungarian Natural History Museum, Budapest;

HWEC, Herbert Weiffenbach Collection, Aschaffenburg;

IBBK, Institue of Biology, Bishkek, Kyrgbyzstan;

INRA, Laboratoire de Faunistique écologique, Station de Zoologie, Versailles;

ISCM, Institut Scientifique Cheripen, Rabat;

IZAS, Institute of Zoology, Beijing;

IZUB, Istituto di Biologia, Bologna;

IZUI, Institut für Zoologie der Universität Innsbruck;

MHNG, Muséum d'Histoire Naturelle, Genève;

MKRC; Manfred Kraus Collection, Nürnberg;
MNHN, Muséum National d'histoire naturelle, Paris;
MRSN, Museo Regionale Scienze Naturali, Torino;
NHMB, Naturhistorisches Museum, Basel;
NHMW, Naturhistorisches Museum, Wien;
NMLS, Natur-Museum, Luzern;
OLML, Oberösterreichisches Landesmuseum, Linz;
RMNH, Rijksmuseum van Naturlijke Historie, Leiden;
SBLC, Stefphan M. Blank Collection; Röhrmoos;
SMNS, Staatliches Museum für Naturkunde, Stuttgart;
TAKC, Takeuchi Collection, Japan;
TAUI, Zoological Museum, Tel Aviv University;
USNM, United States National Museum of Natural History, Washington;
UWCP, Department of Entomology, University of Wroclaw;
ZHMB, Zoologisches Museum der Humboldt Universität, Berlin;
ZKON, Zoologisches Museum, Königsberg (Kaliningrad), Russia;
ZMAS, Zoological Museum, Academy of Sciences, St.Petersburg (Leningrad);
ZMUC, Zoological Museum, University of Copenhagen;
ZSMC, Zoologisches Museum der Bayerischen Staates, München.

Morphological terminology

The morphological terms used herein follow those in Richards (1977) and in Gauld and Bolton (1988), those for sculpture follow Eady (1968) and the majority of those for the genitalia structures follow Ross (1945).

Cephalic morphology is expressed as ratios between measurements taken from the vertex, lower face, mouthparts and antennae. 'EA' represents the 'eye angle' (see character assessment) (Figs 1 and 2). A is the distance between the rear ocellus and the eye and B is the distance between the rear ocelli; these are compared in the ratio 'A:B'. C is the diameter of the rear ocellus (Fig. 3) and is compared with B in the ratio 'B:C'. 'D:E' is the ratio of the length of the third antennal segment in comparison with that of the pedicel and 'D:F' compares the former with the sum of the lengths of the fourth and fifth antennal segments.

The relative length of the third antennal flabella is used for the identifications of both groups and species and its definition is, therefore, important. The apex of the flabella should be examined in relation to a perpendicular line (or pair of lines), drawn from the dorsal apex (or apices) of the flagellar segment(s). For nearly all taxa, particularly those with long flabellae, this estimation will lie between two points of origin and is expressed in terms of 'as long as the following 1-2 (Fig. 4) or 5-6 (Fig. 5) segments', for example. An antennal segment is defined as being without a flabella when

there is no distinct ventral projection at its apex. All measurements of relative sizes of antennal segments are based upon viewing the inner face of the antenna. Lengths of segments are based upon measurements along their dorsal surface and widths upon the maximum apical distance between dorsal and ventral surfaces.

Wing terminology follows Gauld and Bolton (1988), although 'area aspera' is preferred to their 'scaly patch' for describing an area of thorn-like cuticular extrusions from the ventral surface of the forewing (Schrott, 1986), which make contact with the cenchri of the metanotum, when the wings are in repose. The following abbreviations are used:

AC1, anal cell 1

R, radial vein

Sc, subcostal vein

Sc1 and Sc2, apical branches of the subcostal vein

M+Cu1, medio-cubital vein

1A, anal vein 1

For all the illustrations of the digitus and cuspis the scale line represents 0.1 mm; for those of the dorsal and ventral views of the male genitalia it is 0.5 mm. Where no scale line is indicated, these have been drawn from photographs and are not to scale. The following abbreviations are used:

aa, aedeagal apodemes

ai, antennal insertion

ao, anterior ocellus

cd, cardo

cp, cuspis

dg, digitus

ds, dorsal sclerotisation of gonostipes

ga, galea

gd, fused remnant of gonocardo

gl, glossa

gp, gonostipes

gy, gonostylus

lp, labial palp segments

mp, maxillary palp segments

pa, planar region of pentagonal area

pg, paraglossa

pm, prementum

pt, trench of pentagonal area

rmv, rounded lateral margin of volsellae

ro, rear occellus

smv, straight lateral margin of volsellae

st, stipes

sv, sclerotised volsellar sac

vp, volsellar pocket.

Terminology for the constituent parts of the male genitalia of sawflies is highly varied, according to authority, and that employed herein follows Ross (1945) in his use of gonocardo, gonostipes, gonomaculae, parapenial lobes, volsellae and penis valves. Smith's (1970) use of digitus and cuspis (the distivolsella and apiceps, respectively, of Ross) is preferred, since Gauld & Bolton (1988) appear to have confused Ross' terms for these structures (referring to them as the gonolacina and distivolsella, repsectively). These terms are compared with those used in Snodgrass (1941) and Gauld and Bolton (1988) and are presented in Table 1. Boulangé's (1924) highly individual and slightly idiosyncratic terminology (for example, the use of 'trébuchet' for digitus) are not discussed, although mention must be made of his delightful hand-written table (between pages 32-33) which provides a helpful comparative summary of genitalic terminology used in sawflies, in particular, and Hymenoptera, in general, from 1742 onwards.

Phylogenetic relationships within Symphyta

The monophyly of the Megalodontidae is supported by the presence of the lamellate digitus in combination with the digitiform cuspis (or their extreme atrophication), flabellate antennae and the presence of the area aspera within cell AC1, their relationships with other orthandrous sawflies (i.e. those with unrotated male genitalia) are uncertain. The Megalodontidae are regarded as the sister-group of Pamphiliidae in the superfamily Pamphilioidea (e.g. Rasnitsyn, 1988) or Megalodontoidea (e.g. van Achterberg and van Aartsen, 1986; Gauld and Bolton, 1988). Pamphilioidea is thought to be a sister-group of Siricoidea (Siricidae+Xiphydriidae+Anaxyelidae) (e.g. Königsmann, 1977). A North American concept of Megalodontoidea has been to associate Xyelidae, Pamphiliidae and Megalodontidae, disregarding the presence of stophandrous (i.e. rotated through 180°) genitalia in some Xyelidae, which follows Rohwer's (1911b) concept, but omitting the Cephidae. MacGillivray's (1906) contentious assertion of the similarity of Megalodontidae with Siricidae, on the basis on similarities in wing venation, is supported by the presence of a hypostomal bridge and the absence of larval abdominal prolegs, characters shared with the Pamphiliidae and Xiphydriidae.

Rasnitsyn's (1988) phylogenetic reconstruction of the Hymenoptera, based upon characters derived from both fossil and extant material, places Megalodontidae+Pamphiliidae as an offshoot from the fossil Xyelydidae. Megalodontidae are suggested to be derived from the fossil Praesiricidae on the basis of the absence of the subcostal vein, possession of a long mesopseudosternum and the virtual medial separation of the pre-episterna. The most convincing synapomorphies of

Megalodontidae+Pamphiliidae are the closure of the cephalic cavity, with separate mandibular cavities, and the presence of a supra-anal hook in the larvae. However, the knowledge of larval Megalodontidae is so limited that the latter requires confirmation. The two families are often associated on the basis of possession of flattened abdominal sclerites. However, no Megalodontidae possess this feature and it is better regarded as an autapomorphy for Pamphiliidae.

Diagnosis

The Megalodontidae are distinguished from other Symphyta by the following synapomorphies: the unique lamellate form of the digitus and its associated digitiform cuspis (or their subsequent atrophication) (Figs 6 and 7), the presence of the area aspera within cell AC1 and the absence of vein Sc and the veinlets Sc1 and Sc2 (Fig. 8). Some Xyelidae and Pamphiliidae have lost Sc1, but Sc is always present (Fig. 9). They may be separated from the closely related Pamphiliidae by their almost tubular abdomen (a symplesiomorphy) which is never dorso-ventrally flattened (this latter an apomorphy for Pamphiliidae), by their flabellate or pectinate antennae and the form of the male genitalia (both synapomorphic within Pamphilioidea). In turn, this distinguishes them from most other Symphyta. Other sawflies with pectinate, flabellate or ramose antennae are members of the Diprionidae (males only) and the genera *Cladius* (Tenthredinidae: Nematinae) and *Cladomacra* (Pergidae: Perreyiinae) and the Megalodontidae may be distinguished from these by the form of the digitus and cuspis, position of the area aspera and the absence of Sc, Sc1 and Sc2.

Description

Adult 9-16 mm in length. Yellow (or yellow-white) and black (or dark brown) in colour; rarely all yellow or all black.

Head. Antennae 11-37 segmented; strongly or weakly flabellate. Apical 1-10 segments without flabellae. Distance between rear ocellus and nearest point of eye margin at least twice as wide as distance between rear ocelli. Malar sulcus present. Post-genal bridge present. Labrum with prominent ventral covering of stout bristles. Clypeus folded back underneath and joined laterally to the post-genae behind so that there are two separate holes for the mandibles and a third for the labio-maxillary complex. Mandibles bidentate; asymmetrical; left closed over right; inner tooth always shorter than outer. Occipital carina absent. Maxillary palps always with six and labial palps always with four segments; insertions of segments end-to-end (Fig. 13).

Thorax. Median scutal line and notaulices strong, dividing notum into left and right prescutal and scutal regions. Hind-coxa posteriorly with incision, apically open or a deep furrow, a fine groove or a slight depression, apically closed. Mid-tibial spur formula 0:2:2; spurs rounded but never completely cylindrical; inner spur longer than outer; spurs

are haired, protruding through fine sclerotised projections or strongly pectinate. Apico-tibial spur formula 2:2:2; similar in form to mid-tibial spurs but, often, distinctly shorter; fore-tibia has massively elongate inner spur, virtually flattened, rarely pointed, distinctly like the blade of a chisel. Wings with Sc, Sc1 and Sc2 always absent and area aspera always within cell AC1 of forewing.

Abdomen. Slightly broader than deep and, thus, virtually tubular/cylindrical: not distinctly flattened dorso-ventrally. Second abdominal tergite undivided medially. Gonocardo fused strongly with base of gonostipes dorsally, less so ventrally. Dorsal surface of gonostipes with internal margins highly varied and with parapenial lobes appearing fused. Gonostyli with gonomaculae and articulated with gonostipes. Gonostyli shorter than gonostipes, rarely longer. Female ovipositional apparatus consisting of paired saws and sawsheaths surrounding folded ovipositor, which appears triangular when flattended.

Larva. Five instars. Fourth instar 15-19 mm and fifth 20-24 mm. Antennae seven-segmented. Three pairs of well-developed thoracic legs present, with coxa, trochanter, femur, tibia and fused tarsus and claw. abdominal prolegs absent. Supra-anal hooks or cerci present (Lorenz and Krauss, 1957; Gauld and Bolton, 1988, Pschorn-Walcher, 1990).

Character assessment

The basis for the character assessment was an examination of 12 species where 10 or more individuals from a single population were available for examination, these being *cephalotes*, *escalerai*, *flabellicornis*, *interruptus*, *judaicus*, *olivieri*, *quinquecinctus*, *spiraeae* and *turcicus*, *Megalodontes* sp.2 and sp.4 and a population similar to the holotype of *plagiocephalus* (hereafter referred to as *M.* cf. *plagiocephalus*). Comparisons were then made with other individuals of the same and other species.

General characters

Overall body colour. Members of all genera of Xyelidae and Pamphiliidae were examined. Xyelidae are predominately yellow or yellow-brown. Pamphiliidae exhibit a great range of body colour from yellow/yellow-brown to all-black or metallic blue. Of the darker Pamphiliidae, where lighter (usually yellow or white-yellow) coloration appeared superimposed upon darker, these lighter areas were highly variable in size and distribution, particularly upon the face, vertex, lateral thoracic sclerites, terga and sterna. In both families, colour patterns of the same sclerites in species which were predominately lighter in coloration, with darker areas superimposed, appeared to be of greater stability. Therefore, since it is accepted that Xyelidae are the most primitve Hymenoptera (e.g. Richards, 1977; Gauld and Bolton, 1988; Rasnitsyn, 1988), and for the purpose of providing an arbitrary coding of colours and colour patterns, this predominant yellow coloration is primitive and its loss or superimposition by black is

considered derived. Thus, it is assumed, that the same occurs within Megalodontidae, i.e. that predominately yellow species are the more primitive and that its loss is derived and it is this protocol which is adopted when scoring colour syndromes within the Megalodontidae. However, it is accepted that the colour of individual sclerites and colour patterns are, possibly, the most labile of all characters of sawflies.

Overall body sculpture. The above was repeated for patterns of sculpture. Predominately yellow species of Xyelidae and Pamphiliidae tended to be smooth or with sparse punctulae and this is assumed to be primitive. However, many predominately black or metallic blue species of Pamphiliidae were equally smooth and no conclusions upon primitive or derived states are drawn from these.

Head

Colour. Vertiginal yellow never contiguous with facial yellow and always contiguous with genal yellow, even when the latter is greatly narrowed (e.g. in *judaicus*, *cephalotes* and *M.* cf. *plagiocephalus*) or vestigial (in *fabricii*). In most species vertiginal yellow is broken by the post ocellar striae or their occipital remnants. Where it is unbroken, the entire occipital and post-genal areas are yellow (e.g. *xanthosomus*) and this is used to assist in the separation of *olivieri* and *phaenicius*.

The presence (20 species) or absence (8 species) of post-ocellar flecks was found to be stable within most species, but unstable in males of *judaicus*, *flabellicornis* and *skorniakowii*. It is not used in key construction or cladistic analysis. The length and width (used regularly in previous descriptions) of these flecks and whether they are contiguous with the vertiginal yellow was inconsistent in all material examined and these characters are not used.

Facial colour was stable in relation to overall colour patterns in all species (see colour syndromes, below) but, where lower facial yellow becomes fragmented the size and form of the individual colour flecks is highly unstable in most males and all females. The degree to which the yellow between the antennal insertions and the eye margins was produced vertically is stable and is used to separate females of *escalerai* and *reitteri* and between *bucephalus* and *capitalatus*.

Mandibular and mouthpart coloration were stable within the populations examined. However, when compared with other populations and individuals of the same species it was either stable, particularly those with entirely yellow faces, or highly unstable (e.g. in *spiraeae* or *interruptus*). The same situation was found for coloration of antennal segments, particularly differences between the colour of the pedicel and basal and apical flagellar segments and between the bases and apices of the flabellae. Scape colour is considered to be more stable and is used in the keys, otherwise these characters are not used.

Colour patterns. In contrast with the overall instability of individual cephalic colour characters, several general patterns of coloration of the vertex and the face of the male

were noted. These syndromes are, arbitrarily, given specific names. Vertiginal colour pattern is divided into: (i) 'olivieri' (Fig. 28); (ii) 'flabellicornis' (Figs 29 and 30); (iii) 'bucephalus' (Fig. 31) and (iv) 'cephalotes' (Fig. 32) syndromes.

'Olivieri' syndrome has the vertex of the head predominately yellow, with only a narrow band of black, between the eyes, passing through the ocelli; 'flabellicornis' has the vertiginal yellow reduced to two longitudinal flecks, posterior to the rear ocelli and extending toward the occiput, either contiguous or discontinuous with the post-genal yellow; 'bucephalus' syndrome has the vertiginal yellow reduced to a narrow strip above the occiput and contiguous with the post-genal yellow and two small occipital remnants of the post-ocellar flecks and 'cephalotes' syndrome is similar to 'bucephalus', with a narrow post-genal stripe of yellow and two lateral flecks of yellow between the occipital remants of the post-ocellar striae (In some species, the medial part is absent, but is scored the same). 'Olivieri' syndrome (found in 4 species) is considered to be the most primitive, with the 'flabellicornis' (11 species), 'bucephalus' (5 species) and 'cephalotes' (6 species) syndromes being progressively more derived. Five species were not scored for these syndromes.

Facial colour pattern is divided into: (i) 'olivieri' (Fig. 33) (12 species); (ii) 'flabellicornis' (Fig. 34) (6 species); (iii) 'cephalotes' (Fig. 35) (12 species) and (iv) 'fabricii' (Fig. 36) (1 species) syndromes. 'Olivieri' syndrome is characterised by an all yellow face; 'flabellicornis' syndrome by the large triangular shape of the lower facial yellow beiong separated from that between the antennal insertions and the eye margins; 'cephalotes' syndrome has the facial yellow reduced to three, roughly equal-sized flecks and 'fabricii' syndrome reduced to two flecks, one between the antennal insertions and the eye margins.

Setosity. Potentially, this is a good and stable character with little variation between species and populations noted. There is a danger of misinterpretation in older, abraded material or that trapped or preseved in alcohol, in which the hairs become matted and brittle. Hairs white/silver (e.g. *judaicus*) or black (*turcicus*), long (more than twice as long as diamater of rear ocellus) (e.g. *judaicus*), short (less than twice as long as diamater of rear ocellus) (e.g. *kuznetzovi*), densely (e.g. *cephalotes*) or sparsely distributed (e.g. *olivieri*). A constant character, with very little variation noted between populations, but highly variable in length and density between sexes. Two general trends were observed: if the scletire is yellow, there is a tendency to less dense, sborter hairs or bristles, in association with less degree of sparser punctation. If predominantly black, tendency to denser, longer and finer hairs, in association with stronger and denser punctation.

Eye angle. This represents the inclination of the inner margin of the eye, in relation to a vertical median line, when both the front ocellus and lower clypeus are in the same plane and is measured as a ratio of the distances between the lower and upper margins of the eyes (Figs 1 and 2). However, it is difficult to distinguish distinct groupings, since

some species have great variation (e.g. *skorniakowii*, *judaicus*) or one of the sexes accounts for all the variation (e.g. *phaenicius*). This ratio is expressed as EA and is given for each species. It is noted that all species with wide malar spaces possessed EA values greater than 0.95, although no other correlations were noted.

Pentagonal (frontal) area and pentagonal crest. Viewed laterally, these regions are not distinct and merge with the inter-scrobal/nasal area of the upper face and lie in an area defined by anterior and downward extensions of ocellar striae, posteriorly and dorsally to the antennal insertions. A small pit lies between the front ocellus and the inclined part of the face, i.e. in the same plane as the ocellar region. Of two forms: (a) region between front ocellus and pit is excavated, in the form of a trough, occasionally deep, (Fig. 37) or (b) the region is planar, with no excavation (Fig. 38). A good character for both purposes, but requires careful examination, especially in relation to light source.

Malar space. Either (a) wide, where it is equal to one-half of the diameter of one of the rear ocelli but never more than than three-quarters or (b) narrow, where it is equal to less than one-half of the diameter of one of the rear ocelli. This character appears to be constant within a species, with only minimal variation noted, either between sexes or populations. A wide malar space is found in both Pamphiliidae and Xyelidae and is considered to be primitive and its narrowing derived.

Genal carinae. Either (a) present (Fig. 10) or obsolete (Fig. 12) or (b) absent (Fig. 11). Megalodontidae do not possess an occipital carina, which lines the vertex and upper part of the head behind the eyes in the majority of sawflies, but most species possess genal carinae, which are considered to be a downward extension of the occipital carina. In common with many sawflies, the genal carinae are useful for separating many species within Megalodontidae. However, their presence or absence does not appear to be associated with other characters on the head and species-groupings defined previously are contradicted definitively by both mouthpart and genitalia characters. Where present, the genal carinae extend upwards but are absent behind the eyes. Obsolescence (e.g. in *skorniakowii*), where a distinct carinae is absent, but a distinct angle is formed between genal/malar and post-genal/malar areas is considered to be equivalent to presence. absence is considered to be when these areas are confluent. This character appears to be constant within a species, with only minimal variation noted, either between sexes or populations, except certain specimens of *xanthosomus* and *olivieri*, where the carina occasionally extended above the upper limit of the eye. Presence is considered to be plesiomorphic and absence apomorphic (Character 3, states 0,1).

Post-ocellar striae. Either (a) incomplete (Fig. 39) or (b) complete and distinct, extending from rear ocelli to occipital margin (Fig. 40), present only posteriorly of ocelli and at occipital margin. Unstable and varies between sexes and populations, particularly so in *cephalotes*. Useful for separating some closely related taxa in keys (e.g. *quinquecinctus* and *spiraeae*) but less so for phylogenetic analysis. Both states are found

in Pamphiliidae and Xyelidae so the scoring is based upon the majority of megalodontids having incomplete striae, although this appears somewhat arbitrary (Character 7, states 0, 1).

Number and form of teeth on mandible. Two, one outer and longer, a second inner and shorter with no variation, e.g. inner tooth missing or tridentate forms. Both inner and outer tooth highly variable in form and length between sexes (e.g. *merceti*) and within one sex of a single population (e.g. *escalerai*, *spiraeae*, *M.* cf. *plagiocephalus*). One male, possibly aberrant, of *olivieri* possessed both teeth of the same length, highly rounded and atrophied. Not used in keys or cladistic analysis.

Form of galea. Either, (a) in lateral view and when planar, galea strongly swollen so that ventral surface is greatly enlarged in the apical one-quarter to one-third of its length (Fig. 14) or (b) elongate. The latter appears to be of two states: one where the maximum enlargement of the ventral surface is in the apical half of the galea only (Fig. 15) or galea greatly elongated apically, so that maximum enlargement of ventral surface is in basal half only (Fig. 16). Both states of (b) require careful examination of precise point of insertion of galeal base into the stipes, for estimation of total length of galea. Setting precise limits on the separation of (b) tended to subdivide, perhaps artificially, other more stable groupings of characters, particularly those based on male genital morphology. The greatly elongated galea is better interpreted as individual specific variation rather than defining a particular grouping of taxa. One of the most significant and stable characters for keys and phylogeny. The swollen state was noted in Pamphiliidae and Xyelidae and is considered primitive (Character 1, states 0,1).

Glossa. Strongly flared apically (Fig. 18), appearing bulbous and strongly downwardly curved(e.g. *merceti*, *phaenicius*) (Figs 14 and 41), longer than galea, strongly downwardly curved and flared, much longer than galea, strongly downwardly curved and slightly flared or elongate and parallel-sided (e.g. sp.3) with with rows of setae on dorsal surface. [In one male (referable to *mundus*) the glossa appeared to be wider basally than apically, i.e. tapering toward the apex. Examination of the female syntype of *mundus* revealed the same, but the value of this condition or whether it repesents an artefact, is uncertain and is not scored and *mundus* is included within species inquirendae.] Viewed laterally the more strongly flared or swollen glossae appear heavily downwardly curved apically, whereas the elongate forms appear straight or very slightly downwardly curved apically. Comments as for galea. The strongly flared state is considered primitve (Character 2, states 0,1,2,3).

Paraglossa. Elliptical (e.g. *phaenicius*) (Fig. 41) or elongate, hemi-cylindrical (e.g. *cephalotes*, *turcicus*) (Figs 17 and 42). May be as long as glossa (e.g. *merceti*) or slightly shorter (e.g. sp.3). Comments as for galea.

Number and insertion of palp segments. Maxillary palps always with six segments (Fig. 13) and Labial palps always with four. Insertions are always end-on (Fig. 13). The

same as in Pamphiliidae. No variation noted and not used in keys or analysis.

Antennal scrobes. The scrobal region is not strongly excavated in the majority of megalodontids and, thus, a medial nasal region is not particularly evident. However in a few (e.g. *spiraeae*, *quinquecinctus*) the excavation is more profound and is in combination with a large pit behind the antennal insertion (Fig. 40).

Number of antennal segments. Number of segments ranges from 11 (female *parvus*) to 34-37 (male*skorniakowii*). All species appear to have a specific number or range and this is stated in the species descriptions. Where there is a large difference between the numbers of segments, e.g. between females of *xanthosomus* and *nitens*, it is employed sparingly in the keys. However, the character is of limited value, since apparently closely species, e.g. *bucephalus*, *capitalatus*, *gratiosus*, *lacourti* and sp.4 possess similar numbers of segments (e.g. males 15, 15, 16, 14 and 15, respectively, and females 14, 15, 17, 14-16 and 14, respectively). Even within the same sex of one species variation may be high (e.g. 16-19 segments in female *cephalotes*). Not used in cladistic analysis.

Form of scape. Strongly constricted immediately above insertion, giving a stalked appearance, then flared gradually toward apex, slightly more profoundly ventrally, giving an impression of slight curvature to the entire segment (Figs 43 and 44). No variation noted between sexes or populations.

Form of pedicel and third antennal segment. Either (a) oblong; (b) square or (c) transverse. Its interpretation is highly dependent upon the angle of orientation of specimen and the degree of deformation during rigor mortis, which often results in partial contraction or extrusion, thus distorting the comparative mesuration. Third antennal segment flared from base to apex appearing much wider apically or cylindrical and only marginally wider apically than at base. The former occurs widely in species with longer antennal flabellae and with galea forms (a) and (b) and the latter tends to be associated with shorter antennal flabellae and galea form (c). The ratio between the lengths of the two (D:E) is useful for distnguishing species in both male and female keys.

Relative length of third antennal flabella. This character has formed the basis for megalodontid classification for many years. One concept of the subdivision of the Megalodontidae was to split the family into groups depending upon whether the flabella was longer than the three following segments or equal or shorter than the three following segments. This is highly artificial and impractical for dividing the family during key construction. It is of very limited value for separating members of the family into monophyletic groups and was not used in the cladistic analysis, but is extremely useful for separating specific pairs of taxa, within a dichotomous key. Of the monophyletic groups retained by the consensus tree, only one (the *phaenicius* clade) contained all the species with the longest third antennal flabella (as long as the following 11-27 segments). Other clades were highly heterogenous in this respect, for example those of *kuznetzovi*

and *interruptus*. The ratio of lengths of the third and fourth flabella was uniformative as it proved to be a homoplasy. One difficulty in using this character is the requirement that the antennal flabellae are in the same plane as their bases. A second is that, since the antennae are curved and the flabellae further recurved from the orientation of their bases, estimation of their relative lengths is based upon the visual estimation of the lengths of two convergent curves.

Number of apical antennal segments without flabellae. Either (a) less than seven apical segments without flabellae or (b) more than seven segments without flabellae. A stable character, but of limited use in the keys as (b) is found in two species alone (fabricii and sp.5) and in all the cladograms a pairing of these is not supported.

Vertginal sculpture. Either (a) smooth or, at most, with widely spaced punctulae and shining interspaces; (b) sparsely punctulate (separated by more or less than the diameter of the punctulae); (c) punctulate-punctate or (d) widely or closely punctate (separated by more or less than the diameter of the punctae). Requires careful examination of specimens and is variable between populations of the same species and varies slightly within a single sex of the same population (e.g. *cephalotes*, *M.* cf. *plagiocephalus*). Greatest variation tends to occur in species where the degree of yellow coloration of sclerites is variable or, more particularly, those of widespread distribution. A weak tendency exists for predominately yellow areas to be smooth to punctulate and for black areas to be more profoundly and coarsely sculptured and is scored assuming smoothness is primitive, although these correlations were not found in members of Xyelidae and Pamphiliidae.

Ocellar-ocular sculpture. As above, but including: (e) punctate-rugulose.

Thorax

Thoracic colouring. Examinations of the populations mentioned above suggested that the colour of the following sclerites was highly varied within these populations and even more so when compared with individuals from other populations of the same species and these are excluded from use in the keys or analysis: pronotum; mespisternum, mesepimeron, metepisternum, metepimeron, tegula and humeral sclerite. The presence or absence of yellow flecks behind the cenchri on the metapostnotum is used as a tertiary clause to assist in the separation of males of *eversmanni* and *escalerai*. The gross coloration of the mesepisternum, propleurae and metasterna in combination is discussed below.

Leg colouring. A heavily used character based upon the relative amount of black or brown colouring from base to apex of femur and, sometimes, yellow from base to apex of tibia. Varies between sexes, fore-, mid- and hind-limbs and within populations (both sexes). A general trend was noted for femoral black colouring to be reduced from fore- to hind- legs and another, corresponding trend for tibial and tarsal segments to become progressively darker. Generally, of very limited use, with the exception of coxal colour,

as a secondary character for distinguishing between closely related species in combination with others (e.g. separation of males of *reitteri* from those of *eversmanni* and *escalerai*). Three gross and stable patterns of female leg colour are distinguished for the cladistic analysis: all yellow or, at most, with very small areas of black at base of the fore-legs (considered primitive); black basally hind-femora predominately yellow or ochraceous; predominately black with with distinct white markings.

Thoracic colour patterns. In similar fashion to the head, several syndromes of colour pattern are evident. Whilst subject to individual and specific variation, eight syndromes were noted, four each from male lateral and ventral colouring and from female leg coloration, excluding the coxae. Lateral and ventral colouring was sub-divided into: (i) predominately yellow laterally and ventrally (considered primitive); (ii) predominately yellow laterally and on propleurae; (iii) mesepisternum predominately yellow, propleurae and mesosterna black and (iv) laterally and ventrally mostly black, yellow on mesepisternum small or absent.

Setosity. Comments as for head and ventral surface of coxa, trochanter and femur; short setae on dorsal and lateral surfaces of femur and all of tibila and tarsal segments, except baso-ventral surface of basi-tarsus which bears longer, stouter and, apically, blade-like setae; dorsal and ventral surfaces of wings with covering of short hairs.

Pronotal collar. Either (a) viewed laterally, collar narrow, appearing steeply angled or almost perpendicular and as a continuation of anterior plane of mesonotum (considered primitive) or (b) collar gradually curving toward anterior and downwards, i.e. away from anterior of mesonotum. This requires careful examination, as this tends to be obscured in extremely hirsute taxa, and, thus is difficult to interpret. Varies between sexes, e.g. curving and collapsing in male and females, respectively, of *reitteri*. Not used in the keys and its significance phylogenetically is doubtful, based upon its sporadic distribution throughout the species

Hind-coxal apical incision. Either (a) open, i.e. suture extends to and is open at coxal apex (Fig. 19) or (b) closed, i.e. suture does not extend to coxal apex or merges with plane of coxa apically (Fig. 20). Usually very difficult to view correctly and to define, especially in relation to light source and is not included in the keys. A similar open groove is found in Pamphiliidae and the open form is considered primitive. (Character 38, states 0,1)

Number of mid- and apico-tibial spurs. The former always in the formula 0 (fore-tibia): 2 (mid-tibia): 2 (hind-tibia) and the latter: 2:2:2. Not used in keys or phylogeny since this is the standard form throughout the Pamphilioidea. No significant variation in form noted between species. Goulet and Huber (1993: 69) cite the hind-tibia as possessing 2 or 3 pre-apical spurs, but this was not noted in any of the material examined.

Dentition of tarsal claws. Either (a) viewed laterally, the inner tooth of tarsal claw is

widely separated from the outer by more than its basal width (Fig. 46) or (b) inner tooth of tarsal claw is proximal to outer with no separation, so that both teeth appear to originate from similar apical regions of the claw (Fig. 45).(An intermediate state is found in *bucephalus*, where the inner and outer teeth are separated, but by less than the basal width of inner tooth. Useful for distinguishing *kuznetzovi* from *merceti* and *levaillantii* but (a) is found in this species alone. Apex of inner tooth is either vertical (in relation to plane of claw) or recurved toward pulvillus and basitarsi. Pamphiliidae have the tarsal teeth widely separated and this is considered to be primitive, but is not informative since it is an autapomorphy for *kuznetzovi*.

Thoracic sculpture. As in ocellar-ocular sculpture but including: (f) punctulate-punctate with median smooth areas on the lateral lobes of the mesonotum. Comments as vertiginal sculpture. Again a very weak tendency exists for sculpture on the lateral lobes of the mesonotum and that of the mesepisternum to be associated with that between the rear ocelli and eyes or for the latter to be one 'grade' coarser than on the thorax in some species. However, examinations of populations of *cephalotes* suggested that the two varied independently of each other and that no genuine association exists. Used sparingly in the keys (e.g, in distinguishing females of the *interruptus* group) and as two characters (31, 32) in the analysis.

Abdomen

Colour. All terga and sterna yellow, yellow-black/-brown or black. One of the most commonly and extensively used characters for distinguishing species, particularly on the width of the apical yellow bands or whether these are medially complete. Examination of the *cephalotes*, *escalerai*, *flabellicornis* and *M.* cf. *plagiocephalus* populations suggested that these were relatively stable, but this was contradicted by some species widely marked with yellow (e.g. *olivieri*) or predominately black (e.g. *interruptus* and *judaicus*). Presence or absence of lateral yellow flecks on terga 1-3 slightly more reliable, but varies between same sex (e.g. *turcicus*) and there is variation between presence/absence on same terga between sexes (e.g. *judaicus*, *turcicus*). There is even greater variation in coloration of sterna between sexes (e.g. *merceti*) and same sex of one population (e.g. *turcicus* males, *spiraeae* females). Used occasionally in the keys, on a presence versus absence basis, but not in the cladistic analysis.

Sclerite above sawsheath. Either (a) yellow or (b) black. A relatively stable colour with little variation and is used for separating female *jucundus*, but not in the cladistic analysis.

Setosity. Comments as for head.

Eighth tergum of male. Either (a) medially with a basally deep and narrow furrow which widens apically and becomes progressively shallower (e.g. *kuznetzovi* and *merceti*, Figs 47 and 48); (b) medially with a furrow with its margins proximal (e.g. *luteiventris*, Fig. 21) or widely separated (e.g. *turcicus*, Fig. 49) (considered

plesiomorphic) or (c) flattened medially, with any distinct impression. A stable character and used in both keys and cladistic analysis.

Basal plate. Either (a) viewed laterally, with strong apical downward curvature, appearing as a prominent lip (considered primitive); (b) apically down-curved, although not greatly so, when viewed laterally, with the appearance of a small lip or (c) not downwardly curved apically and without any appearance of a lip. Viewed laterally, the sub-genital plate is gradually or sharply curved or angled toward the dorsal surface. This is very stable and the apical region should be oriented so that it is viewed ventrally, at right-angles to this plane. Apical margin is either (a) concave, (b) truncate (appearing 'squared-off') or (b) convex. Apical surface is either (a) impressed or (b) flattened or slightly rounded.

Male genitalia. Orthandrous, i.e. unrotated, like the Pamphiliidae. Gonocardo strongly fused dorsally with base of gonostipes, less so ventrally. Dorsal inner bases of gonostipes proximal but not fused. Inner margins of gonostipal dorsum sub-parallel, subsequently divergent towards apices (e.g. *merceti*, Fig. 24) or divergent from base to apex (e.g. *capitalatus*, Fig. 25).

Sclerotisation of dorsal surface gonostipes. Extending apically from gonocardo to apex of gonostipes (e.g. *kuznetzovi*, Fig. 24) (primitive) or imcomplete (e.g. *capitalatus*, Fig. 25).

Upper and lower points of articulation between gonostipes and gonostylus. Either parallel (e.g. *merceti*, Fig.22) (primitive) or upper projecting more apically (e.g. sp.4, Fig.23).

Dorsal surface of gonostylus. Viewed laterally, either curved upwards toward apex (e.g. *merceti*, Fig. 22) (primitive) or straight (e.g. sp.4, Fig. 23). Surfaces of gonostyli hirsute, inner and ventral surfaces with shorter setosity than outer and dorsal. Setosity uniform in length and colour (e.g. *merceti*) or composed of longer, stouter and darker setae interspersed with shorter, finer and lighter hairs (e.g. *capitalatus*). Gonomaculae hemi-elliptical, semi-circular, circular or deformed oblong. (Neither scored.)

Volsellae. All species with reticulate sculpture and latero-ventral surfaces rounded (most species, e.g. *cephalotes*, Fig. 26) (primitive) or virtually straight (those with atrophied digiti and cuspides, e.g. *olivieri*, Fig. 27). Medio-apical region of volsellae relatively unsclerotised (Fig. 26) (most species) (considered primitve) or enlarged and strongly sclerotised (Fig. 27) (*olivieri* and *phaenicius*).

Digitus. Viewed ventrally, laminiform, sclerotised and projecting prominently from the volsellae (most species, e.g. *cephalotes*, Fig. 6) (primitive) or in the form of a small and almost unsclerotised apical projection of the volsellae (five species, e.g. *phaenicius*, Fig. 7). Where projecting strongly from the volsellae the digitus is of six forms: a small oblong, or slightly dorsally convex, lamina which is apically pointed (e.g. *kuznetzovi*, Fig. 52, called Form 1) (considered plesiomorphic); (ii) a long lamina with dorsal surface

straight baso-dorsally and slightly concave medially, rounded apically, with ventral surface slightly concave (e.g. *eversmanni*, Fig. 50, Form 2); (iii) similar to (ii), but convex baso-dorsally and distinctly angled or pointed apically (e.g. *jucundus*, Fig. 55, Form 3); (iv) a rotated lamina, appearing no longer vertical in orientation but horizontal (e.g. *bucephalus*, Fig. 51, Form 4); a basally narrow lamina with apex appearing as a large and deformed square or rhombus (e.g. *interruptus*, Fig. 53, Form 5); (v) a narrow lamina, basally, medially concave to a narrow rounded or pointed (appearing beaked) apex, apico-ventrally slightly convex, medio-ventrally concave (e.g. *cephalotes*, Fig. 7, Form 6) and (vi) similar to (v) but dorso-medially, strongly concave and then almost straight to apex, which is distinctly truncate, apico-ventrally convex, medio-ventrally slightly concave (e.g. turcicus, Fig. 54, Form 7).

Cuspis. Viewed ventrally, digitiform or sub-clavate, apically, (Fig. 7) and without basal protuberance or deformed into a thumb-like apical projection and a more basal protuberance (Fig. 8) (considered as primitive and scored in combination with the digitus). In most species, between the digitus and cuspis is a reflexed lamina or pocket, directed basally (Fig. 7). Where the cuspis projects distinctly more apically than the digitus this is considered derived. It is absent or vestigial in species where the digiti are not lamellar and the cuspidides are deformed (Fig. 94). Generally, the apex of this lamina or pocket is wider than the base of digitus at its meeting with the volsellae, although in *escalerai* it is distinctly narrower, but this is not used in key construction or in cladistic analysis.

Apex of aedegal apodemes. Rounded or slightly flared and angular. Apodemes never longer than penis valves.

Penis valves. Viewed laterally digitiform (25 species, called Forms 1-5), or blade-like (Fig. 59) (4 species, Form 6) or massively swollen apico-ventrally (Fig. 61) (1 species, Form 7). The digitiform penis valves are subdivided into swollen digitiform (where the baso-ventral region is strongly swollen) (Fig. 56) (6 species, termed Form 1); apically unciform (with a pronounced hook-shape, apico-ventrally) (Fig. 58) (4 species, Form 2); narrow with remnant of hook, appearing angled apico-ventrally (Fig. 60) (6 species, Form 3); narrow with dorso-base distinctly rounded, not angled (Fig. 105) (4 species, Form 4); swollen digitform but with apex distinctly rod-like (Fig. 62) (2 species); in the formed of a highly deformed or inclined shallow S-shape (Fig. 57) (3 species, Form 5). Maximum width of lateral lobes of penis valve as wide as maximum width of penis valve (Fig. 64), or wider than maximum width of penis valve (Fig. 63).

Seventh sternum of female. Apical margin appearing produced so that the sclerite is asymmetrical. Usually in the form of two apico-medial convexities, strongly or weakly concave or truncate in between. In *judaicus* the apical margin is in the form of a single prominent but rounded projection. In many species the apical margins are laterally bent toward the dorsum and this gives the impression that the apico-medial projections are

more prominent than in reality.

Abdominal sculpture. Both terga and sterna are usually smooth with occasional and irregular fine punctulae. Only on the most punctate species (e.g. *cephalotes*) is this modified to punctulate-punctate. Comments as for cephalic sculpture and not used in keys or analysis.

Abdominal setosity. Only tergum 1 and laterally on tergum 2 regularly exhibit setosity similar to that of the head; dorsally on terga 2-8 with short stout black (e.g. sp.1) or brown (e.g. sp.2) setae; laterally on remainder of terga setae much shorter (diameter of rear ocellus) and sparser than head; ventrally as head but much sparser, particularly medially; occasionally, tergum 8 and basal plate with sparse coating of much shorter hairs (about twice diameter of rear ocellus) laterally. Comments as for cephalic setosity and not used in keys or analysis.

Key to the identification of male Megalodontidae

1 Galea swollen strongly; eighth tergum with semi-circular or horseshoe-shaped impression medio-apically or crimped or folded ventrally at apical margin 2

- Galea slightly or strongly elongate; eighth tergum with median furrow, deep and narrow or broad and becoming obsolete apically, or virtually flat without any impression 5

2 Genal carinae absent; flabellae reduced to small apico-ventral projections; basal plate without lip; digitus and cuspis as in Fig. 126 ..... *judaicus* Lepeletier

- Genal carinae present; basal plate with lip; flabellae of standard type 3

3 Teeth of tarsal claws widely separated, flabella of third antennal segment as long as the 5-6 following segments ..... *kuznetzovi* Dovnar-Zapolskij

- Teeth of tarsal claws proximal, flabella of third antennal segment, at most, as long as the 3-4 following segments 4

4 Flabella of third antennal segment as long as the 3-4 following segments .....
..... *merceti* Konow

- Flabella of third antennal segment as long as the 1-2 following segments .....
..... *levaillantii* Lucas

5 D:E 0.8-1; if greater than 1 then flabella of third antennal segment as long as the 8-9 following segments and tergum 8 flattened medially but without distinct impression or furrow; digiti and cuspidides reduced as in Fig. 7 6

- D:E more than 1, if less then scrobes deep and with pit behind antennal insertions and genal carinae absent or with penis valve strongly unciform apically 10

6 Flabella of third antennal segment as long as the 25-27 following segments; genal carinae obsolete ..... *skorniakowii* Freymuth

- Flabella of third antennal segment, at most, as long as the 12-13 following segments; genal carinae complete 7

7 Eighth tergum with distinct V-shaped impression, widening and becoming obsolete

apically; flabella of third antennal segment as long as the 11-13 following segments; volsellar sac strongly sclerotised apico-medially 8

- Eighth tergum flattened medially without distinct impression or furrow; flabella of third antennal segment as long as the 8-9 following segments; volsellar sac strongly unsclerotised apico-medially 9

8. Head behind eyes and in genal and post-genal areas widely marked in black; gonostyli appearing strongly produced apically, as in Figs 65 and 66... *phaenicius* Lepeletier

- Head behind eyes and in genal and post-genal areas entirely yellow; gonostyli with dorsal surface straight and of standard form ..... *olivieri* Brullé

9 D:E 1; gonostyli shorter than ventral length of gonostipes and with dorsal surface straight ..... *nitens* Freymuth

- D:E 1.5; gonostyli longer than ventral length of gonostipes (Fig. 67) and with dorsal surface strongly curved upwardly (Fig. 68) ..... *xanthosomus* Zhelochovtsev

10 Vertiginal colour as flabellicornis syndrome; penis valve laterally strongly unciform apically (e.g. Figs 58 and 60) or as in Fig. 119..... 11

- Vertiginal colour as in bucephalus or cephalotes syndromes; penis valve laterally, not unciform apically 18

11 Gena acarinate; very finely and sparsely punctulate between rear ocelli and eyes; remainder of head and thorax appearing smooth or with a few punctulae; scrobes deep and with pit behind antennal insertions (cf. Fig. 40).....
.....*parvus* Dovnar-Zapolskij

- Gena carinate; at least punctulate-punctate between rear ocelli and eyes and remainder of head and thorax more coarsely sculpted; scrobes shallow and without pit behind antennal insertions 12

12 Facial coloration as in flabellicornis syndrome; glossa parallel-sided toward apex .. 13

- Face yellow; glossa slightly flared toward apex ..... *jucundus* Mocsáry

13 Penis valve strongly unciform apically; dorsal sclerotisation of gonostipes complete, if incomplete then genal carinae absent 14

- Penis valve at most slightly angled apico-ventrally; dorsal sclerotisation of gonostipes incomplete 16

14 Thorax, laterally and ventrally, and sterna yellow; coxae yellow; D:E 0.83; digitus as in Fig. 102; aedeagal apodemes parallel-sided and rounded apically .....
..... *reitteri* Konow

- Thorax, laterally and ventrally, strongly marked with black and sterna marked with black, at least baso-laterally; coxae black with yellow longitudinal fleck; D:E 1:1 or greater; digitus as in Figs 50 and 134; aedeagal apodemes flared apically 15

15 D:F 0.86; B:C 1.67; yellow flecks on metapostnotum present; digitus as in Fig. 134..
.....*escalerai* Klug

- D:F 1.15-1.67; B:C 1.38-1.58; yellow flecks on metapostnotum absent; digitus as in

Fig. 50..... *eversmanni* Freymuth

16 Head between rear ocelli and eyes closely and coarsely punctate to punctate-rugulose. ..... *luteiventris* Konow

- Head between rear ocelli and eyes, at most, punctate 17

17 D:E 1 or slightly more; closely puncate on mesoscutum without lustrous interspaces on lateral lobes; flabella of third antennal segment as long as the 5-6 following segments; 10-11 mm in length ..... *flabellicornis* Germar

- D:E 1.4-1.7; mesoscutum sparsely punctate to punctate, becoming punctulate with lustrous interspaces on lateral lobes; flabella of third antennal segment as long as the 4-5 following segments; 8-9.5 mm in length sp.3

18 Vertiginal coloration as in bucephalus syndrome; digitus oriented laterally rather than vertically 19

- Vertiginal coloration as in cephalotes syndrome; digitus oriented vertically rather than laterally 23

19 Face yellow (cf. olivieri syndrome) 20

- Facial colour as in flabellicornis syndrome 22

20 Thorax, laterally and ventrally, and sterna predominately yellow; genal carinae obsolete; flabella of third antennal segment as long as the following segment; penis valves without enlarged lateral lobes; dorsally as in Fig. 64, laterally as in Fig. 62; digitus as in Fig. 51..... *bucephalus* Klug

- Thorax, laterally and ventrally, and sterna strongly marked with black; genal carinae present; flabella of third antennal segment barely half the length of the following segment or as long as the following 1-2 segments; penis valves with enlarged or massively enlarged lateral lobes; dorsally as in Fig. 63, laterally as in Figs 70 or 72; digiti as in Figs 71, 74 or 75 21

21 B:C 1.38; flabella of third antennal segment as the following 1-2 segments; dorsal sclerotisation of gonostipes incomplete; penis valves with enlarged lateral lobes (Fig. 63); digitus as in Fig. 71; dorsal surface of gonostylus straight..... *capitalatus* Konow

- B:C 2-2.2; flabella of third antennal segment barely half the length of the following segment; dorsal sclerotisation of gonostipes complete; penis valves without enlarged lateral lobes (Fig. 69); digitus as in Fig. 73; dorsal surface of gonostylus strongly curved upwardly ..... *lacourti* Chevin

22 D:E 1.73; genal carinae present; flabella of third antennal segment as long as the 2 following segments; dorsal sclerotisation of gonostipes incomplete; digitus as in Fig. 74 ..... *gratiosus* Mocsáry

- D:E 2.92; genal carinae present but distinct only in malar region; flabella of third antennal segment as the following 1-2 segments; dorsal sclerotisation of gonostipes complete; digitus as in Fig. 75 ..... sp.4

23 Antennal scrobes deep and with pit behind antennal insertions; penis valve laterally as in Fig. 40 24

- Antennal scrobes shallow and without pit behind antennal insertions; penis valve laterally as in Figs 57, 81, 82 or 83 25

24 Face yellow (cf. olivieri syndrome); flabella of third antennal segment, at most, as long as the 5 following segments; D:E 1.9-2 26

- Face cephalotes syndrome; flabella of third antennal segment as long as the 6-9 following segments; D:E 1.38-1.5 ..... *interruptus* Gussakovskij

25 Predominately yellow, laterally and ventrally on thorax and on sterna; flabella of third antennal segment as long as the 3-4 following segments; post-ocellar striae incomplete ..... *quinquecinctus* Klug

- Strongly marked with black, laterally and ventrally on thorax and on sterna; flabella of third antennal segment as long as the 4-5 following segments; post-ocellar striae complete ..... *spiraeae* Klug

26 Apical 7-9 segments of antennae without flabellae 27

- At most, 4-5 apical segments of antennae without flabellae 28

27 Face coloration fabricii syndrome, longitudinal sclerotisation of gonostipes incomplete; thorax laterally and ventrally and sterna predominately black; A:B 2.4-2.7; B:C 1.67-2; digitus as in Fig. 78; penis valve laterally as in Fig. 81 .... *fabricii* Leach

- Face coloration cephalotes syndrome, longitudinal sclerotisation of gonostipes complete; thorax laterally and ventrally and sterna predominately yellow; A:B 3 or more; B:C 1.4-1.5; digitus as in Fig. 79; penis valve laterally as in Fig. 82 ..... sp.5

28 Facial coloration as in flabellicornis syndrome; closely and coarsely punctate to punctate rugulose between rear ocelli and eyes; metepisternum and metepimeron with postero-dorsal fleck of yellow sp.1

- Facial coloration as in cephalotes syndrome; at most closely and coarsely punctate, but never punctate-rugulose, between rear ocelli and eyes; metepisternum and metepimeron black 29

29 Scape black; sterna 3-7 with small white-yellow markings apico-medially; flabella of third antennal segment as long as the following two segments; digitus as in Fig. 54 ..... *turcicus* Mocsáry

- Scape yellow or ochraceous, sometimes marked with black longitudinally on outer face; sterna 3-7 with narrow white-yellow or yellow band apically; flabella of third antennal segment as long as the following segment or slightly shorter or as long as the following 1-2 segments; digiti as in Figs 6 and 85 30

30 B:C 1.39-1.44; digitus as in Fig. 6; penis valve, laterally, as in Fig. 57; wings lightly fuscous throughout ..... *cephalotes* Fabricius

- B:C 2.67; digitus as in Fig. 85; penis valve, laterally, as in Fig. 83; wings fuscous

anteriorly, hyaline posteriorly sp.2

Key to the identification of female Megalodontidae

1 Galea swollen strongly 2

- Galea slightly or strongly elongate 4

2 Genal carinae absent; flabellae reduced to small apico-ventral projections.....
.....*judaicus* Lepeletier

- Genal carinae present; flabellae of standard type 3

3 Teeth of tarsal claws widely separated, flabella of third antennal segment as long as the 4-6 following segments; pedicel square; A:B 1.86; B:C 1.75; D:E 1.5; D:F 1.6
..... *kuznetzovi* Dovnar-Zapolskij

- Teeth of tarsal claws proximal, flabella of third antennal segment as long as the 3-4 following segments; pedicel transverse; A:B 3; B:C 1.75; D:E 1.1; D:F 1.2 .....
..... *merceti* Konow

4 Antennal scrobes shallow and without pit behind antennal insertions 5

- Antennal scrobes deep and with pit behind antennal insertions 28

5 Vertiginal colour cephalotes syndrome..... 6

- Vertiginal colour entirely yellow behind eyes (cf. olivieri syndrome) or flabellicornis or bucephalus syndromes 10

6 At most, 4-5 apical segments of antennae without flabellae 7

- Apical 7-10 segments of antennae without flabellae 9

7 Flabella of third antennal segment as long as the following segment or slightly shorter; tergum 1 black with large apico-lateral fleck of yellow; closely, but not coarsely punctate between rear ocelli and eyes.....*cephalotes* Fabricius

Flabella of third antennal segment, at least, as long as the following 1-2 segments; tergum 1 black; closely and coarsely punctate between rear ocelli and eyes..... 8

8 Scape black basally, dark-brown apically; pedicel brown to dark-brown; flabella of third antennal segment as long as the following 2-3 segments; sterna 2-4 and 7 black; B:C 2.45-2.65 ..... *turcicus* Mocsáry

- Scape and pedicel ochraceous; flabella of third antennal segment, at least, as long as the following 1-2 segments; B:C 2.9-3.2; sterna 2 black.....sp. 2

9 Face coloration fabricii syndrome; scape ochraceous to testaceous with large black longitudinal fleck on upper surface; pedicel black..... *fabricii* Leach

- Face coloration cephalotes syndrome; scape yellow, ochraceous to testaceous fleck on upper surface; pedicel brown basally, testaceous apically..... sp. 5

10 Vertiginal colour entirely yellow behind eyes (cf. olivieri syndrome) or flabellicornis syndrome; if bucephalus syndrome then flabella of third antennal segment as long as the following 19-20 segments.....11

- Vertiginal colour bucephalus syndrome; flabella of third antennal segment, at most as

long as the following 2-3 segments 24

11 Entirely yellow behind eyes or with flabella of third antennal segment longer than the following 7 segments 12

- Vertiginal coloration as in flabellicornis syndrome and with flabella of third antennal segment shorter than the following 7 segments 16

12 Genal carinae present; head between rear ocelli and eyes, at most, punctate with lustrous interspaces; flabella of third antennal segment, at most, as long as the following 12-13 segments 13

- Genal carinae obsolete; head between rear ocelli and eyes closely punctate; flabella of third antennal segment as long as the following 19-20 segments; vertiginal coloration as in bucephalus syndrome ..... *skorniakowii* Freymuth

13 Flabella of third antennal segment as long as the following 7-8 segments; antennae with 12-14 segments ..... *xanthosomus* Zhelochovtsev

- Flabella of third antennal segment at least as long as the following 10 segments; antennae 18-21 segmented 14

14 Flabella of third antennal segment at least as long as the following 10-11 segments; upper head much less punctate than mesepistemum; malar space narrow..... ..... *nitens* Freymuth

- Flabella of third antennal segment as long as the following 12-13 segments; upper head not less punctate than mesepisternum; malar space wide 15

15 Facial yellow complete; pedicel longer than third antennal segment..... *olivieri* Brullé

- Facial yellow incomplete; medial yellow separated from yellow between antennal insertions and eye margins and broken into medial oblong between antennal insertions and, occasionally with two large transverse lateral flecks; pedicel and third antennal segment of equal length ..... *phaenicius* Lepeletier

16 Legs yellow, at most fore-legs marked or ringed in black basally; hind-coxal apical incision open 17

- Only hind-femora yellow or ochraceous entirely, fore- and mid- strongly marked with or predominately black; hind-coxal apical incision closed..... 20

17 Medial facial yellow complete, extending into malar region, in the form of a deformed triangle 18

- Medial facial yellow greatly reduced to a small campaniform mark above a smaller roundel ..... *eversmanni* Freymuth

18 Sclerite above sawsheath yellow or yellow ochraceous; mesoscutum closely punctate 19

- Sclerite above sawsheath black; mesoscutum very sparsely punctulate-punctate..... ..... *jucundus* Mocsáry

19 Yellow between antennal insertions and eye margins produced vertically and inwardly toward ocelli with its most apical point lying posterior to a lateral line drawn

through the anterior ocellus ..... *escalerai* Konow

Yellow between antennal insertions and eye margins produced vertically and slightly inwardly toward ocelli with its most apical point lying anterior to a lateral line drawn through the anterior ocellus ..... *reitteri* Konow

20 Tergum 1 black without yellow markings or dark-brown to black with small white-yellow fleck apico-laterally.....21

- Tergum 1 with large yellow fleck apico-laterally 22

21 Tergum 1 black; flabella of third antennal segment as long as the following 4-5 segments; body length 10-11.5 mm; genal carinae present; vertiginal/occipital margin rounded.....*flabellicornis* Germar

Tergum 1 dark-brown to black with small white-yellow fleck apico-laterally; flabella of third antennal segment as long as the following 3-4 segments; body length 7-8 mm; genal carinae absent; vertiginal/occipital margin strongly angled.....
..... *parvus* Dovnar-Zapolskij

22 Head between rear ocelli and eyes and mesoscutum coarsely and closely punctate to punctate-rugulose; pedicel square or transverse.....23

- Head between rear ocelli and eyes and on mesoscutum, at most, punctate; pedicel oblong.....sp. 3

23 Flabella of third antennal segment as long the following 4 segments.....
..... *luteiventris* Konow

Flabella of third antennal segment as long the following 1-2 segments .....sp. 1

24 Yellow between antennal insertions and eye margins contiguous with lower facial yellow 25

- Yellow between antennal insertions and eye margins widely or narrowly separated from lower facial yellow.....

25 Yellow between antennal insertions and eye margins produced vertically and inwardly toward ocelli with its most apical point lying posterior to a lateral line drawn through the anterior ocellus; flabella of third antennal segment barely longer than the following segment; genal carinae present but becoming obsolete, only clearly visible in malar region..... *bucephalus* Klug

- Yellow between antennal insertions and eye margins produced vertically and slightly inwardly toward ocelli with its most apical point lying anterior to a lateral line drawn through the anterior ocellus; flabella of third antennal segment as long as the following 1-2 segments; genal carinae present and distinct..... *capitalatus* Konow

26 Flabella of third antennal segment not more than half the length of the following segment; eye margins narrowly separated from lower facial yellow. *lacourti* Chevin

- Flabella of third antennal segment at least as long as the following 1-2 segments; eye margins widely separated from lower facial yellow.....

27 Genal carinae present; flabella of third antennal segment as long as the following 2-3

segments; scape yellow throughout; D:F 1.55..... *gratiosus* Mocsáry

- Genal carinae present but becoming obsolete, only clearly visible in malar region; flabella of third antennal segment as long as the following 1-2 segments; scape yellow with broad longitudinal black stripe on dorso-lateral face; D:F 1.1 .... sp. 4

28 Closely and coarsely punctate between rear ocelli and eyes; flabella of third antennal segment as long as the following 5-6 segments; D:F 1.7-1.8 .... *interruptus* Gussakovskij

- At most, closely but not coarsely punctate between rear ocelli and eyes; flabella of third antennal segment, at most, as long as the following 4-5 segments; D:F 2.1-2.25 ... .29

29 Punctulate-punctate with lustrous interspaces between rear ocelli and eyes; flabella of third antennal segment as long as the following 2-3 segments; pedicel square; genal yellow broad and extending to malar region ..... *quinquecinctus* Klug

- Closely punctate between rear ocelli and eyes; flabella of third antennal segment, as long as the following 4-5 segments; pedicel transverse; genal yellow narrow and not extending to malar region ..... *spiraeae* Klug

MEGALODONTES Latreille

Megalodontes Latreille, 1802: 302; Rohwer, 1911a; Abe and Smith, 1991. Type species: *Tenthredo cephalotes* Fabricius, 1781, by monotypy.

Tarpa Fabricius, 1804: 19; Rohwer, 1911a; Abe and Smith, 1991. Type species: *Tenthredo cephalotes* Fabricius, 1781, by subsequent designation in Westwood (1840); objective synonym of *Megalodontes* Latreille.

Megalodontes (Rhipidioceros) Konow, 1897: 2; Abe and Smith, 1991. Type species: *Tarpa flabellicornis* Germar, 1817, by subsequent designation in Rohwer, 1911a.

Melanopus Konow, 1897: 12; Rohwer, 1911a; Abe and Smith, 1991. Type species: *Tarpa fabricii* Leach, 1817, by monotypy.

Tristactus Konow, 1897: 12; Rohwer, 1911a; Abe and Smith, 1991. Type species: *Tarpa judaica* Lepeletier, 1823, by monotypy.

Megalodontes (Forifculotarpa) Pic, 1915: 12; Abe and Smith, 1991. Type species. *Tarpa levaillantii* Lucas, 1848, by monotypy.

Clada Pic, 1915: 12. Nomem nudum.

Tristactoides Chevin, 1985: 73. Type species: *Tristactoides lacourti* Chevin: 73, by original designation and monotypy.

Included taxa

anatolicus Mocsáry, 1883

aquilus Konow, 1902b
bucephalus (Klug, 1824)
    hispanica Spinola, 1843
capitalatus Konow, 1904
cephalotes (Fabricius, 1781)
    laticeps Konow, 1897
escalerai Konow, 1899
eversmanni Gussakovskij, 1935
eversmanni (Freymuth, 1870)
    loewii Stein, 1876
    multicincta Mocsáry, 1891
exornata (Zaddach, 1865)
fabricii (Leach, 1817)
    megacephala Klug, 1824
flabellata Eversmann, 1847
flabellicornis (Germar, 1817)
    albicincta Stein, 1876
    coronata Zaddach, 1865
    speciosa Mocsáry, 1877
flavicornis (Klug, 1824)
gratiosus (Mocsáry, 1881)
    castiliensis Enslin, 1913
interruptus Gussakovskij, 1935
    antoniae Zombori, 1971
jucundus (Mocsáry, 1891)
judaicus (Lepeletier, 1823)
    candidatus Konow, 1899
    caesariensis Lepeletier, 1823
    leucosticta Zaddach, 1865
    punctatus Konow, 1898
klugii (Leach, 1817)
kuznetzovi Dovnar-Zapolskij, 1930
    andromorphus Dovnar-Zapolskij, 1930
lacourti (Chevin, 1985)
levaillantii (Lucas, 1848)
luteiventris (Konow, 1894)
medius Konow, 1904
merceti Konow, 1904
mocsáryi (André, 1881)

mundus Konow, 1904
nigritegulis Konow, 1904
nitens (Freymuth, 1870)
    decussatus Konow, 1906
olivieri (Brullé, 1846)
panzeri (Leach, 1817)
parvus Dovnar-Zapolskij, 1930
phaenicius (Lepeletier, 1823)
    caucasica André, 1881
    dusmeti Enslin, 1913
    imperialis Konow, 1897
    kohli Konow, 1897
plagiocephala (Fabricius, 1804)
quinquecinctus (Klug, 1824)
    apakensis Togashi, 1973
    nitidus Maa 1949
    tsunekii Togashi, 1973
reitteri Konow, 1894
scythicus Zhelochovtsev, 1988
skorniakowii (Freymuth, 1870)
    lamellata André, 1881
    victoriosa Jakovlev, 1892
spiraeae (Klug, 1824)
    borealis Jakovlev, 1892
    coreensis Takeuchi, 1927
    pectinicornis Klug, 1824
    ruthena Jakovlev, 1888
    sibiriensis Rohwer, 1925
spissicornis (Klug, 1824)
sulphurea (Lucas, 1848)
turcicus Mocsáry, 1881
    orientalis Mocsáry, 1881
xanthocerus Gussakovskij, 1935
xanthosomus Zhelochovtsev,1927
    curticornis Dovnar-Zapolskij, 1930
sp.1
sp.2
sp.3
sp.4

sp.5

Species descriptions

Megalodontes bucephalus (Klug)

(Figs 31, 51, 62, 64, 84, 88, 129)

Tarpa bucephala Klug, 1824: 185; Konow, 1897. SYNTYPES ♂, ♀, Portugal (ZHMB), [examined].

Tarpa hispanica Spinola, 1843: 117. SYNTYPES ♂, ♀, Spain (V. Ghiliani) (MRSN), [not examined]. Synonymised by Zaddach, 1865.

Megalodontes bucephalus (Klug); Kirby, 1882.

Male

Length 8.5-10 mm; EA: 0.94; A:B 2.09; B:C 1.64; D:E 2.38; D:F 1.38 (2 specimens measured)

Colour: predominately black on head and thorax, dorsally; predominately yellow on venter of head and thorax and dorsally and ventrally on abdomen. Vertiginal yellow contiguous with genal yellow; facial yellow, in a W-shape, contiguous with fleck between antennal insertion and eye margin. Mouthparts dark-brown basally, strongly marked ochraceous to testaceous apically. Scape black, inner ventral face yellow; pedicel black; third antennal segment black, anterior apical face and flabella testaceous; flagellum testaceous to red-brown; flabellae dark-brown to black. Pronotum yellow, except dorso-medially and anterior collar. Four yellow flecks on mesoscutum. Yellow flecks behind cenchri present (usually vestigial) or absent. Tegula and humeral sclerite yellow. Mesepisternum yellow, except for ventral one-sixth to one-fifth, metepisternum and mesepimeron yellow, except anterior margin; metepimeron yellow, except ventrally. Fore- and mid-coxae yellow, marked with black on outer face; hind-coxae yellow. Fore- and mid-femora yellow, ringed black basally and with black fleck dorsally in basal one-third; hind-femora yellow. Wings slightly fuscous anteriorly and basally, hyaline posteriorly and apically. Venation brown anteriorly and basally, testaceous posteriorly and apically. Tergum 1 black, yellow fleck, apico-laterally; terga 2-4 black, yellow fleck laterally, extended medially; terga 5-7 apical yellow band complete; basal plate yellow, black baso-medially only, furrow black. Sterna 2-8 yellow, black at extreme latero-bases, all sterna medially smudged darker.

Head Sculpture: closely punctulate-punctate between rear ocelli and eyes, remainder punctulate, except between anterior ocellus and antennal insertions which is closely punctate. Setosity: coating of long black hairs, almost bare between antennal insertion and malar region. Post-ocellar striae complete, but indistinct in occipital region. Pentagonal area flat, virtually unexcavated, with small anterior puncture. Genal carinae present but becoming obsolete, only clearly visible in malar region. Malar space narrow. Galea

elongate; glossa longer than galea, curved downward apically, parallel-sided; paraglossa: hemi-tubular, shorter than glossa. Antennae 15 segmented, 3-4 without flabella; pedicel oblong; flabella of third antennal segment: as long as the following segment.

Thorax Sculpture: yellow areas smooth, black areas sparsely punctulate-punctate with lustrous interspaces. Setosity: as head. Pronotal collar: collapsing (anterior ledge of pronotum very narrow). Hind-coxal apical incision closed.

Abdomen Sculpture: dorsally smooth to very finely and sparsely punctulate, ventrally similar but with even fewer punctulae. Setosity: dorsally on tergum 1, dorso-medially on tergum 2 and laterally on terga 1-3 as head; laterally on terga 4-8 similar to head, but hairs shorter and sparser; dorsally on terga 3-8 with very short and sparse setae; ventrally as head, but sparser. Eighth tergum with broad shallow impression, becoming obsolete apically. Basal plate curved gradually toward apex, apical surface impressed distinctly; without lip; apical margin slightly convex. Dorsal inner margins of gonostipes sub-parallel basally, diverging to three-quarter length and curved laterally to apex. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus projecting more anteriorly than ventral. Dorsal surface of gonostylus straight, slightly upwardly curved at apex; setosity of gonostylus sparse coating of long, stout and dark hairs interspersed with shorter, fine and lighter hairs; gonomaculae large, appearing truncate basally, semi-circular apically. Lateral surface of volsellae rounded. Digitus (Fig. 51), latero-ventrally appears as a flared lamina, extremely broad apically and with massive concavity on outer surface. Cuspis digitiform, appearing sub-clavate in some specimens; volsellar pocket wide and asymmetrical apically. Laterally, penis valves massive, straight to slightly concave dorsally, almost semi-circular at apex, ventrally divergent from base to mid-length then angled strongly toward dorsum and strongly concave to rounded apex, thus appearing tapered; dorsally mitriform, lateral lobes wider than maximum width of one of the valves; aedeagal apodemes flared, albeit marginally.

Female

Length 8.5-10 mm; EA 0.94:1; A:B 2.45; B:C 1.82; D:E 2.21; D:F 1.41 (2 specimens measured)

Colour: as male dorsally, but more extensively yellow; predominately black ventrally. Vertiginal yellow contiguous with genal yellow, the latter more extensive than in males; yellow colouring between antennal insertion and eye margin produced vertically more extensively than in males and produced toward anterior ocellus. Mouthparts predominately dark-brown, palp segments and galea ochraceous to testaceous. Scape yellow; third antennal segment black, testaceous extreme dorso-apically; flagellum testaceous; flabellae dark-brown, lighter apically. Yellow on dorsum of pronotum as males but much reduced laterally. Four yellow flecks on mesoscutum larger. Yellow flecks behind cenchri larger. Mesepisternum with yellow fleck occupying dorsal half of sclerite, strongly produced downwardly posteriorly, remainder black; metepisternum and

metepimeron with yellow stripe dorsally. Propleurae and mesostema black. Fore-coxae black, yellow on apico-anterior surface; mid-coxae black; hind-coxae predominately black, lateral yellow fleck. Fore-femora yellow, ringed black basally and with black fleck on dorsal surface in basal one-third to half; mid-femora yellow, ringed black basally and with black fleck on dorsal surface in basal one-quarter to one-third; hind-femora yellow. Wings venation testaceous to red-brown; pterostigma yellow, except median region; veins R, M+Cu1 and 1A dark-brown to black basally. Terga 1-2 black, with large yellow fleck laterally; terga 3-7 apical yellow band complete, occasionally broken apico-medially on tergum 3; tergum 8 yellow, black in baso-medial one-quarter only. Sternum 1 black; sternum 2 black, yellow flecks at extreme latero-apices only; sterna 3-4 black, yellow fleck laterally, produced toward median, sterna 5-7 apical yellow band complete. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Sculpture: closely punctate between rear ocelli and eyes, otherwise punctulate-punctate, closely punctate between anterior ocellus and antennal insertions. Setosity: dense coating of long black hairs, virtually bare between antennal insertion and malar region. Antennae 14 segmented, 3 without flabella; flabella of third antennal segment barely longer than the fourth.

Material examined: SYNTYPES ♂,♀ and 2♂♂, 3♀♀ (RMNH, ISCM)

Distribution: Portugal (Algarve) and Spain (Malaga and Cadiz regions).

Comments: male often more strongly marked with black on mesepisternum, mesepimeron, metepisternum and metepimeron, often throughout on mesepimeron. Related to *lacourti* and *capitalatus*, and may distinguished from them by its obsolete genal carinae and the unenlarged lateral lobes of the penis valves. Females are separated from *capitalatus* by the obsolescence of the genal carinae and the greater vertical production of the upper facial yellow.

Megalodontes capitalatus Konow

(Figs 25, 63, 70, 71, 86, 130)

Megalodontes capitalatus Konow, 1904: 227; Gussakovskij, 1935. SYNTYPES ♂,♀, Spain: Aranjuez (R.G.Mercet) (DEIC), [examined].

Male

Length 10-11 mm; EA 0.98; A:B 2.53:1; B:C 1.38; D:E 2.11; D:F 1.18 (2 specimens measured)

Colour: head and thorax predominately black, dorsally and ventrally, abdomen predominantely yellow, dorsally and ventrally. Vertiginal yellow contiguous with genal yellow; facial yellow, in a W-shape, contiguous with fleck between antennal insertion and eye margin and produced vertically slightly. Mouthparts predominately dark-brown, apical palp segments and galea ochraceous to testaceous. Scape black, inner ventral

surface marked with yellow; pedicel black; third antennal segment: black, inner apical quarter testaceous; flagellum testaceous; flabellae testaceous, becoming darker at apices. Pronotum yellow dorsally, except postero-medially, dorso-laterally and latero-ventrally. Four yellow flecks on mesoscutum. Tegula and humeral sclerite yellow. Yellow flecks behind cenchri present. Mesepisternum black, yellow occupying dorsal one-quarter, strongly produced downwards posteriorly; metepisternum yellow, except anterior margin; metepimeron with dorsal yellow fleck. Propleurae and mesostema black. Fore- and mid-coxae black; hind-coxae black, marked with yellow laterally and apically. Fore-femora black in basal two-thirds, yellow in apical one-third; mid-femora yellow, ringed black in basal one-third; hind-femora yellow, ringed black in basal one-sixth to one-fifth. Wings slightly fuscous anteriorly and basally, hyaline posteriorly and apically; venation brown anteriorly and basally, testaceous posteriorly and apically. Tergum 1 black; terga 2-4 black with large lateral yellow fleck; terga 5-7 apical yellow band complete; tergum 8 yellow, only extreme base black. Sternum 1 black; stema 2-6 yellow band complete, occupying all of sclerite laterally, but only apical three-quarters medially; sternum 7 yellow band complete, black at extreme latero-bases; basal plate yellow.

Head Sculpture: closely punctulate-punctate between rear ocelli and eyes, remainder punctulate, except between anterior ocellus and antennal insertions which is closely punctate. Setosity: coating of long black hairs, almost bare between antennal insertion and malar region. Post-ocellar striae incomplete. Pentagonal area wide but shallow excavation by anterior ocellus, otherwise flattened toward anterior puncture. Genal carinae present. Malar space narrow. Galea elongate; glossa longer than galea, curved downward apically, parallel-sided; paraglossa hemi-tubular, shorter than glossa. Antennae 15 segmented, 3 without flabella; pedicel square; flabella of third antennal segment as long as the following 1-2 segments.

Thorax Sculpture: yellow areas smooth, black areas sparsely punctulate-punctate with lustrous interspaces. Setosity: as head. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: virtually smooth with a few sparse and fine punctulae dorsally, ventrally with even fewer punctulae. Setosity: dorsum of terga 1and 2, laterally and ventrally as head, but slightly sparser; remainder dorsally with shorter and sparser coating of hairs. Eighth tergum with broad and deep impression, becoming obsolete apically. Basal plate curved gradually toward apex; without lip; apical surface flattened; apical margin convex or truncate. Dorsal inner margins of gonostipes sub-parallel basally, gradually divergent, slightly concave beyond mid-length then curved abruptly laterally to apex. Dorsal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostipes and gonostylus projecting more anteriorly than ventral. Dorsal surface of gonostylus straight; gonostyli with a dense coating of long, stout and dark hairs interspersed with one of shorter, finer and lighter hairs; gonomaculae, large, appearing truncate basally but

semi-cicular apically. Lateral surface of volsellae rounded. Latero-ventral form of digitus as *bucephalus*, less flared apically and thus appearing less profoundly concave on outer (ex-dorsal) surface, but more extensively so along its length (Fig. 71); cuspis digitiform; volsellar pocket wide apically. Penis valves laterally strongly concave on dorsal surface, sharply angled ventrally at mid-length; dorsally similar to *bucephalus*, lateral lobes wide; form of aedeagal apodemes very slightly flared apically.

Female

Length 9.5-10 mm; EA 0.94; A:B 2.76; B:C 1.42; D:E 1.93; D:F 1.08 (2 specimens measured)

Colour: similar to male but more extensively yellow dorsally; laterally and ventrally predominately black. More extensively yellow on vertex and occiput than male; vertiginal yellow contiguous with genal yellow. Facial yellow similar to males, but lateral fleck between antennal insertions and eyes produced slightly vertically toward anterior ocellus. Mouthparts predominately dark-brown, palp segments and galea predominately testaceous. Scape yellow; third antennal segment yellow; flagellum ochraceous, becoming testaceous apically; flabellae red-brown; flabella of third antennal segment testaceous. Dorsum of pronotum more extensively yellow medially, reduced laterally and latero-ventrally or latero-ventral yellow contiguous with that dorso-laterally. Four yellow flecks on mesoscutum more extensive than males, particularly in axillary region. Yellow flecks behind cenchri present and larger. Mesepisternum black, with yellow marking in dorsal one-third to half, strongly produced downwards posteriorly; yellow on metepisternum and metepimeron reduced to small postero-dorsal flecks. Fore- and mid-coxae black; hind-coxae black, marked with yellow apico-anteriorly, sometimes greatly reduced. Fore-femora yellow, ringed black in basal one-fifth; mid-femora yellow, ringed black in basal one-sixth; hind-femora yellow. Tergum 1 black, yellow fleck apico-laterally; terga 2-3 black, large yellow fleck apico-laterally, extended medially; terga 4-7 apical yellow band complete; tergum 8 yellow. Sterna 2-3 black, small yellow fleck apico-laterally; sterna 4-6 black, large lateral yellow fleck widely broken medially; sternum 7 black, large lateral yellow fleck narrowly broken medially. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Setosity: coating of long black hairs, almost bare between antennal insertion and malar region. Antennae 15 segmented, 3 without flabella; flabella of third antennal segment as long as the following 1-2 segments.

Abdomen Sculpture: appearing smooth, with very fine and sparse punctulae dorsally and ventrally. Setosity: as head laterally, shorter and sparser dorsally and ventrally.

Material examined: SYNTYPES ♂,♀ and 4♂♂, 3♀♀ (MKRC, RMNH, ZSMC).

Distribution: Spain (Zaragoza, Teruel, Madrid and Cuenca regions).

Comments: Related to *bucephalus* and *lacourti*. It may be distinguished from the

former by its possession of genal carinae and from the latter by B:C and the longer flabella of the third antennal segment. Females are distinguished form those of *bucephalus* by the upper facial yellow coloration and the flabella of the third antennal segment.

Megalodontes cephalotes Fabricius

(Figs 6, 26, 32, 57, 87)

Tenthredo cephalotes Fabricius, 1781: 408; Latreille, 1802, 1810. SYNTYPE ♀, Germany: Hattorf (ZMUC), [examined].

Megalodontes laticeps Konow, 1897: 10. SYNTYPES ♂,♀, Romania: Mehadia. (NHMW), [examined].

Megalodontes cephalotes (Fabricius); Latreille, 1802.

Male

Length: 9-11 mm; EA 0.85-0.89; A:B 2.72-2.88; B:C 1.39-1.44; D:E 2.09-2.62; D:F 1.04-1.41 (10 specimens measured)

Colour: predominately black. Vertiginal yellow narrowly broken medially or absent and contiguous with genal yellow. Post-ocellar flecks absent. Facial yellow greatly reduced, represented only by an oblong fleck between antennal insertion and ocular margin and a smaller oblong fleck between the antennal insertions. Mouthparts predominately black, apical palp segments testaceous to light-brown. Scape yellow with longitudinal black fleck on outer face; pedicel black; third antennal segment and flagellum ochraceous; flabellae ochraceous, testaceous apically. Pronotum with yellow flecks dorso-laterally. Two or four yellow flecks on mesoscutum, anterior pair often absent. Yellow flecks behind cenchri absent. Tegula yellow; humeral sclerite testaceous. Mespisternum black with yellow fleck in dorsal one-sixth. All coxae black. Fore-femora black, ochraceous in apical one-third; mid-femora black, ochraceous in apical half; hind-femora ochraceous, marked black ventro-basally. Wings lightly fuscous throughout, except the hyaline apex of the fore-wing. Venation testaceous basally and anteriorly, ochraceous apically and posteriorly. Terga 1-3 black with yellow flecks apico-laterally; terga 4-7 apical yellow band complete, widest on tergum 4; tergum 8 yellow band narrowly broken medially. Sternum 2 apical band of yellow narrow and broken irregularly; sternum 3-7 apical band of yellow complete; basal plate black, yellow apically.

Head Sculpture: closely punctate betwen rear ocellus and eye, becoming punctate with lustrous interspaces on vertex and punctate-rugulose between anterior ocellus and antennal insertions. Setosity: dense coating of long hairs (nearly three times the diameter of rear ocellus), longer and denser in post-genal region. Post-ocellar striae incomplete. Pentagonal area with a slight excavation anterior of anterior ocellus, otherwise planar to anterior puncture Genal carinae present. Malar space narrow. Galea elongate; glossa

distinctly longer than galea, slightly downwardly curved, parallel-sided, even appearing tapered; paraglossa slightly shorter than glossa, slightly downwardly curved, between laminar and hemi-cylindrical. Antennal 16-18 segmented, 3-4 without flabella; pedicel oblong, flabella of third antennal segment as long as the following segment or slightly shorter.

Thorax Sculpture: punctate, although not closely so, on lateral lobes of mesocutum, punctate to punctulate-punctulate on its anterior and on mesoscutellum. Setosity: as head, longer and denser on propleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Setosity: tergum 1 and laterally on terga 2-3 as head, laterally on remaining terga with shorter hairs (little more than the diameter of rear ocellus), remainder of terga 2-7 with short hyaline setae, tergum 8 with apical row of short hairs; ventrally as head but shorter and sparser. Sculpture: smooth with very fine and occasional punctulae. Tergum 8 wide shallow impression becoming obsolete apically. Basal plate curved gradually toward dorsum; flattened apically; without lip and concave apically. Dorsal internal margins of gonostipes divergent gradually from base to three-quarter length, slightly concave at mid-length, angled abruptly laterally to apex. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting more anteriorly than ventral. Dorsal surface of gonostylus straight; sparse coating of long dark hairs; gonomaculae circular. Lateral surface of volsellae rounded. Digitus dorsally straight to mid-length, strongly convex, secondarily concave to rounded apex; ventrally weakly concave throughout its length and recurved to apex (Fig. 6); cuspis digitiform; volsellar pocket wide apically, asymmetrical and wider than base of digitus. Penis valve, dorsally, divergent from base to one-third of its length then tapering gradually to apex, lateral lobes not enlarged; laterally, basally perpendicular to dorsal surface which is straight to mid-length and then weakly convex to bluntly rounded apex; ventral surface straight to mid-length and then weakly concave to apex; aedeagal apodemes parallel-sided and rounded apically

Female

Length: 9-11 mm; EA 0.86-0.93; A:B 2.43-3.18; B:C 1.31-1.95; D:E 2.35-2.45; D:F 1.2-1.32 (10 specimens measured)

Colour: similar to males. Mouthparts black throughout. Scape yellow basally, ochraceous apically; pedicel testaceous to brown; flagellum and flabellae dark ochraceous throughout. Two or four yellow flecks on mesoscutum, anterior pair often lost or vestigial and indistinct, axillary flecks usually larger than males. Yellow flecks behind cenchri absent. Mespisternum black with yellow fleck in dorsal one-sixth. Fore-femora black in basal half, becoming brown towards apex, yellow to ochraceous only at apex; mid-femora black to dark-brown in basal one-third becoming brown towards apex, yellow to ochraceous in apical one-quarter only; hind-femora dark-brown only basally,

remainder testaceous to ochraceous. Wings: hyaline strongly fuscous on anterior half, less so on posterior; venation brown basally and anteriorly, testaceous apically and posteriorly. Terga 1-3 black with apico-lateral spots or flecks of yellow, tergum 2 occasionally black throughout; terga 4-8 apical yellow band complete, widest on tergum 4. Sterna 2-3 black; sternum 4 black with apical margin of yellow, broken medially; sternum 5-7 apical band of yellow, broken narrowly medially. Sclerite above sawsheath black.

Morphology as males with the exception of the following.

Head Setosity: as males on post-gena and lower face, slightly shorter on vertex. Antennae 17 segmented, 5 without flabella; flabella of third antennal segment as long as the following segment or slightly shorter.

Material examined: SYNTYPES 1♀ of *cephalotes*, 1♂ 2♀ of *laticeps*; non-type material 35♂♂, 74♀♀ (ZMUC, MHNG).

Distribution: Germany, Switzerland, Romania.

Comments: Males of *cephalotes* may be distinguished from *Megalodontes* sp.2 by the form of the digitus and the lateral form of the penis valves and its lightly fuscous wings. Females may be separated from turcicus and *Megalodontes* sp.2 by their shorter third antennal flabellae and the punctation between the rear ocelli and the eyes.

Megalodontes escalerai Konow

(Fig. 134)

Megalodontes escalerai Konow, 1899: 203; Gussakovskij, 1935. SYNTYPES ♂,♀, Turkey: Akbes, Gülex (DEIC), [examined].

Male

Length 11-12 mm; EA 0.92; A:B 2.45; B:C 1.67; D:E 1.14; D:F 0.86 (2 specimens measured).

Colour: dorsally, head and thorax predominately black, except dorsum of pronotum; abdomen predominately yellow. Ventrally head and thorax predominately black; abdomen predominately yellow. Vertiginal yellow contiguous with genal yellow. Face yellow with lateral colouring produced toward anterior ocellus. Strial flecks proximal to vertiginal yellow, separated by posterior of strium. Mouthparts dark brown; testaceous to ochraceous apically. Scape yellow, pedicel brown, third antennal segment testaceous with darker fleck apically; flagellum testaceous, becoming lighter in apical eight segments; flabellae: testaceous, becoming lighter in apical eight segments. Pleural region yellow, lined with black. Four yellow flecks on mesonotum. Tegula yellow. Mesoscutellum black. Lateral yellow flecks on metapostnotum present. Mesepisternum dorsal three-quarters yellow, produced downwardly at anterior but not greatly so; mesepimeron with small yellow spot dorso-posteriorly; metepisternum with dorsal yellow stripe; metepimeron predominately yellow. Fore- and mid-coxae black, yellow on inner

face; hind-coxae predominately yellow with black fleck near insertion continuing to apical incision. Wings: hyaline to slightly yellow; venation ochraceous to testaceous basally and anteriorly, ochraceous apically and posteriorly. Tergum 1 black with large lateral yellow flecks; tergum 2 black with large lateral yellow flecks extended medially; tergum 3-7 yellow complete apically, but occupying only apical quarter medially; tergum 8: yellow; sterna 2-7 yellow, with black flecks latero-basally; sternum 8 yellow.

Head Sculpture: punctate, closely so between rear ocellus and eye; punctate-rugulose between anterior ocellus and antennal insertions. Setosity: dense coating of long hairs, sparser in lateral yellow regions of face. Post-ocellar striae incomplete. Pentagonal area slightly excavated in region of anterior ocellus, otherwise flat to anterior puncture. Genal carinae present. Malar space narrow. Galea slightly elongate; glossa elongate, parallel-sided or slightly tapering toward and downwardly curved at apex; paraglossa hemi-tubular, slightly shorter than glossa. Antennae 16 segmented, 1 without flabella, pedicel oblong; flabella of third antennal segment as long as the following 5-6 segments.

Thorax Setosity: dense coating of long hairs, sparser in yellow regions. Sculpture: closely punctate, similar to head but less so anteriorly. Pronotal collar collapsing. Hind-coxal apical incision open.

Abdomen Sculpture: dorsally, smooth with occasional very fine and sparse punctulae, ventrally, smooth. Setosity: ventrally similar to head, terga 1-3 and 7 similar to head but sparser, remainder with very short and sparse hairs, laterally similar to head but sparser. Tergum 8 with deep furrow, narrowing and becoming obsolete toward apex. Basal plate curved gradually, but strongly narrowed towards dorsal surface of abdomen; without lip; apical surface slightly rounded; apical margin slightly convex. Dorsal inner margins of gonostipes divergent basally, curving laterally from mid-length to apex. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus projecting apically of ventral. Dorsal surface of gonostylus straight. Gonostylus with dense coating of long hairs, sparser apically; gonomaculae deformed circular. Lateral surface of volsellae rounded. Digitus, viewed latero-ventrally, as a large lamina, dorsal surface straight; ventral surface divergent to between one-third and mid-langth, convex to apex (Fig. 134). Cuspis digitoid, slightly shorter than digitus, projecting distinctly anteriorly of parapennial lobes; volsellar sac symmetrical, wide apically. Penis valves laterally digitiform, unciform apically and dorsally slightly divergent from base to beyond mid-length, tapering to apex, lateral lobes narrow; aedeagal apodemes flared apically.

Female

Length 9-12 mm; EA 0.9; A:B 2.72; B:C 1.64; D:E 0.92-0.93; D:F 1.25 (2 specimens measured)

Colour: simlar to male; ventrally predominately black throughout. More extensively yellow on vertex, longer flecks along striae; fleck between antennal insertion and eyes

greatly extended vertically and inwardly toward anterior ocellus. Mouthparts as males but, generally, darker throughout. Flabellae testaceous, all but apical three segments darkened apically. Pleurae, black. Four yellow flecks on mesoscutum. Mesepistemum marked with yellow in dorsal quarter, strongly downwardly produced posteriorly. Mespimeron, metepisternum and metepimeron black. Mesoscutellum black. (One specimen with a single lateral yellow fleck on left side.) Fore- and mid-coxae black, hind-coxae black, anterior apical face and laterally yellow. Terga 1-2 black with large lateral yellow flecks extended medially on tergum 2; terga 3-7 apical yellow band complete; tergum 8 yellow, black at extreme base only. Sterna 2-3 black; sternum 4 black, small yellow fleck apico-laterally; sterna 5-6 apical yellow band yellow complete, occupying apical third; sternum 7 large yellow fleck apico-laterally, broken medially. Sclerite above sawsheath yellow to ochraceous.

Morphology as males with exception of the following.

Head Setosity: dense coating of long hairs, sparser in lateral yellow regions of face, almost bare between antennal insertions and malar region. Antennae 15 segmented, 1 without flabella; flabella of third antennal segment as long as the following 5-6 segments.

Thorax Setosity: dense coating of long hairs, sparser in yellow regions. Sculpture: closely punctate, similar to head but less so anteriorly.

Abdomen Sculpture: virtually smooth dorsally, with a few sparse punctulae; ventrally smooth. Setosity: laterally, ventrally and terga 1, 2 and 8 with dense coating of long hairs, tergum 7 similar, but shorter and sparser, remaining terga bare.

Material examined: Syntypes ♂, ♀ and 2♂♂, 8♀♀ (BMNH, TAUI).

Distribution: Turkey, Israel.

Comments: one male from Israel is considerably darker on terga and sterna and missing yellow flecks behind cenchri, however, its head and thoracic colour are the same as the other material examined. Males may be separated from *eversmanni* by the ratios D:F and B:C. Females are distinguished from those of *reitteri* by the greater degree of upper facial yellow.

Megalodontes eversmanni (Freymuth)

(Figs 44, 50, 58)

Tarpa eversmanni Frejmuth, 1870: 225. SYNTYPE ♂, M(lady) K(avkaz) (ZMUM), [examined].

Tarpa loewii Stein, 1876: 56. HOLOTYPE ♀, Turkey: Patara (F.H. Loew) (ZMHB), [not examined].

Megalodontes loewii (Stein); Kirby 1882.

Tarpa (Megalodontes) multicincta Mocsáry, 1891: 157. SYNTYPE ♀, Caucasus (HNHM), [examined].

Male

Length 10-13 mm; EA 0.88-0.89; A:B 2.53-2.91; B:C 1.38-1.58; D:E 1-1.23; D:F 1.15-

1.67 (6 specimens measured).

Colour: predominately black, dorsally, and apprearing much darker than other members of the group. Ventrally, predominately black, although sterna are mostly yellow. Vertiginal yellow contiguous with genal yellow. Yellow colouring between antennal insertion and eye margin produced toward anterior ocellus, but separated from lower facial colouring. Strial flecks proximal to vertiginal yellow, separated by posterior remnant of strium. Mouthparts predominately dark brown, ochraceous to testaceous apically. Scape yellow with brown fleck on outer face, enlarged apically; pedicel black; third antennal segment and flagellum ochraceous; flabellae ochraceous becoming testaceous apically. Four yellow flecks on mesoscutum or anterior pair absent and smaller in comparison with *escalerai*. Tegula yellow, humeral sclerites ochraceous. Mesoscutellum black. Lateral and median yellow flecks on metapostnotum absent. Mesepisternum black, yellow occupying only dorsal one-fifth of sclerite, mespimeron, metepisternum and metepimeron black. Fore- and mid-coxae black; hind-coxae black with large yellow fleck apically. Wings slightly fuscous throughout on both fore- and hind-wings, more strongly so apically of pterostigma; venation testaceous testaceous anteriorly, ochraceous posteriorly of both fore- and hindwings. Tergum 1 black, with small yellow fleck laterally; terga 2-3 black, with yellow fleck laterally, produced toward median line; terga 4-7 apical yellow band complete; tergum 8 with yellow band complete, black only baso-medially and in basal half laterally. Sternum 2 black, marked with yellow laterally and apico-medially; sternum 3 yellow, black baso-medially; sterna 4-7 yellow, black basally; sternum 8 yellow, black basally only and in a narrow strip laterally.

Head Sculpture: punctate between rear ocellus and eye; punctulate to punctulate-punctate toward occiput; punctate-rugulose between anterior ocellus and antennal insertions. Setosity: coating of long hairs, sparser in lateral yellow regions of face. Post-ocellar striae incomplete. Pentagonal area slightly excavated in region of anterior ocellus, otherwise flat to anterior puncture or excavated in region of anterior ocellus, narrowing and flattened in region of anterior puncture. Genal carinae present. Malar space narrow. Galea slightly elongate; glossa elongate, parallel-sided, downwardly curved at apex; paraglossa hemi-tubular, slightly shorter than glossa. Antennae 18 segmented, 1 without flabella; pedicel oblong; relative length of flabella of third antennal segment: as long as following 5-7 segments.

Thorax Setosity: as head, slightly denser on propleurae. Sculpture: punctate on lateral lobes of mesonotum with lustrous interspaces and on mesoscutellum; punctulate to punctulate-punctate toward anterior, on lateral sclerites and on propleurae; meso- and metapleurae sparsely punctulate. Pronotal collar collapsing. Hind-coxal apical incision open.

Abdomen Sculpture: virtually smooth dorsally and ventrally, with the exception of a few sparse and fine punctulae. Setosity: as head on sterna, laterally on all terga, dorsally

on terga 1 and 2 and dorso-medially on tergum 3; dorsally on tergum as head but hairs much shorter; dorsally on remainder of terga with sparse and short setae. Tergum 8 with deep and narrow furrow, becoming obsolete apically. Basal plate curved toward apex, but not abruptly so; without lip; slightly flattened apically; apical margin convex. Dorsal inner margins of gonostipes sub-parallel to mid-length then curving gradually laterally to apex. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus projecting apically of ventral. Dorsal surface of gonostylus slightly curved to apex; gonostylus with coating of long hairs, dense baso-dorsally and ventrally, becoming sparser and shorter toward apex and laterally; gonomaculae deformed circular. Lateral surface of volsellae curved. Digitus, viewed latero-ventrally, as a large lamina, dorsal surface straight to mid length, concave in apical half; ventral surface divergent to between one-third and mid-langth, weakly convex to apex (Fig. 50). Cuspis digitoid, slightly shorter than digitus. Penis valves laterally digitoid, unciform apically and dorsally divergent from base to beyond three-quarter length, tapering to apex, lateral lobes narrow; aedeagal apodemes flared apically

Female

Length 11.5-13 mm; EA 0.88-0.89; A:B 2.67-3.1; B:C 1.43-1.8; D:E 1; D:F 1.07-1.25 (6 specimens measured)

Colour: similar to male, except slightly lighter dorsally and less extensively yellow ventrally. Vertiginal yellow contiguous with yellow flecks along remnants of post-occipital striae. Facial yellow much less extensive, reduced to one large yellow triangular fleck between antennal insertions and a smaller circular fleck on the upper clypeus. Fleck between antennal insertion and eye margin not produced along latter and only slightly produced toward anterior ocellus. Mouthparts as male, with the exception of the palp segments which are lighter throughout. Scape yellow, ochraceous apically; pedicel ochraceous to testaecous third antennal segment ochraceous to testaecous; flagellum ochraceous to testaecous basally, testaecous in apical 11-13 segments; flabellae testaceous basally, becoming red-brown apically on segments 4-12. Four yellow flecks on mesonotum. Humeral sclerite yellow. Mesoscutellum black. Mesepisternum black, with yellow fleck on dorsal one-fifth to one quarter, slightly produced downwards posteriorly. Fore- and mid-coxae black; hind-coxae black with large yellow fleck antero-apically. Wings as males, stronger fuscosity slightly more extensive in costal and sub-costal areas. Terga 3-7 with apical yellow band complete; tergum 8 with yellow band broken medially, occupying apical half of sclerite. Sterna 2-4 black; sterna 5-6 yellow band complete, occupying apical half of sclerite throughout; sternum 7 black, lateral yellow fleck extended medially. Sclerite above sawsheath black.

Morphology as males except for the following.

Head Setosity: as male, but slightly denser.

Pentagonal area with slightly greater excavation near anterior ocellus, otherwise as male.

Antennae 17-18 segmented, 1 without flabella.

Thorax Setosity: as male, slightly denser dorsally and ventrally. Sculpture; as male, lustrous areas on lateral lobes of mesonotum less distinct since punctation more proximal; more punctulate-punctate on pleural sclerites.

Abdomen Sculpture: as males, but slightly more punctulate dorsally. Setosity: as males, very slightly longer throughout.

Material examined: SYNTYPES ♂ of *eversmanni*, ♀ of *multicincta* and 10♂, 4♀ (BMNH, DEIC, IZUI, RMNH, ZMHB, ZMUC, ZMUM, ZSMC).

Distribution: Russia (Lower Caucasus, Pyatigorsk region), Armenia, Turkey (Hakkari, Adana, Tufanbeley), Greece (Lesbos).

Comments: Males separated from those of *escalerai* by the ratios D:F and B:C. Females are distinguished by the extreme reduction of their medial facial yellow.

Megalodontes fabricii (Leach)

(Figs 78, 81, 137)

Tarpa fabricii Leach, 1817: 130; Konow, 1897. SYNTYPE ♀, Europe (W.E. Leach.) (BMNH), [examined].

Tarpa megacephala Klug, 1824: 190. SYNTYPES ♂,♀, Germany: Tauria (Pallas) (ZMHB), [examined]. Synonymised by Zaddach, 1865.

Megalodontes fabricii (Leach); Kirby 1882.

Male

Length: 9.5-11.5mm; EA 0.85; A:B 2.4-2.7:1; B:C 1.67-2:1; D:E 1.83:1; D:F 1:1 (2 specimens measured).

Colour: predominately black throughout, yellow or white yellow markings greatly reduced. Occipital white-yellow broken medially and discontinuous with genal yellow, which is greatly reduced, present only posterior of lower eye and malar region. Post-ocellar flecks absent. Facial white-yellow absent and white-yellow between antennal insertions and eye margin present in the form of a trapezoidal longitudinal fleck, produced vertically slightly along eye margin above line of antennal insertions. Mouthparts predominately brown to dark-brown, palp segments lighter apically. Scape dark-brown to black; pedicel dark-brown to black; third antennal segment ochraceous; flagellum basal 6-7 segments ochraceous, remainder testaceous; flabellae ochraceous basally, testaceous apically. White-yellow dorso-laterally and laterally, although not ventrally on pronotum. Two small white-yellow flecks on mesoscutum in axillary region. Tegula black basally and medially, white-yellow apically; humeral sclerite black. Flecks behind cenchri absent. Mesepisternum black, white-yellow fleck on dorsal one-fifth. Fore- and mid-coxae black, hind-coxae dark-brown. Fore-femora ringed dark-brown basally, testaceous, becoming yellow apically; mid-femora testaceous, becoming yellow apically; hind-femora testaceous, becoming yellow apically. Wings fuscous throughout

but distinctly more so anteriorly. Venation testaceous basally and anteriorly; pterostigma red-brown, lighter posteriorly; ochraceous to testaceous apically and posteriorly. Terga 1-3 black; tergum 4 white-yellow band complete, occupying apical half of sclerite laterally, but only apical one-third medially; tergum 5 black, with large white-yellow fleck laterally, greatly extended medially; tergum 6 black, with white-yellow fleck laterally, slightly extended medially; tergum 7 black; tergum 8 white-yellow band complete, occuping only apical one-quarter laterally but apical two-thirds medially. Sternum 2 black; sternum 3 black, white-yellow transverse fleck apico-medially; sterna 4-7 wide band of white-yellow apico-medially; basal plate white-yellow, basally and laterally edged in black.

Head Sculpture: closely punctate between rear ocelli and eyes, becoming punctate toward occiput and on face; punctate-rugulose between anterior ocellus and antennal insertions. Setosity: dense coating of long hairs (more than twice diameter of rear ocellus), slightly shorter on lower face and clypeus, shorter and sparser on white-yellow markings and almost bare between antennal insertions and malar region. Post-ocellar striae incomplete. Pentagonal area with very slight impression in region of anterior ocellus, otherwise planar. Genal carinae present. Malar space narrow. Galea elongate; glossa distinctly longer than galea, slightly downwardly curved apically, parallel-sided; paraglossa slightly shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 18-21 segmented; 8-9 without flabella; pedicel oblong; flabella of third antennal segment as long as the fourth segment or slightly shorter.

Thorax Sculpture: punctate on mesoscutum, with lustrous smooth interspaces on lateral lobes, punctation becoming sparser toward pronotum; mesocscutellum punctate; laterally punctate; pleurae punctulate-punctate to punctate. Setosity: as head, distinctly longer on propleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth with occasional fine punctulae dorsally, ventrally smooth. Setosity: as head on terga 1-3, laterally on terga 4-8 dense coating of shorter hairs (slightly longer than diameter of rear ocellus); dorsally on terga 4-8 and basal plate coating of short setae (diameter of rear ocellus); ventrally, except basal plate, as head but much sparser. Tergum 8 with broad, widely separated and shallow impression. Basal plate curved gradually toward dorsum; without lip; impressed apically; apical margin convex. Dorsal internal margin of gonostipes divergent from base to thre-quarter length, curved laterally abruptly to apex, strongly indented medio-apically. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting more anteriorly than ventral. Gonostylus, viewed laterally, very slightly upwardly curved toward apex; gonostyli with sparse coating of short hairs; gonomacula between apically rounded square and a highly deformed circle. Lateral surface of basivolsella rounded. Digitus broad basally, dorsally strongly concave from base to apex,

ventrally virtually straight to mid-length, then concave to apex, although much less so than dorsally (Fig. 78). Cuspis digitiform, sub-clavate apically; apex of volsellar pocket wide. Penis valve, dorsally, sub-parallel in basal half, appearing constricted between base and median, tapering from median to apex; lateral flaps undeveloped; laterally as in Fig. 81; aedeagal apodemes strongly flared apically.

Female

Length: 10-12mm; EA 0.88-0.9; A:B 2.73-3.1; B:C 1.57-1.67; D:E 2.09-2.15; D:F 1.1-1.27 (3 specimens measured)

Colour: similar to males but with white-yellow colouring much reduced throughout, except in axillary region. Genal yellow slightly more extensive than in males. Apical palp segments slightly lighter. Scape ochraceous to testaceous, large black fleck on outer face; pedicel black; flagellum basal 3-4 segments ochraceous, becoming testaceous toward apex, apical 2-3 segments brown; flabellae ochraceous to testaceous on basal segments, testaceous on apical segments. Dorso-lateral white-yellow extended medially but absent latero-ventrally on pronotum. Two white-yellow flecks on mesoscutum in axillary region, slightly larger than males. Tegula black. Flecks behind cenchri absent. Mesepisternum black, white-yellow fleck on dorsal one-fifth. Fore-femora ringed dark-brown in basal one-third to half, testaceous, becoming ochraceous apically; mid-femora ringed brown basally, testaceous, becoming yellow apically; hind femora testaceous, becoming ochraceous apically. Tergum 4 apical white-yellow band wider; tergum 5 white-yellow band complete, occupying apical half of sclerite laterally but reduced to an extrmely narrow apical line medially; tergum 7 black, thin apical white-yellow band, often incomplete laterally; tergum 8 white-yellow, black baso-laterally. Sternum 3 black; sternum 4 black, small transverse white-yellow fleck apico-medially; sternum 5 white-yellow band complete, occupying apical one-quarter of sclerite laterally and apical one-third medially; sternum 6 black, with large transverse white yellow fleck apically; sternum 7 black. Sclerite above sawsheath black.

Morphology as males with the exception of the following.

Head Sculpture: as males, slightly coarser between rear ocelli and eyes. Setosity: as males. slightly denser on lower face and on postgena. Antennae 18-22 segmented, 9-10 without flabella; pedicel square or oblong.

Thorax Setosity: as head, distinctly longer on propleurae. Sculpture: punctate on mesoscutum, without lustrous smooth interspaces on lateral lobes.

Abdomen Setosity: as head on terga 1 and 8, laterally on terga 2 and 3 and on sterna 7, dorsally on terga 2-7 and laterally on terga 4-7 with coating of shorter hairs; remaining sterna as head but sparser. Sculpture: finely punctulate dorsally, smooth to finely and very sparsely punctulate ventrally.

Material examined: SYNTYPES ♀ of *fabricii*, ♂, 2♀ of *megacephala*, 5♂, 7♀ (BMNH, PMSL, UWCP, ZMUM).

Distribution: Russia (Kherson), Poland, Czechoslovakia, Germany, Hungary, Macedonia, western Turkey.

Comments: Both sexes may be distinguished from those of *Megalodontes* sp.5 by the fabricii clour syndrome. Males may further be distinguished by the ratios A:B and B:C, the incomplete sclerotisation of the gonostipes and the lateral form of the penis valve.

Megalodontes flabellicornis (Germar)

(Figs 29, 34, 133, 135)

Tarpa flabellicornis Germar, 1817: 12; Konow, 1897; Rohwer, 1911a. SYNTYPE ♀, Illyria (= Yugoslavia, Croatia) (Ullrich) (ZMHB), [examined].

Tarpa coronata Zaddach, 1865: 198. SYNTYPE(S) ♀, Europe (ZKON), [Type(s) lost or destroyed]. Synonymised by Konow, 1897.

Tarpa albicincta Stein, 1876: 55. SYNTYPES ♂, ♀, Greece (?): Macedonia (♂) (Kruper); Greece: Mount Olympus (♀) (Kruper) (ZMHB), [not examined]. Synonymised by Konow,1897 (under *exronatus*).

Tarpa speciosa Mocsáry, 1877: 88-89. SYNTYPE ♀, Bosnia: Biela Gora (HNHM), [examined]. Synonymised by Konow, 1897.

Megalodontes flabellicornis (Germar); Kirby 1882.

Megalodontes coronatus (Zaddach); Kirby, 1882.

Megalodontes speciosus (Mocsáry); Kirby, 1882.

Megalodontes flabelliformis;:Dalla Torre, 1894: 416; mis-spelling.

Male

Length 10-11 mm; EA 0.86-0.88; A:B 2.61-2.7; B:C 3.6-4.29; D:E 1.07-1.13; D:F 1.03-1.07 (4 specimens measured).

Colour: predominately black; sterna strongly marked with yellow. Vertiginal yellow broken medially, contiguous with genal yellow, but not with small and narrow post-ocellar flecks. Facial yellow separated from yellow between antennal insertions and eye margin. Where the facial yellow is campaniform or triangular the quadrilateral flecks between the antennal insertions and ocular margin are wider dorsally than ventrally, whereas when the facial yellow is sub-divided that between the antennal insertions and ocular margin is wider ventrally than dorsally. Mouthparts predominately black, sub-apical palp segments testaceous. Scape yellow, strongly marked with black on outer or dorsal faces; pedicel black; third antennal segment ochraceous, often ringed black basally; flagellum ochraceous; flabella ochraceous becoming testaceous at apices. Pronotum strongly marked with yellow dorso-laterally and with small yellow spot latero-ventrally, former often much reduced and latter often absent. Four yellow flecks on mesoscutum. Yellow flecks behind cenchri absent. Tegula yellow; humeral sclerite yellow to ochraceous. Mesepisternum marked yellow in apical one-quarter to one-third. Propleurae

and mesosterna black. Fore- and mid-coxa black; hind-coxae black, marked with two apical flecks of yellow. Fore- and mid-femora ringed black in basal half, remainder yellow to ochraceous; hind-femora yellow, ringed black basally. Wings slightly fuscous anteriorly, remainder yellow-hyaline. Venation testaceous basally and anteriorly, except ochraceous costal vein of fore-wing; apically and posteriorly ochraceous to testaceous. Tergum 1 black throughout or with two small apico-lateral yellow spots; tergum 2 black with large apico-alteral yellow flecks; tergum 3-7 apical yellow band complete; tergum 8 yellow. Sternum 2-7 yellow, marked black latero-basally; basal plate yellow, lined black basally.

Head Sculpture: punctate between rear ocelli and eyes and on lower face, becoming punctulate-punctate on vertex; punctate-rugose between anterior ocellus and antennal insertions. Setosity: dense coating of long hairs (more than twice diameter of rear ocelli), slightly longer in post-genal region and slightly shorter on areas marked with black on face. Post-ocellar striae incomplete. Pentagonal area consisting of a broad and shallow excavation to anterior puncture. Genal carinae present. Malar space narrow. Galea slightly elongate; glossa distinctly longer than galea, slightly downwardly curved throughout its length, parallel-sided; paraglossa slightly shorter than glossa, slightly downwardly curved throughout, between laminar and hemi-cylindrical. Antennae 16 segmented, 2 without flabella; pedicel oblong; flabella of third antennal segment as long as the following 5-6 segments.

Thorax Sculpture: closely punctate on mesoscutum becoming punctulate-punctate anteriorly; mespisternum punctate. Setosity: as head, longer on mesoscutellum and propleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: terga 1-2 smooth to very finely and sparsely punctulate; remainder and sterna smooth. Setosity: as head on tergum 1 and laterally on terga 2-3; shorter and sparser than head laterally on remainder of terga; tergum 8 with coating of short hairs (about the diameter of rear ocellus) apically; remainder of terga with short fine hairs on apical yellow bands or with hyaline setae; sterna as head; basal plate with dense coating of shorter hairs. Tergum 8 with broad and relatively shallow impression, becoming obsolete apically. Basal plate without lip; apically impressed; apical margin convex. Dorsal inner margin of gonostipes curving laterally gradually to beyond three-quarter length and secondarily abruptly curved laterally to apex. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting anteriorly to ventral. Dorsal silhouette of gonostylus, viewed laterally straight, slightly concave medially and slightly upwardly curved towards apex. Gonostylus with sparse coating of short hairs, longer and denser baso-ventrally. Gonomaculae deformed circular. Lateral surface of volsellae rounded. Digitus dorsally straight basally, angled downwards and weakly concave to apex, which is rounded bluntly; ventrally weakly convex throughout (Fig. 133). Cuspis digitiform, volsellar pocket wide apically. Penis

valve, dorsally, parallel-sided or appearing weakly divergent to three-quarter length, tapering to fine apical point; laterally, curved at dorso-base, straight to mid-length, curved upwards and, secondarily, downward at apex, ventrally virtually straight and weakly concave apically giving a slightly downwardly-curved appearance to the penis valve; aedeagal apodemes slightly flared apically

Female

Length 10-11.5 mm; EA 0.83-0.86; A:B 2.9-2.95; B:C 1.5-1.54; D:E 1.23-1.67; D:F 1-1.25 (3 specimens measured)

Colour: predominately black throughout, more extensively marked with yellow dorsally. Post-ocellar flecks longer and wider than males. Facial yellow between antennal insertions generally campaniform and smaller than males. Mouthparts as males, more widely marked with brown. Scape ochraceous; pedicel testaceous to dark-brown; third antennal segment and flagellum ochraceous to testaceous; flabella ochraceous to testaceous, becoming brown apically. Either more extensively yellow or much reduced in comparison with males dorso-laterally on pronotum and latero-ventral yellow absent. Four yellow flecks on mesoscutum, larger than males. Yellow flecks behind cenchri absent. Mesepistemal yellow in dorsal one-quarter. All coxae black. Mid-femora occasionally more extensively black basally than fore-femora. Wings as males, except costal vein of fore-wing ochraceous to testaceous. Tergum 1 black or with apico-lateral spot of yellow; tergum 2 as males; terga 3-7 apical yellow band complete; tergum 8 narrow apical band of yellow irregularly broken. Sterna 2-3 black; sternum 4 black with indistinct yellow flecks apico-laterally; sterna 5-6 apical yellow band complete; sternum 7 black, yellow apico-lateral flecks and an indistinct medio-apical yelow stripe. Sclerite above sawsheath black.

Morphology as males with the exception of the following.

Head Setosity: similar to males but shorter throughout (about twice the diameter of rear ocellus), except for post-genal area which is as males, much sparser on yellow markings between antennal insertions and eye margin. Pentagonal area as males, more widely excavated by anterior ocellus. Antennae 16-17 segmented, 2-3 without flabella; flabella of third antennal segment as long as the following 4-5 segments.

Thorax Sculpture: as males but with lustrous interspaces on lateral lobes of mesoscutum.

Abdomen Setosity: as males, sclerite above sawsheath as basal plate.

Material examined: SYNTYPES ♀ of flabellicornis, ♀ of *speciosa* and 7♂, 13♀ (BMNH, MKRC, MWEC, PMSL, SBLC, ZSMC)

Distribution: Greece (Mount Pieria, Aspropotomas, Ioannina) Croatia (Krk), Slovenia, Italy (Trieste).

Comments: dorsal longitudinal sclerotisation of gonostipes appearing complete in three specimens from Krk. Males may be separated from the related *Megalodontes* sp.3

by the ratio D:E, the degree of punctation of the mesoscutum and the slightly longer flabella of the third antennal segment. Females are distinguished form those of *parvus* by their all black tergum 1 and the presence of genal carinae.

Megalodontes gratiosus Mocsáry

(Figs 74, 120-123)

Tarpa gratiosa Mocsáry, 1881: 36; Konow, 1897. SYNTYPE ♀, Spain: Granada (H.Ribbe) (HNHM), [examined].

Megalodontes castiliensis Enslin, 1913: 168. SYNTYPES ♂, ♀, Spain: Castille, Cuenca, 3.vi.1887 (♂), 18.-19.iv. 1890 (♀) (ZSMC), [examined].

Megalodontes gratiosus (Mocsáry), Kirby, 1882.

Male

Length 9-10 mm; EA 0.89; A:B 2.35-2.4; B:C 2.22; D:E 1.67-1.73; D:F 1.18 (2 specimens measured).

Colour: predominately black, dorsally and ventrally, on head and thorax; predominately yellow, dorsally and ventrally, on abdomen. Occipital yellow contiguous with genal yellow; facial yellow in the form of an inverted T-shape or campaniform of yellow medially and a large fleck between the antennal insertion and the eye margin. Mouthparts dark brown, apical palp segments and galea ochraceous to testaceous. Scape yellow with small apico-lateral brown fleck; pedicel dark brown to black; third antennal segment: dark-brown to brown basally, testaceous apically; flagellum testaceous; flabellae testaecous, becoming darker apically. Dorsum and dorso-lateral surfaces of pronotal collar yellow, the former divided postero-medially. Four yellow flecks on mesoscutum. Tegula and humeral sclerite yellow. Mesepisternum black with yellow fleck on dorsal one-third, slightly produced downwards apically. All coxae black. Fore-femora yellow, basal half black; mid-femora yellow, basal one-third black; hind-femora yellow, basal one-fifth to one-quarter. Wings slightly fuscous anteriorly and basally, hyaline posteriorly and apically; venation brown anteriorly and basally, testaceous posteriorly and apically. Tergum 1 black; terga 2-4 black, with large lateral yellow fleck, narrowly separated apico-medially on tergum 4; terga 5-7 black, yellow band complete; tergum 8 yellow band complete, black only at extreme base. Sternum 2 yellow; sternum 3-4 black, yellow fleck apico-laterally; sterna 5-7 yellow band complete, occupying apical two-thirds of sclerite throughout; basal plate 8 yellow, black only baso-medially.

Head Sculpture: closely punctulate-punctate between rear ocelli and eyes, remainder punctulate, except between anterior ocellus and antennal insertions which is closely punctate. Setosity: dense coating of long black hairs; almost bare between antennal insertion and malar region. Post-ocellar striae incomplete. Pentagonal area flat, virtually unexcavated, with small anterior puncture. Genal carinae present. Malar space narrow. Galea elongate; glossa longer than galea, curved downward apically, parallel-sided;

paraglossa hemi-tubular, shorter than glossa. Antennae 16 segmented, 2-3 without flabella; pedicel square; flabella of third antennal segment as long as the following 2 segments.

Thorax Sculpture: yellow areas smooth, dorsally and laterally; dorsum punctulate-punctate; punctulate laterally; pleural region smooth to punctulate. Setosity: as head. Pronotal collar collapsing (anterior ledge of pronotum very narrow). Hind coxal apical incision closed.

Abdomen Sculpture: smooth to very finely and sparsely punctulate dorsally, similar ventrally but with even fewer punctulae. Setosity: as head, but hairs slightly shorter and sparser in comparison. Tergum 8 with broad and deep impression becoming obsolete apically. Basal plate curved gradually toward apex; apical surface flattened; without lip; apical margin convex. Dorsal inner margins of gonostipes diverging from base to three-quarter length and abruptly angled laterally to apex. Dorsal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostipes and gonostylus projecting more anteriorly than ventral. Dorsal surface of gonostylus straight; gonostylus sparse coating of short, stout and dark hairs, interspersed with shorter, finer and lighter hairs; gonomaculae deformed circular. Lateral surface of volsellae rounded. Digitus, in latero-ventral view, more apically flared than *bucephalus*, inner face longer than outer and latter less profoundly concave (Fig. 74). Cuspis digitiform, appearing sub-clavate, volsellar pocket wide apically. Penis valves, lateral, curved dowardly abrubtly baso-dorsally, slightly concave, much less so than *capitalatus* and secondarily convex, less rounded and appearing slightly tapered or pointed apically, ventrally slightly divergent to mid-length, then angled and straight to slightly convex to apex; dorsally mitriform, lateral lobes so strongly developed (more than twice the width of one of the valves) that the entire structure appears constricted baso-medially; aedeagal apodemes flared apically

Female

Length 9 mm; EA 0.92:1; A:B 2.25:1; B:C 2.22:1; D:E 2.38:1; D:F 1.55:1 (1 specimen measured)

Colour Genal yellow more extensive than in males. Scape yellow, but without brown fleck; pedicel black; third antennal segment: testaceous throughout; flabellae as males, but distinctly darker, almost brown apically. Four yellow flecks on mesoscutum larger than in males. Flecks behind cenchri absent. Mesepisternum yellow fleck on dorsal one-quarter, strongly produced downwards posteriorly. Mid-femora yellow, basal one-third to half black; hind-femora yellow, basal one-sixth to one-fifth. Terga as males but apico-lateral and apical yellow flecks and bands wider. Sterna 2-3 black; sterna 4-5: black, narrow flecks apico laterally, extended medially; sterna 6-7 yellow band complete, occupying apical one-third of sclerite laterally and less than apical one-fifth medially. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Genal carinae present, as males but slightly longer. Antennae 17 segmented flabellae, 2-3 without flabella, flabella of third antennal segment as long as the following 2-3 segments.

Thorax Sculpture as males, but dorsum less densely punctate. Pronotal collar collapsing, anterior ledge very narrow.

Abdomen Sculpture: very finely and sparsely punctulate in black areas, smooth in yellow. Setosity: as head, but hairs slightly shorter and sparser in comparison.

Material examined: SYNTYPES 1♀ of *gratiosus*, 1♀ of *castiliensis* and 2♂, 1♀ (ZHMB, ZSMC).

Distribution: southern Spain (Andalucia, Granada).

Comments: Both sexes may be separated from those of *Megalodontes* sp.4 by the presence of genal carinae, their longer third antennal flabella and by incomplete dorsal sclerotisation of the gonostipes in males.

Megalodontes interruptus Gussakovskij

(Figs 55, 127)

Megalodontes interruptus Gussakovskij, 1935: 204. SYNTYPES ♂,♀, USSR: Eastern Siberia (ZMAS) [not examined].

Megalodontes antoniae Zombori, 1971: 234. HOLOTYPE ♂, Mongolia: central aimak, 30 km. east of Somon Nalajch, 14.vi.1966 (HNHM), [not examined].

Male

Length 10-11 mm, EA 0.91-0.93:1; A:B 2-2.27:1; B:C 1.83-2:1; D:E 1.38-1.55:1; D:F 1.17-1.25:1 (2 specimens measured).

Colour: predominately black or dark-brown, except where noted. Vertiginal yellow continuous (discontinuous on one specimen from Irkutsk) and contiguous with genal yellow. Post-ocellar flecks absent. Facial yellow discontinuous with yellow between antennal insertions and eye margin and in the form of a campaniform fleck between antennal insertions and two large transverse flecks on the clypeus. Median and lateral colouring greatly reduced and clypeal colouring often absent (in 2 specimens examined). Yellow between antennal insertions and eye margin produced slightly vertically along eye margin but not greatly above antennal insertions. Mouthparts predominantely dark-brown. Scape ochraceous with dark-brown fleck on upper surface; pedicel dark-brown to black; third antennal segment ochraceous to testaceous; flagellum ochraceous to testaceous, apical 2 segments brown; flabella testaceous to red-brown basally becoming brown apically. Dorso-lateral area of pronotum yellow and with small spot latero-ventrally. Two yellow flecks on mesoscutum, in axillary region. Tegula black; humeral sclerite testaceous to brown. Flecks behind cenchri absent. Mesepisternum black, except for small yellow fleck at extreme dorsum, strongly downwardly produced posteriorly. Fore- and mid-coxae

dark-brown to black; hind-coxae dark-brown, yellow apico-anteriorly. Wings: anterior fuscous, posterior hyaline to fuscous; venation ochraceous to testaceous basally and anteriorly, ochraceous apically and posteriorly; costal vein ochraceous and posterior of pterostigma yellow to ochraceous. Tergum 1 black; terga 2-4 black, small apico-lateral yellow fleck; terga 5-6 black, small apico-lateral yellow fleck, slightly extended medially; tergum 7 black, small apico-lateral yellow fleck and one larger medially; tergum 8 black, yellow margin complete, occupying apical one-quarter of sclerite, produced slightly baso-medially in region of tergal impression. Sterna 2-7 dark-brown to black, yellow margin complete; basal plate ochraceous basally, ochraceous to testaceous apically.

Head Sculpture: closely and coarsely punctate between rear ocelli and eyes becoming punctulate to punctulate-punctate towards occiput; punctate-rugulose between anterior ocellus and antennal insertions. Setosity: dense coating of long hairs, more than twice as long as rear ocellus, slightly shorter stouter and sparser on yellow flecks between antennal insertions and between these and the eye margins. Post-ocellar striae incomplete. Pentagonal area shallow excavation by anterior ocellus, extending to anterior puncture. Genal carinae present as sharp angle between gena and post gena. Malar space narrow. Galea slightly elongate; glossa distinctly longer than galea, parallel-sided and slightly downwardly curved apically; paraglossa slightly shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 19-22 segmented, 2 without flabella; pedicel tranverse; flabella of third antennal segment as long as the following 6-9 segments.

Thorax Sculpture: punculate-punctate to punctate on lateral lobes of mesonotum, with lustrous interspaces; punculate-punctate anterior of notaulices, becoming sparsely punctulate at border with pronotum; mesoscutellum punctate; laterally and ventrally punctulate-punctate to punctate. Setosity: as head, slightly longer in pleural regions, particularly propleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth dorsally and ventrally with the exception of a few very sparse punctulae. Setosity: as head on tergum 1 and laterally on tergum 2; laterally on all terga and dorsally on tergum 8 with sparse coating of short (the diameter of rear ocellus) and stout setae; sterna with setae of same length as on head but distributed much more sparsely. Tergum 8 with broad, widely separated and shallow impression. Basal plate curved gradually toward dorsum; slightly flattened apically; without lip; apical margin slightly convex. Dorsal inner margins of gonostipes diverging from base to apex, secondarily curved medially and strongly notched. Dorsal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting more anteriorly than ventral. Dorsal surface of gonostylus, viewed laterally, straight; gonostyli with dense coating of short hairs; gonomaculae circular to elliptical. Lateral surface of volsellae rounded. Digitus with

dorsal surface concave to mid-length, massively convex to apex; ventrally concave to three-quarter length, concave to apex, appearing slightly rounded apically (Fig. 53). Cuspis digitiform, volsellar pocket symmetrical slightly wider than base of digitus. Penis valve, dorsally, sub-parallel in basal two-thirds, appearing constricted between base and median, tapering from median to apex and appearing secondarily constricted between the two; lateral flaps undeveloped; laterally as in fig.; aedeagal apodemes flared apically

Female

Length: 11-12 mm; EA 0.89-0.91; A:B 2.7-2.89; B:C 1.43-1.67; D:E 1.67-1.83; D:F 1.43-1.83 (2 specimens measured)

Colour: similar to males but distinctly lighter on terga; laterally and ventrally distinctly darker. Vertiginal white-yellow continuous and contiguous with genal white-yellow. Facial white-yellow reduced to a small circular fleck between antennal insertions; white-yellow between antennal insertions and eye margin reduced to irregular quadriangular flecks and only very slightly produced vertically above antennal insertions. Scape ochraceous; third antennal segment testaceous to red-brown; flagellum brown, apical 2-3 segments testaceous to red-brown. Latero-ventral white-yellow flecks on pronotum absent. Two flecks of yellow on mesoscutum (one with four, the two anterior very small). Tegula brown to dark brown, at apex white-yellow or yellow; humeral sclerite testaceous. Flecks behind cenchri absent. Mesepisternum: black, except for small yellow fleck at extreme dorsum, strongly downwardly produced posteriorly. Fore- and mid-coxae brown; hind-coxae dark-brown. Wings: fore-wing slightly fuscous throughout, more so anteriorly and basally; hind-wing slightly fuscous anteriorly, hyaline/fuscous posteriorly; venation testaceous basally and anteriorly, ochraceous to testaceous apically and posteriorly, costal vein of forewing ochraceous to testaceous. Tergum 1 dark-brown; tergum 2 dark-brown, small white-yellow spot apico-laterally; terga 3-5 dark-brown, white-yellow fleck apico-laterally, extended medially on terga 4-5; terga 6-8 dark-brown, apical white-yellow band complete. Sterna 2-3 dark-brown; sternum 4 dark-brown, thin apical margin of white-yellow, broken regularly; sternum 5-6 dark-brown, apico-lateral fleck of white-yellow, greatly extended toward median; sternum 7 dark-brown, very thin apical margin of white-yellow. Sclerite above sawsheath ochraceous to testaceous, two specimens black.

Morphology as males with the exception of the following.

Head Setosity: much shorter (little more than diameter of rear ocellus) but much denser than males, particularly on lower face, genal and postgenal regions, less dense on white-yellow areas. Sculpture: closely and coarsely punctate between rear ocelli and eyes becoming punctulate to punctulate-punctate towards occiput; punctate-rugulose between anterior ocellus and antennal insertions. Antennae 16-19 segmented,

1 without flabella; pedicel square; flabella of third antennal segment as long as the following 5-6 segments.

Thorax Sculpture: punculate-punctate to punctate on lateral lobes of mesonotum, with lustrous interspaces; punculate-punctate anterior of notaulices, becoming sparsely punctulate at border with pronotum; mesoscutellum punctate; laterally and ventrally punctulate-punctate to punctate.

Abdomen Setosity: as male, except for sternal setae which are as long as those on tergum 1.

Material examined: 6♂, 10♀ (BMNH, ZMUM)

Distribution: Russia (Irkutsk, Ushmin), Mongolia, China (Harbin).

Comments: Female wing colour varies between yellow-hyaline/ slightly fuscous throughout (material from Manchuria) to fuscous throughout (specimen from 'Ushmin'). Venation varies from yellow to ochraceous throughout (material from Manchuria) to testaceous throughout (specimen from 'Ushmin'). Males may be separated from those of *spiraeae* and *quinquecinctus* by the facial colour pattern and the much longer third antennal flabella, which also assist in separating the females which, in turn, may be distinguished by the degree of punctation between the rear ocelli and eyes. The synonymy of *antoniae* (Zombori, 1971) is based upon the original and detailed description which agrees well with all material examined of *interruptus*.

Megalodontes jucundus Mocsáry

(Figs 55, 60)

Tarpa (Megalodontes) jucunda Mocsáry, 1891: 157; Konow, 1897. SYNTYPE ♂, Mesopotamia (=Turkey): Malatia (HNHM), [examined].

Megalodontes jucundus (Mocsáry); Konow, 1897. Synonymised by Konow, 1897 (under *phaenicius*).

Male

Length 9-11 mm; EA 0.87-0.9; A:B 2.65-2.81; B:C 1.46-1.48; D:E 0.9-0.94; D:F 0.73-0.82 (2 specimens measured).

Colour: predominately black on head and dorsum of thorax, remainder predominately yellow. Vertiginal yellow broken, and separated from narrow post-ocellar flecks of yellow, but contiguous with genal yellow. Face yellow, except for tentorial pits, and contiguous with yellow between antennal insertions and eye margin, the latter produced vertically slightly along eye margin. Mouthparts predominately ochraceous to testaceous, although marked with black and yellow. Scape yellow with longitudinal black fleck on dorsal face; pedicel black; third antennal segment; flagellum testaceous, flabellae testaceous becoming brown apically. Pronotum yellow dorso-laterally and almost entirely so laterally. Four yellow flecks on mesoscutum. Yellow flecks behind cenchri absent. Tegulae and humeral sclerites yellow. Mes-, metepisternum, mes-, metepimeron,

'propleurae and mesostema yellow; mesepisternum and metepimeron occasionally marked black ventrally. All coxae and femora yellow. Wings yellow-hyaline; venation ochraceous; pterostigma yellow, marked testaceous medially. Terga 1-2 black with apico-lateral spot or fleck of yellow; tergum 3 apical yellow narrowly or widely broken medially: terga 4-8 apical yellow band complete, occasionally widely broken medially on tergum 4. All sterna and basal plate yellow.

Head Sculpture: closely and coarsely punctate between rear ocelli and eyes, becoming smooth at vertex; punctate-rugulose between anterior ocellus and antennal insertions. Setosity: dense coating of long (more than twice diameter of rear ocellus) hairs, sparser on yellow and denser on black post-genal regions, shorter on face. Post-ocellar striae incomplete. Pentagonal area broadly excavated at anterior ocellus, shallow trench not extending to anterior puncture. Genal carinae present. Malar space narrow. Galea slightly elongate; glossa distinctly longer than galea, downwardly curved throughout its length, weakly flared to apex; paraglossa slightly shorter than glossa, curved like glossa, between laminar and hemi-cylindrical. Antennae 15-16 segmented, 2 without flabella; pedicel oblong or square; flabella of third antennal segment as long as the following 5-6 segments.

Thorax Sculpture: very sparsely punctulate-punctate with lustrous interpaces throughout; lateral lobes of mesoscutum with small punctate areas. Setosity: as head, slightly longer on pronotum, mesoscutellum and propleurae and sparser on areas marked with yellow. Pronotal collar collapsing. Hind-coxal apical incision open.

Abdomen Sculpture: terga smooth with fine and occasional punctulae; sterna smooth. Setosity: as head on tergum 1 and laterally on terga 2-3, laterally on remainder of terga with sparse coating of short (little more than the diameter of rear ocellus) hairs, terga 2-8 with short hyaline setae; sterna as head, except basal plate which has coating of short hairs, slightly shorter than those laterally on terga. Tergum 8 with deep furrow becoming obsolete apically, relatively broad apically. Basal plate flattened apically; without lip; apical margin convex. Dorsal inner margin of gonostipes divergent from base to mid-length, weakly concave then curving laterally to apex. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting more anteriorly to ventral. Dorsal surface of gonostylus, viewed laterally, straight; gonostyli with dense coating of short hairs; gonomaculae deformed circular. Lateral surface of volsellae rounded. Digitus, in latero-ventral view, dorso- and ventro-basally divergent, strongly convex dorso-medially and then strongly concave to apex, ventrally strongly convex from mid-length to apex (Fig. 55). Cuspis digitiform, volsellar pocket wide apically. Penis valve, dorsally, slightly divergent from base to beyond mid-length, subsequently tapering gradually to apex, lateral lobes undeveloped, similar to *M. eversmanni*; laterally baso-dorsally gently rounded, virtually straight for most of dorsal surface strongly upwardly curved apically, apex rounded; ventrally straight to mid-

length, angled toward dorsum and weakly convex to apex; aedeagal apodemes flared apically.

Female

Length 9-10 mm; EA: 0.89-0.9:1; A:B 2.67-3:1; B:C 1.5-1.67:1; D:E 1-1.1:1; D:F 1-1.1:1 (2 specimens measured)

Colour: similar to males, more extensively yellow dorsally but much less so, laterally and ventrally. Post-ocellar flecks longer and broader. Facial yellow campaniform and separated from irregular quadrilateral flecks of yellow between antennal insertions and eye margin. Mouthparts predominately black, palp segments ochraceous to testaceous. Scape yellow with longitudinal black fleck on dorsal face; pedicel black; third antennal segment and flagellum testaceous, flabellae testaceous becoming brown apically. Third antennal segment and flagellum ochraceous to testaceous. Pronotal yellow much reduced laterally. Four yellow flecks on mesoscutum, larger than males. Yellow flecks behind cenchri absent. Mesepisternum black with large yellow fleck in dorsal one-third, produced downwardly strongly posteriorly; metepimeron with dorsal stripe of yellow. Propleurae and mesosterna black. All coxae black with small apical yellow markings. All femora ochraceous. Terga 1-2 black, with apico-lateral fleck of yellow; tergum 3 black with lateral flecks narrowly separated medially; terga 4-8 apical band of yellow complete. Sterna 2-3 black; sternum 4 black with small apico-lateral flecks of yellow; sternum 5-6 apical band of yellow complete; sternum 7 black with apical margin of indistinct yellow. Sclerite above sawsheath black.

Morphology as males with the exception of the following.

Head Sculpture: coarsely punctate between rear ocelli and eyes, becoming smooth at vertex; closely and coarsely punctate becoming punctate-rugulose between anterior ocellus and antennal insertions. Setosity: slightly shorter than males on head, particularly on lower face, post-genal setosity as males. Antennae 17-18 segmented, 3 without flabella; pedicel square; flabella flabella of third antennal segment as long as the following 5-7 segments.

Thorax Setosity: as head on mesoscutum and yellow region of mespisternum, as males on mesoscutellum, propleurae and black region of mespisternum.

Abdomen Setosity: as males, slightly longer on apical yellow bands.

Material examined: SYNTYPE ♂, 2♂, 2♀ (BMNH, HNHM, MKRC)

Distribution: Turkey (Ankara, Tokat, Erzinçan).

Comments: Males of *jucundus* are separated from taxa such as *parvus* and *luteiventris* by the complete facial yellow and their slightly flared glossa and the females from species such as *escalerai* by the black coloration of the sclerite above the sawsheath and the degree of punctation on the mesoscutum.

Megalodontes judaicus Lepeletier

(Figs 126, 128)

Tarpa judaica Le Peletier, 1823: 17; Konow, 1897. HOLOTYPE ♀, Syria (MHNP), [not examined].

Tarpa caesariensis Lepeletier, 1823: 17. HOLOTYPE ♀, Syria (MHNP), [not examined]. Synonymised by Konow, 1897.

Tarpa leucosticta Zaddach, 1865: 200. SYNTYPE(S) ♂, Syria (ZKON), [type lost or destroyed]. Synonymised by Konow, 1897.

Tristactus punctatus Konow, 1898: 108. SYNTYPE ♀ Turkey: Cilic (DEIC), [examined].

Tristactus punctatus var. *canadidatus* Konow, 1899: 204. SYNTYPE ♀ Turkey: Akbes (DEIC), [examined].

Megalodontes judaicus (Lepeletier); Kirby, 1882.

Male

Length 8-9.5 mm; EA 0.90-0.95; A:B 2.56; B:C 1.29; D:E 2.1; D:F 1.14 (3 specimens measured).

Colour: predominately black throughout; only lower face, dorsum of pronotum and basal plate predominately white-yellow. Vertiginal white-yellow discontinuous with that of genal region which, in turn, is greatly reduced; very short and narrow flecks of white-yellow posterior of rear ocelli; facial white-yellow complete, medially produced vertically toward anterior ocellus, laterally produced vertucally along eye margin. Scape white-yellow basally with fleck extending toward median ventrally; remainder and all of flagellum black. Two white-yellow flecks in axillary region of mesonotum, often vestigial. Hind-femora and tibiae marked white-yellow apico-dorsally and baso-dorsally, respectively. Wings: strongly fuscous; venation dark-brown to black anteriorly and basally, becoming red-brown posteriorly and apically; pterostigma marked with white-yellow. Tergum 1 black; terga 2-8 usually with white-yellow markings apico-laterally and -medially but rarely complete as an apical band of colour. Sternum 2 black; sterna 3-4 strongly marked with white-yellow; sterna 4-7 and basal plate white-yellow.

Head Sculpture: sparsely punctulate-punctate between rear ocelli and eyes; smooth to sparsely punctulate on vertex and occiput; punctate between anterior ocellus and antennal insertions; lower face smooth. Setosity: coating of long and stout hairs; shorter and sparser in white-yellow region of face; region around antennal insertions bare. Post-ocellar striae incomplete. Pentagonal area in the form of a deep triangular excavation extending from anterior ocellus to anterior puncture. Genal carinae present, but greatly reduced. Malar space narrow. Galea swollen; glossa flared apically, downcurved strongly and barely longer than galea; paraglossa more or less laminate, not distinctly hemi-tubular. Antennae 14 segmented, 1 without flabella; pedicel oblong; flabella of third antennal segment strongly reduced to small projection.

Thorax Sculpture: sparsely and finely punctulate on lateral lobes on mesonotum

with large smooth areas; almost smooth anterior of notaulices; punctulate on mesoscutellum; punctulate-punctate on mesepisternum and closely so on pro-pleurae; meso- and meta-pleurae similar to lateral lobes of mesonotum. Setosity: as head dorsally and laterally, but much longer denser and lighter on pleural sclerites, particularly on pro-pleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth, with occasional and fine punctulae. Setosity: as head on tergum 1, laterally on terga 2-3, apically on sterna 2-4, apico-medially on sterna 5-7; basal plate with hairs shorter, stouter and darker; shorter and sparser laterally on terga 4-8; remainder bare. Tergum 8 without indentation or furrow and strongly crimped apically. Basal plate slightly curved toward apex; without distinct lip; slightly impressed apically; apical margin appearing truncate when viewed ventrally but actually slightly convex. Dorsal inner margins of gonostipes widely separated but sub-parallel in basal one-quarter, diverging slightly to apical two-thirds and strongly secondarily divergent to apex. Dorsal sclerotisation of gonostipes complete but indistinct apically. Dorsal articulation of gonostipes and gonostylus not projecting anteriorly of ventral. Dorsal surface of gonostylus slightly angled ventrally and secondarily recurved dorsally toward apex; gonostylus with sparse coating of short setae, slightly denser on dorsal and ventral surfaces; gonomaculae deformed circular to hemi-elliptical. Lateral surface of volsellae rounded. Digitus, latero-ventral view as in Fig. 126. Cuspis digitiform, tapering toward apex. Penis valves, laterally, as in Fig. 56; dorsally; sub-parallel to mid-length, then convex toward apex and abruptly rounded apically; aedeagal apodemes flared apically.

Female

Length 6.5-9.5 mm; EA: 0.91-0.95; A:B 2.88; B:C 1.33; D:E 1.85; D:F 1.2 (3 specimens measured)

Colour: slightly lighter than males dorsally but, otherwise, similar. Vertiginal white-yellow discontinuous with genal white-yellow, which is greatly reduced; flecks posterior of rear ocelli longer and broader than in males, but still discontinuous with vertiginal white-yellow, lateral fleck between antennal insertion and eye margin is discontinuous with remainder of facial yellow. Thoracic colour similar to males, but pronotal dorsal and lateral white-yellow coloration reduced in comparison. Two white-yellow flecks on mesonotum, slightly larger than in males. Lateral yellow flecks on metapostnotum absent. Femora marked white-yellow, at least apically and more extensively on hind femur and tibia white-yellow basally on outer face. Tegula white-yellow, black at extreme base. Terga more widely marked with white-yellow, particularly laterally, than males but rarely any tergum with complete apical band of this colour. Sclerite above sawsheath white-yellow.

Morphology as males except for the following.

Head 1-2 antennal segments without flabella.

Abdomen Setosity: as males, longer at apex of sternum 7. Seventh sternum:

produced strongly apically to a median point.

Material examined: SYNTYPES 1♀ of *punctatus*, 1♀ of *candidatus* and 14♂, 12♀ (BMNH, TAU1, UCWP)

Distribution: Israel, Syria, Turkey.

Comments: one female from Israel (Qiryat Shemona) with white-yellow contiguous medially of remnants of post-ocellar striae and one female from eastern Turkey (Diyarbakir) with white-yellow fleck posterior to the cenchri. Both sexes may be separated from other species with swollen galea, by their overall black colour, the form of the antennae and the absence of genal carinae. The uniquely crimped apical margin of tergum 8 is diagnostic for the males.

Megalodontes kuznetzovi Dovnar-Zapolskij

(Figs 5, 33, 52, 56)

Megalodontes kuznetzovi Dovnar-Zapolskij, 1930: 92; Gussakovskij, 1935. SYNTYPE ♂, Turkestan: Alexander-Gebirge (N. N. Kuznetzov-Ugamskij) (ZMAS), [not examined].

Megalodontes andromorphus Dovnar-Zapolskij, 1930: 93. SYNTYPE ♂, Turkestan: Alexander-Gebirge (N. N. Kuznetzov-Ugamskij) (ZMAS), [not examined]. Synonymised by Gussakovskij, 1935.

Megalodontes kusnetzovi Dovn.: mis-spelling or error Zhelochovtsev 1976: 15.

Male

Length 14-15 mm; EA 1; A:B 2.1-2.3; B:C 1.67-1.75; D:E 1.67; D:F 1.54-1.6 (2 specimens measured).

Colour: predominately yellow. Vertex and occiput of head, with the exception of two small and narrow post-ocellar flecks, dorsum of thorax, except for four yellow flecks on mesonotum (the axillary pair appearing subdivided); a pair of metapostnotal yellow flecks posterior of the cenchri; wings hyaline; venation ochraceous to testaceous basally and anteriorly; pterostigma marked yellow; remainder of venation apically and posteriorly yellow to ochraceous. bases of all except apical 2-3 terga and all except laterally on tergum 1 black.

Head Sculpture: punctulate-punctate between rear ocelli and eyes; punctulate between anterior ocellus and antennal insertions; face, genal, post-ocular,vertiginal and occipital areas smooth to sparsely and finely punctulate.Setosity: sparse coating of fine and short, hyaline hairs, shorter and sparser in lower face, denser and longer in genal region. Post-ocellar striae incomplete. Pentagonal area excavated anteriorly, with narrow and shallow trench extending to anterior puncture. Genal carinae present. Malar space wide. Galea swollen; glossa flared apically, downcurved strongly and barely longer than galea; paraglossa more or less laminate, not distinctly hemi-tubular. Antennae 15 segmented, 1 without flabella; pedicel square; flabella of third antennal segment as long as

the following 5-6 segments (Fig. 5).

Thorax Sculpture: punctate on lateral lobes of mesonotum and anterior of notaulices; mesoscutellum punctulate; laterally and ventrally smooth to punctulate. Setosity: mesepisternum, postero-dorsal and lateral regions of pronotum and pro-pleurae as genal region; remainder with sparse coating of fine and short, hyaline hairs. Pronotal collar curving. Hind-coxal apical incision open. Teeth of all tarsal claws widely separated.

Abdomen Sculpture: smooth to very finely and sparsely punctulate, dorsally and ventrally. Setosity: median of tergum 1 as head; median of all sterna with a few sparse and shorter setae; remainder with covering of short hyaline setae, particularly dense upon basal plate. Tergum 8 with deep inverted V-shaped impression basally, widening toward apex (Fig. 47). Basal plate strongly curved toward apex and then sharply re-curved to produce prominent apical lip; apical surface impressed and apical margin appearing strongly concave, viewed ventrally, but actually convex. Dorsal inner margins of gonostipes sub-parallel basally, then widely divergent and slightly recurved toward apex. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus not projecting more anteriorly than ventral. Dorsal surface of gonostylus slightly upwardly curved; gonostylus with dense coating of short setae; gonomaculae hemi-elliptical. Lateral surface of volsellae curved basally and subsequently sharply angled antero-medially. Digitus, latero-ventrally, between a highly deformed ellipse and caputoviform, not projecting greatly from volsellae (Fig. 52). Cuspis digitiform, sub-clavate, secondarily indented apically but not rounded; projecting apically of digitus. Penis valves, laterally, digitiform (Fig. 56) and dorsally parallel and tapering in apical one-third without pronounced lateral lobes; aedeagal apodemes strongly flared apically.

Female

Length: 12.5-14.5 mm; EA 1; A:B 1.86; B:C 1.75; D:E 1.5; D:F 1.62 (1 specimen measured)

Colour: more extensively yellow on vertex of head than males, with the exception of the syntype of *andromorphus* which is distinctly darker; antennae slightly darker apically, otherwise as males; yellow markings on pronotum larger than males and only 4 yellow flecks on mesonotum, i.e. axillary pair undivided (cf. males); predominately yellow laterally but less so than males; wings as males; ventrally darker and terga slightly darker with yellow banding on tergum 2 broken widely medially; sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Flabella of third antennal segment: as long as 4-6 following segments

Thorax Sculpture: punctate on lateral lobes of mesonotum and anterior of notaulices; mesoscutellum punctulate; laterally and ventrally smooth to punctulate on yellow regions, becoming punctulate-punctate on black regions. Setosity: mesepisternum,

postero-dorsal and lateral regions of pronotum and pro-pleurae as genal region in males; remainder with sparse coating of fine and short, hyaline hairs.

Abdomen Setosity: as males, with the exception of basal plate, although similarly short setae are found on seventh sternum.

Material examined: 2♂, 4♀ (BMNH, DEIC, ZMAS, ZMUM).

Distribution: Turkmenistan, Uzbekistan

Comments: On one specimen gold label suggests that Gussakovskij (?) selected the male lectotype, without designating it subsequently; both syntypes agree well with their respective description (with the exception that *andromorphus* is male and not female, as stated in the original description); pink label written in Cyrillic on male lectotype; male syntype bears the specific name 'gynandromorphus' (Taeger, pers. comm.); minor colour variation in both sexes with some males slightly darker on terga and some females with more extensive yellow coloration throughout. *M. kuznetzovi* is closely related to *levaillantii* and *merceti*, but is distinct from all three by the wide separation of the teeth of the tarsal claws, its longer third antennal flagellum and the medial angling of the volsellar sclerotisation.

Megalodontes lacourti Chevin

(Figs 69, 72, 73, 111, 112, 114)

Tristactoides lacourti Chevin, 1985: 74. HOLOTYPE ♀, Morocco: Moulay Bou Selham, 8.iv.1971 (J. and V. Lacourt) (INRA), by original description [not examined].

Male

Length 9-10 mm; EA 0.91-0.93; A:B 2.6-2.9; B:C 2-2.2; D:E 2.08-3.22; D:F 1.25-1.53 (2 specimens measured).

Colour: predominately black dorsally, laterally and ventrally on head and thorax, predominately yellow dorsally and ventrally on abdomen. Vertiginal yellow broken medially but contiguous with genal yellow. Post-ocellar flecks present only in occipital region and greatly reduced. Facial yellow contiguous with yellow between antennal insertions and eye margin, the latter produced vertically along eye margin. Mouthparts predominately dark-brown to black, marked with yellow; galea and palp segments predominately yellow to ochraceous. Scape black, marked ochraceous to testaceous basally on inner face; pedicel black; third antennal segment black basally, becoming dark-brown at apex and marked red-brown apically on outer face; flagellum red-brown on outer face, brown on inner; flabellae red-brown to brown. Dorso-lateral and lateral regions of pronotum yellow. Two yellow flecks on mesonotum in axillary region. Tegula yellow; humeral sclerite yellow to ochraceous. Yellow flecks behind cenchri absent. Mesepistemum black with large yellow fleck on dorsal one-third, strongly produced downwardly anteriorly; metepisternum yellow, except for anterior margin; metepimeron with large dorsal yellow stripe. Propleurae yellow. Fore- and mid-coxae black, marked

yellow on apical inner face; hind-coxae black, with longitudinal yellow fleck on outer face. Fore-femora black, yellow in apical one fifth with longer ventral fleck of yellow in apical half; mid-femora yellow, ringed black basally with longer basal black fleck on inner and outer faces; hind-femora yellow, ringed black basally. Wings: fuscous throughout on both wings, slightly less so on hind wing; venation dark-brown basally and anteriorly, brown apically and posteriorly; costal vein ochraceous to testaceous, pterostigma marked yellow. Tergum 1 black; tergum 2: black, with large lateral yellow fleck; terga 3-4 black, with large lateral yellow fleck, greatly extended medially; terga 5-7 yellow band complete, occupying all of sclerite laterally but only apical half medially; tergum 8 yellow with very narrow basal black margin; Sternum 2 yellow, appearing smudged with black apico-laterally; sterna 3-5 yellow, black fleck baso-medially; sternum 6-7 and basal plate yellow.

Head Sculpture: closely and coarsely punctate between rear ocelli and eyes becoming punctate with lustrous interspaces toward occiput; punctate-rugulose between anterior ocellus and antennal insertions; smooth on lower face. Setosity: coating of long hairs (more than three times diameter of rear ocellus), slightly sparser on yellow markings and almost bare between antennal insertions and malar region. Post-ocellar striae complete. Pentagonal area planar. Genal carinae present. Malar space narrow. Galea elongate; glossa distinctly longer than galea, slightly downwardly curved apically, parallel-sided; paraglossa distinctly shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 14 segmented, 3-4 without flabella; pedicel oblong or tranverse; flabella of third antennal segment barely half the length of the fourth segment.

Thorax Sculpture: punctate with lustrous interspaces on lateral lobes of mesoscutum and on mescoscutellum; punctulate-punctate anterior of notaulices, yellow region of mespistemum smooth, remainder punctulate-punctate; propleurae smooth, remainder of pleurae punctulate-punctate. Setosity: as head, longer on propleurae and mesoscutellum. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth with few sparsely distributed and fine punctulae, ventrally smooth. Setosity: as head on tergum 1 and laterally on terga 2-8; remainder dorsally with sparse coating of short and stout setae; ventrally as head but extremely sparse, except basal plate with denser coating of much shorter setae. Tergum 8 with broad, widely separated and shallow impression. Basal plate curved gradually toward dorsum; without lip; apical surface impressed; apical margin convex. Dorsal internal margin of gonostipes divergent from base to median then sharply angled to apex. Dorsal longitudinal sclerotisation of gonostipes complete, but indistinct apically. Dorsal articulation of gonostylus and gonostipes projecting more apically than ventral. Dorsal surface of gonostylus, viewed laterally in the form of an elongate cone, strongly upwardly curved; gonostyli with dense coating of hairs, slightly longer ventrally;

gonomaculae between square and slightly rectangular with corners rounded. Lateral surface of volsellae rounded. Digitus baso-dorsally concave, massively convex from mid-length; ventrally virtually straight or very slightly convex to beyond mid-length and convex to apex (Fig. 73). Cuspis digitiform; volsellar pocket slightly wider apically than base of digitus. Penis valve, dorsally, divergent from base to median and then convergent from median to apex, with small lateral lobes; laterally as in Fig. 72; aedeagal apodemes very slightly flared apically.

Female

Length 10-11 mm; EA 0.92-0.93; A:B 2.1-2.2; B:C 1.67; D:E 2.5-2.8; D:F 1.33-1.71 (2 specimens measured)

Colour: more extensively marked with yellow dorsally than males, but distinctly darker laterally and ventrally. Vertiginal yellow continuous and contiguous with genal yellow and with occipital remants of yellow posterior of rear ocelli, all three slightly larger than in males. Facial yellow separated by a very thin black stripe from yellow between antennal insertions and eye margin. Yellow between antennal insertions and eye margin produced vertically. Mouthparts as males but slightly darker throughout. Scape yellow to ochraceous with longitudinal brown to dark-brown fleck on dorsal face; pedicel black, with testaceous to red-brown inner face; third antennal segment testaceous; flagellum testaceous to red-brown; flabella brown to dark-brown. Dorso-lateral yellow on pronotum narrowly separated medially, but reduced laterally. Four yellow flecks on mesonotum larger in axillary region than pair anterior of notaulices. Yellow flecks behind cenchri absent. Mespisternum black with yellow fleck in apical one-quarter, greatly produced postero-ventrally; metepisternum black; metepimeron with narrow dorsal stripe of yellow. Fore- and mid- coxae black. Pleurae black. Fore-femora black, yellow in apical one quarter with longer ventral fleck of yellow in apical half. Tergum 1 black; tergum 2 black, with large lateral yellow fleck; terga 3-4 black, with large lateral yellow fleck, greatly extended medially; terga 5-7 yellow band complete, occupying all of sclerite laterally but only apical half medially; tergum 8 yellow with very narrow basal black margin; Sternum 2 yellow, appearing smudged with black apico-laterally; sterna 3-5 yellow, black fleck baso-medially; sternum 6-7 and basal plate yellow. Sterna 2-4 black; sterna 5-6 black, yellow fleck apico-laterally; sternum 7 black, with thin apical yellow margin. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Setosity: as males, but much shorter on yellow markings and denser on lower face and clypeus.Antennae 14-16 segmented, 4-5 without flabella; pedicel square or oblong.

Thorax Sculpture: punctate with lustrous interspaces on lateral lobes of mesoscutum and on mescoscutellum; punctulate-punctate anterior of notaulices, yellow region of mespisternum smooth, remainder punctulate-punctate; pleurae punctulate-

punctate. Setosity: as head, longer on propleurae and mesoscutellum.

Abdomen Setosity: as males, as long as on head on terga 7 and 8 and on sclerite above sawsheath.

Material examined: 2♂, 3♀ (MKRC)

Distribution: Morocco (Al-Gharb: Moulay Bou Selham; western Rif: Chefchaouen).

Comments: variable in antennal coloration, particularly the pedicel; relative lengths of third, fourth plus fifth antennal segments variable; all material examined (from Chefchaouen) collected on same day. Males may be distinguished from those of *bucephalus* by their possession of genal carinae, the much shorter third antennal flabella and from those of *capitalatus* by the ratio B:C and also by the shorter third antennal flabella.

Megalodontes levaillantii Lucas

(Fig. 4)

Tarpa levaillantii Lucas, 1848: 343; Konow, 1897. HOLOTYPE ♂, Algeria: Oran, (Levaillant) (MNHN), [examined].

Megalodontes (Forficulotarpa) levaillanti Pic, 1918: 12) mis-spelling.

Megalodontes levaillantii (Lucas); Kirby, 1882.

Male

Length 12.5 mm; EA 1; A:B 3.1; B:C 1.91; D:E 1.7; D:F 1.42 (1 specimen measured)

Colour: predominately yellow. Major areas of black coloration: vertex; occiput; antero-dorsal, medial, latero-basal and latero-posterior regions of pronotum, dorsum of thorax, except paired anterior and axillary yellow flecks on mesoscutum, a pair of small lateral flecks on mesoscutellum and tegulae; entirety of tergum 1, except apico-laterally, basally and apico-medially on tergum 2 and basally but becoming narrower on remainder of terga; wings yellow-hyaline, venation yellow-ochraceous.

Head Sculpture: smooth to very finely and sparsely punctulate throughout, except anterior and dorsal surfaces of the mandibles which are punctulate-punctate to punctate. Setosity: fine white-yellow hairs on face and vertex, sparser and shorter in geno-occipital region, shorter and stouter on latero-posterior regions of mandibles. Post-ocellar striae incomplete. Pentagonal area excavated anteriorly, with narrow and shallow trench extending to anterior puncture. Galea elongate (see comments); glossa, paraglossa and all palp segments missing. Genal carina present. Malar space wide. Antennae 15 segmented, 1 without flabella; projection on penultimate segment extremely small; pedicel oblong; flabella of third antennal segment as long as following 1-2 segments.

Thorax Sculpture: smooth to very finely and sparsely punctulate throughout, except anterior, dorsal surfaces of the pronotum, lateral regions of the mesoscutum and mesoscutellum, which are punctulate-punctate to punctate. Setosity: as head, except

longer on posterior and lateral regions of pronotum, sparser and longer on latero-posterior edges of axillae, antero-lateral regions of metanotum, pleural and sternal sclerites. Pronotal collar curving. Hind-coxal apical incision open.

Abdomen Sculpture: smooth to very finely and sparsely punctulate throughout. Setosity: a few short and sparse hairs on lateral portions of basal terga, becoming even less dense on apical terga; sterna with a few long and very sparse hairs apically; basal plate with a sparse covering of much shorter hairs. Tergum 8 strongly indented apically with a semi-circular depression. Basal plate curved gradually toward dorsum; strongly indented, apically, with a semi-circular depression; viewed laterally, basal plate strongly downwardly curved apically, i.e. with a lip; apical margin appearing concave when viewed ventrally, although convex in reality. Genitalia: see comments.

Female

Unknown (but see comments). Possibly similar to that of *M. mercerti.*

Material examined: HOLOTYPE, ♂, Algeria: Oran, (Levaillant) (MNHN).

Distribution: western Algeria (Oran, Mekhalia).

Comments: The holotype bears two labels, one marked "Type" and the other "Tarpa levaillantii, Lu.".An extremely rare species, known from the holotype and another male, collected by Pic. The holotype, itself, is in an extremely poor condition, with no genitalic capsule, and the second specimen was unavailable for examination. Kirby's (1882) list of Hymenoptera in the British Museum (Natural History) indicates the existence of both sexes in the collections, but these were not found. This is particularly strange and infuriating, since no other specimens are known. Kirby was thorough and meticulous and it is unlikely that his records represent a lapsus. However, despite the poor condition of the holotype, it is quite obvious that Konow's putative (1897) and, later, confirmed (1901?) synonymy of *levaillantii* with *bucephalus* Klug, accepted by Gussakovskij (1935), was unjustified. Whilst the galea is damaged, the apical surface is intact sufficiently and this and its lipped and apically impressed basal plate indicate its proximity to *judaicus*, *kuznetzovi* and *mercerti*. It is distinguished from *judaicus* by its wide malar space and its distinctly flabellate antennae. The proximal nature of the teeth of the tarsal claw suggests that *levaillantii* may be more closely related to *mercerti* than to *kuznetzovi*.

Megalodontes luteiventris Konow

(Figs 21, 113)

Tarpa luteiventris Konow, 1894: 129; Konow, 1897. SYNTYPES ♂,♀, Algeria (DEIC), [examined].

Megalodontes luteiventris (Konow); Konow, 1897.

Male

Length 9-11mm; EA 0.85-0.88; A:B 3.14; B:C 2.33; D:E 1.18; D:F 0.87 (2 specimens

measured)

Colour: predominately black dorsally, laterally and ventrally on thorax and abdomen; predominately yellow dorsally and ventrally on abdomen. Occipital yellow broken medially (continuous in one specimen) and contiguous with genal yellow and with remnants of post-ocellar flecks (discontinuous in one specimen), which are present in occipital region only. Post-ocellar flecks reduced to remnants in occipital region only. Facial yellow, a large triangular marking between antennal insertions and occupying most of lower face and clypeus, discontinuous with yellow between antennal insertions and eye margin, in the form of a large longitudinal quadriangular fleck, which is produced vertically slightly above antennal insertions. Mouthparts predominately dark-brown; palp segments predominately ochraceous. Scape yellow, black fleck along length of dorsal surface; pedicel ochraceous, ringed brown basally; third antennal segment ochraceous; flagellum and flabellae yellow to ochraceous. Dorso-lateral and ventral regions of pronotum yellow. Four yellow flecks on mesonotum. Tegula yellow. Yellow flecks behind cenchri present (greatly reduced in one specimen and absent in another. Mespisternum black, yellow in dorsal quarter, not produced downwardly; antero-ventral region of metepimeron with yellow fleck. Propleurae yellow lined with black. Fore-coxae yellow, longitudinal black fleck along entire length or predominately black; mid-coxae black; hind-coxae black, marked with yellow laterally and sometimes apically. Fore-femora black, yellow at apex on outer face and on apical inner half; mid-femora black, yellow on outer face at apex and inner apical half to two-thirds; hind-femora yellow, ringed black basally and with small black fleck on basal one fifth on inner face. Wings: slightly fuscous throughout, less so on hind wing; venation testaceous basally and anteriorly, ochraceous apically and posteriorly; costal vein of both wings yellow basally. Tergum 1 black; tergum 2 black with large yellow fleck apico-laterally, greatly extended medially; terga 3-7 apical yellow band complete; tergum 8 yellow, only black in region of median impression. Sterna 2-7 black, yellow band complete occupying apical half of sclerite throughout; basal plate yellow.

Head Sculpture: closely and coarsely punctate to punctate-rugulose between rear ocellus and eye becoming punctate toward ocellus and on face, except yellow areas which are punctulate-punctate; rugulose between anterior ocellus and antennal insertions. Setosity: dense coating of long (more than twice diameter of rear ocellus) setae, particularly in genal and postgenal regions, slightly shorter and sparser on yellow marking of face and clypeus. Post-ocellar striae incomplete. Pentagonal area with very slight excavation in region of anterior ocellus, otherwise planar to anterior puncture. Genal carinae present. Malar space narrow. Galea elongate; glossa distinctly longer than galea, slightly downwardly curved apically, parallel-sided; paraglossa slightly shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 14-16 segmented, 2-3 without flabella; pedicel square; flabella of third

antennal segment as long as the following 4-5 segments.

Thorax Sculpture: punctulate-punctate on black regions of pronotum; propleurae, mesepimeron, metepisternum and metepimeron smooth; closely punctate-rugulose on mesonotum; mesepistemum and meso- and metapleurae punctate. Setosity: as head, distinctly longer on propleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth with a few fine and very sparse punctulae, dorsally and ventrally. Setosity: as head on tergum 1 and medially and laterally on tergum 2; laterally on remainder of terga with shorter and much sparser setae; dorsally remainder of terga with short and sparse setae; ventrally of same length as head but extremely sparsely distributed; basal plate with coating of shorter and finer setae. Tergum 8 with broad, widely separated and shallow impression. Basal plate curved gradually toward dorsum; without lip; apical surface flattened; apical margin distinctly convex. Dorsal internal margin of gonostipes parallel basally, diverging slightly medially, sharply curved apically. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting more anteriorly than ventral. Dorsal surface of gonostylus, viewed laterally, straight, appearing slightly downwardly angled apically; gonostyli with very sparse coating of long hairs; gonomaculae hemi-elliptical. Lateral surface of basivolsellae rounded. Digitus dorsally slightly convex basally and concave apically, ventrally convex from base to dorsal apex, thus giving the digitus the appearance of being slightly pointed dorso-apically (Fig. 113). Cuspis digitiform, volsellar pocket wide but asymmetrical apically. Penis valve, dorsally, sub-parallel in basal two-thirds, appearing constricted between base and median, tapering from median to apex and appearing secondarily constricted between the two; lateral lobes undeveloped; aedeagal apodemes flared apically.

Female

Length 9-10 mm; EA 0.84-0.87; A:B 2.27-2.6; B:C 1.67-1.83; D:E 1.73-1.9; D:F 1.06 (2 specimens measured)

Colour: similar to males, but more extensively yellow dorsally and darker laterally and ventrally. Yellow between antennal insertions and eye margin produced slightly vertically and toward rear ocelli. Scape yellow; pedicel ochraceous; flagellum and flabellae ochraceous. Dorso-lateral yellow markings on pronotum more widely separated than in males. Ventro-lateral yellow on pronotum absent. Four yellow flecks on mesoscutum, anterior larger than axillary or vice versa. Yellow flecks behind cenchri present, very large or greatly reduced. Metepisternal yellow absent; remainder laterally and pleural sclerites black. Fore-coxae yellow, longitudinal black fleck along entire length or black; mid-coxae brown or black; hind-coxae dark brown or black. Sternum 2-3 black; sternum 4 black, small apical transverse fleck laterally; sterna 5-6 black, large apical transverse fleck, greatly extended medially; sternum 7 black, apical margin of

yellow. Sclerite above sawsheath dark-brown.

Morphology as males with the exception of the following.

Head Setosity: as males, shorter but much denser on lower face and clypeus, bare between antennal insertions and malar region. Antennae 15-16 segmented, 3 without flabella; pedicel tranverse or square; flabella of third antennal segment as long as the following 4 segments.

Thorax Setosity: as males, but distinctly longer on mesepisternum.

Abdomen Sculpture: dorsally punctulate throughout, ventrally smooth with a few sparse and fine punctulae. Setosity: coating of long setae, as head in length but sparser, except for apical terga and sterna.

Material examined: SYNTYPES ♂,♀ and 3♂, 2♀ (DEIC, ISCM, MNHN).

Distribution: Algeria (Annaba, Teniet El Had).

Comments: Closely related to *flabellicornis* and *Megalodontes* sp.3 and males are easily separated fom them by its much coarser punctation between the rear ocelli and eyes. Females are separated from *Megalodontes* sp.1 by their longer third antennal flabella.

Megalodontes merceti Konow

(Figs 18, 22, 24, 48, 115)

Megalodontes merceti Konow, 1904: 226; Gussakovskij, 1935. SYNTYPES ♂,♀, Spain: Escorial, Vaciamadrid (R.G.Mercet.) (DEIC), [examined].

Male

Length 14-15 mm; EA 0.96-0.98; A:B 2.64; B:C 1.38; D:E 1.35; D:F 1.21 (2 specimens measured)

Colour: predominately yellow. Vertex, occiput and upper postgenal area of head, with the exception of two narrow post-ocellar flecks, upper scrobal region (check terminology), upper region of frons, dorsum of thorax black, except for four yellow flecks on mesonotum, tegulae and a pair of metapostnotal yellow flecks posterior of the cenchri; wings yellow-hyaline; venation ochraceous to testaceous basally and anteriorly; pterostigma marked yellow; remainder of venation apically and posteriorly yellow to ochraceous. bases of all except apical 2-3 terga and all except apico-laterally on tergum 1 black.

Head Sculpture: closely punctulate between rear ocelli and eyes; smooth to punctulate on vertex and occiput; region between anterior ocellus and upper scrobal region closely punctate; face smooth. Setosity: coating of fine short hairs, slightly longer in genal region. Post-ocellar striae incomplete. Pentagonal area with deep triangular excavation extending from anterior ocellus to anterior puncture. Genal carinae present. Malar space wide. Galea swollen; glossa flared apically, downcurved strongly and barely longer than galea; paraglossa more or less laminate, not distinctly hemi-tubular. Antennae

16 segmented, 1-2 without flabella, penultimate segment with extremely short process; pedicel oblong; flabella of third antennal segment as long as the following 3-4 segments.

Thorax Sculpture: closely punctate on mesonotum; punctulate anterior of notaulices; laterally and ventrally smooth except for setal insertions. Setosity: as head, slightly longer on dorso-lateral of pronotum and on mesepisternum. Pronotal collar curving. Hind-coxal apical incision open.

Abdomen Sculpture: smooth with a very fine and sparse punctulae, dorsally and ventrally. Setosity: median of tergum 1 as head; median of sterna 3 and 4 with a few sparse amd shorter setae: remainder with covering of short hyaline setae, particularly dense upon basal plate. Tergum 8 with deep horseshoe-shaped depression. Basal plate strongly curved toward apex and then sharply re-curved to produce prominent apical lip; apical surface impressed; apical margin appearing strongly concave, viewed ventrally, but actually convex. Dorsal inner margins of gonostipes sub-parallel basally, except for a distinct indentation near junction of gonostipal dorsal surfaces, curving away strongly from median line toward apex. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus articulation not projecting anteriorly of ventral. Dorsal surface of gonostylus strongly upwardly curved; gonostyli with dense coating of short setae; gonomaculae semi-circular. Lateral surface of volsellae rounded. Digitus, in latero-ventral view, in the form of a highly deformed ellipse (Fig. 115). Cuspis digitiform, projecting apically of digitus; volsellar pocket asymmetrical, wide apically. Penis valves viewed laterally digitiform (as in Fig. 56) and parallel-sided from base to mid-length and tapering to apex when viewed dorsally; aedeagal apodemes flared apically.

Female

Length 14-16 mm; EA 0.97-0.98; A:B 3.1; B:C 1.22; D:E 1.14; D:F 1.2 (2 specimens measured)

Colour: predominately black dorsally, on head and thorax, pronotum excepted; laterally and ventrally predominately black. Facial yellow discontinuous with fleck between antennal insertion and eye margin, reduced to a campaniform or oblong fleck between antennal insertions and two rectangular flecks in lateral regions of clypeus. Four yellow flecks on mesonotum, lateral yellow flecks on metapostnotum present but, usually, very indistinct and tegula yellow. Tergum 1 marked yellow apico-laterally, but often indistinct, tergum 2 with larger apico-lateral yellow flecks and terga 3-8 yellow in, at least, apical half, appearing distinctly narrower apico-medially on tergum 3. Sclerite above sawsheath yellow to ochraceous.

Morphology as males with the exception of the following.

Head Sculpture: punctate between rear ocelli and eyes, smooth to punctulate-punctate in vertiginal and occipital areas; between anterior ocellus and antennal insertions closely and coarsely punctate to punctate-rugulose. Antennae 17 segmented, 1-2 without

flabella, process on penultimate and anti-penultimate segments greatly reduced.

Thorax Sculpture: as males, dorsally, but laterally and ventrally punctulate-punctate to punctate. Setosity: as males, slightly longer on lateral and pleral sclerites.

Abdomen Sculpture: very finely but closely punctulate dorsally and ventrally. Setosity: tergum 1 and yellow regions of sterna with long but sparse hairs; remainder with dense covering of hyaline setae, particularly dense laterally and ventrally.

Material examined: SYNTYPES ♂,♀ and 2♂, 3♀ (BMNH, IZUB, MNHN).

Distribution: central Spain (Madrid and Avila regions).

Comments: post ocellar flecks wider and longer than in *kuznetzovi*, occipital and post genal black more extensive than in *kuznetzovi*, intra-antennal area projecting more dorso-anteriorly than in *kuznetzovi*. The predominately black hind coxa differs from the entirely yellow colouring of that of *kuznetzovi*. The degree of yellow colouring on terga in both sexes reduced in comparison with *kuznetzovi*.

Megalodontes nitens (Freymuth)

(Figs 59, 116, 118)

Tarpa nitens Freymuth, 1870: 222; Konow, 1897; Gussakovskij, 1935. SYNTYPES ♂,♀, Uzbekistan: Zaravshanskaya dolina, Ak' Dar'ya, steppe between Katti-Kurgan and Ulus 1 (and 9?).v. (A.P.Fedchenko) (ZMAS), [not examined].

Megalodontes decussatus Konow, 1906: 254. SYNTYPES ♂,♀, Turkmenistan: Tedzhen (ZMAS), [not examined]. Synonymised by Gussakovskij, 1935.

Megalodontes nitens (Freymuth); Kirby, 1882.

Male

Length 9-10 mm; EA 0.92-0.96; A:B 2.1; B:C 1.67; D:E 1; D:F 1.6 (2 specimens measured)

Colour: predominately black dorsally, entirely yellow laterally and ventrally, except ventral region of mesepisternum, all except upper or anterior of mesepimeron and all except median of propleurae and mesosterna. Post-ocellar flecks of yellow present, vestigial or absent. Face and frons yellow entirely with black only below antennal insertions or yellow only on clypeus, lower face and laterally toward frons and widely black below and between antennal insertions and in pentagonal area. Mouthparts predominately yellow. Four yellow flecks on mesoscutum. Mesoscutellum black basally, strongly marked with yellow apically. Lateral yellow flecks on metapostnotum present. Tegula yellow. Wings hyaline; venation predominately ochraceous to testaceous; base of costal vein and median of pterostigma yellow. Tergum 1 with yellow fleck apico-laterally, terga 2-7 with complete apical band of yellow and tergum 8 yellow entirely.

Head Sculpture: smooth to extremely finely and sparsely punctulate between rear ocelli and eyes, remainder of head smooth except for punctulate-punctate region between anterior ocellus and antennal insertions. Setosity: sparse coating of long and stout bristles

on upper face and genal region, becoming sparser and slightly shorter on vertex and occiput, but denser on lower face. Post-ocellar striae incomplete. Pentagonal area with broad triangular but not deep excavation in region of anterior ocellus, extending to, but flattened, toward anterior puncture. Genal carinae present. Malar space narow. Galea slightly elongate; glossa linguiform, downwardly curved and slightly flared apically; paraglossa lamelliform, downwardly curved apically. Antennae 17 segmented, 1 without flabella; pedicel transverse; flabella of third antennal segment as long as the following 8-9 following segments.

Thorax Sculpture: punctate on anterior portion of lateral lobes of mesonotum and anterior of notaulices, smooth to punctulate-punctate on remainder of notum; laterally and ventrally smooth apart from setal insertions. Setosity: sparse coating of long and stout bristles on pro-pleural sclerites, becoming sparser but slightly longer on dorsal and lateral sclerites. Pronotal collar curving. Hind-coxal apical incision open.

Abdomen Sculpture: smooth. Setosity: sparse coating of long and stout bristles on dorsum of tergum 1, sparser and shorter on sterna, becoming considerably shorter on apical sterna; sternum 8 with sparse coating of short hyaline setae. Tergum 8 with broad shallow impression. Basal plate curved toward apex; without distinct lip but strongly impressed on apical surface; apical margin truncate. Dorsal inner margins of gonostipes diverging from base to apex, notched near apex and curving laterally abruptly. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus not projecting more apically than ventral. Dorsal surface of gonostylus virtually straight; gonostyli with dense coating of short hairs; gonomaculae semi-cicular to hemi-elliptical. Lateral surface of volsellae straight. Digitus in the from of a small digitiform projection (Fig. 118). Cuspis in the form of small antero-lateral protuberance from volsellae. Penis valves lateral and dorsally tapering gradually from base to apex, more abruptly so in apical one-quarter to form a sharp point; aedeagal apodemes widely flared apically

Female

Length 9-10.5 mm; EA 0.90-0.92; A:B 1.; B:C 1.83; D:E 1.11; D:F 1.67 (2 specimens measured)

Colour: yellow more extensive than males, dorsally; more extensively dark-brown or black laterally and ventrally but still predominately yellow. Head yellow throughout, with the exceptions of the dark-brown to black scrobal regions, a black marking beneath each antennal insertion, and a transverse dark-brown to black band passing through the rear ocelli but separated from eye margins; vertex appearing smudged with brown. Mouthparts predominately yellow to ochraceous. Four yellow flecks on mesoscutum much larger than in males. Mesoscutellum: yellow, basal margin brown. Mesepisternum yellow, ventral one-fifth to one-quarter dark-brown to black; mesepimeron yellow entirely. Median yellow flecks on metapostnotum: present. Pterostigma more extensively marked in yellow. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Sculpture: smooth to very fine and sparse punctulae throughout. Setosity: similar in density to males but shorter throughout. Pentagonal area similar to males but much broader triangular area in region of anterior ocellus, but less excavated than in males. Antennae 18 segmented, 1 without flabella; pedicel oblong; flabella of third antennal segment as long as 10-11 following segments.

Thorax Sculpture: dorsum punctate, except for smooth pronotum; laterally and ventrally as males, except for dark-brown to black regions which are punctulate.

Abdomen Setosity: as males, except setae much stouter on sternum 7.

Material examined: 4♂, 4♀ (BMNH, DEIC, ZMAS, ZMUM)

Distribution: Turkmenistan (Dzhizak, Kerki), Uzbekistan (Samarkand) Tadzhikistan (Guzar).

Comments: a highly variable species in coloration, particularly the degree of yellow colouration of the face and terga in males and a female which is more extensively yellow throughout. Males may be distinguished from the closely related *xanthosomus* by their far shorter and dorsally straight gonostyli and by D:E and the females by the length of the third antennal flabella and by A:B.

Megalodontes olivieri Brullé

(Figs 27, 28, 117)

Tarpa olivieri Brullé, 1846: 660. HOLOTYPE ♀, Iraq: Baghdad (C.M.Olivier) (MNHN), [not examined].

Megalodontes olivieri (Brullé); Kirby, 1882.

Male

Length 8-10 mm; EA 1; A:B 2.22-2.3; B:C 1.5; D:E 0.8-0.85; D:F 1.45-1.6 (2 specimens measured)

Colour: predominately yellow throughout, except vertex of head and dorsum of thorax, which are predominately black. Vertiginal yellow broken medially at occiput but contiguous with genal yellow, which is complete, and also contiguous with broad long flecks of yellow posterior of rear ocelli; facial yellow complete, laterally extended along eye margins and medially toward rear ocelli. Scape yellow; pedicel ochraceous, marked brown: basal flagellar segments yellow to ochraceous becoming ochraceous to testaceous apically; flabellae ochraceous to testaceous basally, becoming brown apically. Mouthparts predominately yellow to ochraceous. Four yellow flecks on mesoscutum, axillary pair large. Mesoscutellum black, 2 yellow flecks latero-apically. Mesepisternum, yellow, black in ventral one-fifth only; mesepimeron yellow. Lateral and median yellow flecks on metapostnotum present. Tegula yellow. Wings: hyaline; venation ochraceous; pterostigma marked with yellow basally. Tergum 1 with large lateral apical fleck and apical margin of yellow. Tergum 2, occasionally tergum 3 black with yellow flecks occupying all of

sclerite laterally and greatly extended medially, but widely separate. Terga 3-7 with apical yellow band complete and tergum 8 yellow. Sterna yellow, occasionally with smudges of darker colour apico-laterally.

Head Sculpture: smooth to very finely and sparsely punctulate between rear ocelli and eyes, remainder smooth except punctate between rear ocelli and antennal insertions. Setosity: sparse coating of long and stout bristles on upper face and genal region, becoming sparser and slightly shorter on vertex and occiput, but denser on lower face; generally very similar to *nitens*. Post-ocellar striae incomplete. Pentagonal area with broad triangular but not deep excavation in region of anterior ocellus, flattened toward anterior puncture. Genal carinae present. Malar space wide. Galea slightly elongate; glossa linguiform, downwardly curved and distinctly flared apically; paraglossa lamelliform, downwardly curved apically. Antennae 18 segmented, 1 without flabella; pedicel square; flabella of third antennal segment as long as the following 12-13 segments.

Thorax Sculpture: smooth on yellow regions, except for setal insertions; sparsely punctate on lateral lobes of mesonotum and anterior of notaulices with large lustrous interspaces. Setosity: sparse coating of long and stout bristles throughout; slightly denser on pro-pleurae. Pronotal collar curving. Hind-coxal apical incision open.

Abdomen Sculpture: smooth, dorsally and ventrally. Setosity: tergum 1, laterally on tergum 2 and ventrally with sparse coating of hairs, slightly shorter than on head and thorax; basal plate with coating of short and fine hyaline setae. Tergum 8 with broad and shallow V-shaped impression. Basal plate curved gradually to apex; without distinct lip; slightly flattened apically; apical margin truncate to very slightly concave. Dorsal inner margins of gonostipes divergent from base to apex and curving laterally near apex. Dorsal sclerotisation of gonostipes incomplete, although apex is proximal to inner dorsal margin. Dorsal articulation of gonostipes and gonostylus projecting marginally more apically than ventral, appearing virtually equal on casual inspection. Dorsal surface of gonostylus straight, slightly upwardly curved at apex; gonostylus with coating of short hairs; gonomaculae hemi-elliptical. Lateral surface of volsellae straight-sided to mid-length, incut abruptly and slightly angled toward apico-median of volsellae. Digitus, in latero-ventral view, strongly reduced to small partially lamellar projection in the form of a seed-crushing bill (Fig. 117). Cuspis reduced to small protuberance on latero-apex of volsellae. Volsellar sac square to slightly oblong and strongly sclerotised. Penis valves rod-like laterally, tapering more so ventrally to a fine point apically and, viewed dorsally, parallel to mid-length and tapering gradually to a fine point apically; aedeagal apodemes widely flared at apex.

Female

Length 7-10 mm; EA 0.97-1; A:B 2.2-2.3; B:C 1.67; D:E 0.8; D:F 1.33-1.35 (2 specimens measured)

Colour: similar to males but generally darker, i.e. more ochraceous; head and dorsum of thorax more extensively yellow than males; pleural region more extensively black and sterna ochraceous rather than yellow. Mouthparts predominately yellow; only ochraceous to testaceous on cardo, stipes and prementum. Yellow flecks on mesoscutum: 4, more extensive than males and flecks at anterior traversing notaulices, thus suggesting six rather than four flecks. Mesoscutellum basally black, apically yellow. Mesepisternum yellow, ventral one-quarter black. Humeral sclerite ochraceous. Wings: hyaline; venation ochraceous to testaceous throughout, pterostigma and costal vein near pterostigma red-brown. Occasionally tergum 2 with yellow apical band widely broken, usually all terga with banding complete, at least apically. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Setosity: similar density to males but considerably shorter throughout. Antennae 21 segmented.

Thorax Pronotal collar collapsing.

Material examined: 6♂, 9♀ (BMNH, SMNS, ZMUM)

Distribution: Iran (Baluchistan, Iranshahr), Iraq(Baghdad), Armenia (Dzhervezh); Israel (Hazeva), Morocco (Erfoud).

Comments: Type female, not male as in original description. Males may be separated from those of *phaenicius* by the entirely yellow post-genal areas and by the form of apex of the gonostylus. Females are separated from those of *phaenicius* by their complete facial yellow.

Megalodontes parvus Dovnar-Zapolskij

(Figs 100, 119)

Megalodontes parvus Dovnar-Zapolskij, 1930: 93; Gussakovskij, 1935. SYNTYPES ♂,♀, Turkestan: Kisiltshi (environs of Guzar) (A. Gerasimov) (ZMAS), [not examined].

Male

Length 6.5-9 mm; EA 0.88; A:B 2.29-2.41; B:C 1.35-1.47; D:E 0.95-1.06; D:F 0.83 (2 specimens measured).

Colour: predominately dark-brown to black dorsally, laterally and ventrally, only sterna predominately white yellow. Occipital white-yellow unbroken or narrowly broken between occipital remnants of post-ocellar striae; contiguous with genal yellow which extends to malar region posterior of oculus and sometimes contiguous with fleck between antennal insertions and eye margin Post-ocellar flecks long extending from immediately posterior of ocellar area to occiput and contiguous with occipital colouring. Facial white-yellow consisting of a lateral trapezoidal fleck between the antennal insertion and oculus and an oblong mark between the former, both separate from lower facial white-yellow which, in turn is broken medially into lateral rectanglar flecks and a central

circular or square of colour. Mouthparts predominately black, apical palp segments light brown. Antennal segments black, with the exception of the baso-venter of the scape, marked white-yellow. Pronotum white-yellow dorsally, except medially and on pronotal collar, laterally and latero-ventrally. Four white-yellow flecks on mesoscutum, axillary pair large. Tegula and humeral sclerite white-yellow. Mesoscutellum with very small fleck of white-yellow apico-medially. Flecks behind cenchri present. Mespistemum marked white-yellow in dorsal one-third, produced downwardly strongly posteriorly; mesepimeron with narrow fleck of white-yellow dorso-posteriorly. All coxae brown to dark-brown. Fore- and mid-femora ochraceous, ringed testaceous to brown in basal one-third; hind-femora ochraceous. Wings fuscous, less strongly so apically and posteriorly on both fore- and hind wings; venation black basally and anteriorly, dark-brown apically and posterioly; costal vein and pterostigma of fore-wing white-yellow, the latter darker medially. Tergum 1 dark-brown with or without small apico-lateral white-yellow spot; tergum 2 with either lateral and medial flecks of white-yellow or a narrow apical band, irregularly broken or unbroken; terga 3-8 with narrow apical band of white-yellow. Sternum 2 brown with small apico-lateral flecks; sterna 3-7 apical band complete, although very narrow on sternum 3; basal plate white-yellow.

Head Sculpture: very finely and sparsely punctulate between rear ocellus and oculus with lustrous interspaces, otherwise smooth. Setosity: sparse coating of long hairs (more than three times diameter of rear ocellus), slightly denser in post-genal region and slightly shorter on lower face. Post-ocellar striae incomplete. Pentagonal area wide and shallow excavation extending to anterior pit. Genal carinae absent. Malar space extremely narrow, may appear absent. Galea slightly elongate; glossa distinctly longer than galea, strongly downwardly curved apically, slightly flared apically; paraglossa slightly shorter than glossa, strongly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 12 segmented, 2 without flabella; pedicel oblong; flabella of third antennal segment as long as the following 4-5 segments.

Thorax Sculpture: smooth with occasional punctulae throughout on black areas, those marked in white-yellow smooth. Setosity: as males but shorter and sparser on mesoscutum; as post-gena on propleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth. Setosity: laterally on tergum 1 as head, medially of same length but only a few hairs medially; laterally on terga 2-7 shorter and much sparser than head; tergum with sparse coating of short hairs (less than diameter of rear ocellus); sterna as head, basal plate as tergum 8. Tergum 8 with shallow impression, broadly separated. Basal plate curved gradually to dorsum; without lip; impressed apically; apical margin convex. Dorsal inner margin of gonostipes divergent from base to three-quarter length, angled abruptly laterally toward apex. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting

anteriorly to ventral. Dorsal surface of gonostylus, viewed laterally straight, upwardly curved at apex; gonostyli with sparse coating of short hairs, slightly longer ventrally; gonomaculae highly deformed circular, almost truncate basally. Lateral margin of volsellae rounded. Digitus straight to weakly concave dorsally, angled downward at apex, ventrally straight to mid-length and convex to dorsal apex (Fig. 100). Cuspis digitiform; volsellar pocket apically wide. Penis valve, dorsally, parallel-sided, tapering to apex from beyond three-quarter length; laterally, dorso-basally almost perpendicular, straight to weakly convex dorsally, concave to apex; ventrally convex from base beyond three-quarter length, apically concave thus giving an unciform appearance ventro-apically; apices of aedeagal apodemes parallel-sided and rounded apically

Female

Length 7-8 mm; EA 0.88-0.89; A:B 2.21-2.26; B:C 1.52-1.62; D:E 1.3-1.35; D:F 0.84-1.08 (2 specimens measured)

Colour: Head coloration as males but more extensively white-yellow throughout, particularly the larger post-ocellar flecks. Antennae as males, scape slightly lighter. Pronotum more extensively white-yellow dorsally; sligbtly less so laterally. Flecks on mesoscutum and behind cenchri larger. Mesoscutellum marked with white-yellow, often extensively. Humeral sclerite slightly darker than tegula. Mesepistemal white-yellow on dorsal quarter and not produced downwards as strongly as in males. Mesepimeron, metepistemum and metepimeron black. Propleurae black with white-yellow spots; mesostema black. Wings and venation as males; costal vein of fore-wing slightly darker. Fore-femora brown in basal three-quarters, apically ochraceous to testaceous; mid-femora brown in basal half apically ochraceous to testaceous; hind-femora ochraceous. Tergum 1 dark-brown with small apico-lateral white-yellow spot and irregular spots basao-medially; tergum 2 with narrow white-yellow apical band, irregularly broken or unbroken; terga 3-8 with narrow apical band of white-yellow. Sternum 2 brown with small apico-lateral flecks; sterna 3-7 apical band complete, although very narrow or irregularly broken on sterna 3-5. Sclerite above sawsheath white-yellow, marked with black

Morphology as males with the exception of the following.

Head Sculpture: smooth with occasional fine punctulae. Setosity: as males but slightly shorter hairs. Antennae 11 segmented, 1 without flabella; flabella of third antennal segment as long as the following 3-4 segments.

Abdomen Setosity: as males, apical margin of tergum 8 with short hairs (slightly longer than the diameter of rear ocellus).

Material examined: 4♂, 4♀ (BMNH, OLML, ZMUM).

Distribution: Tadzhikistan (Guzar), Turkmenistan (Golodnaya steppe).

Comments: A very distinctive species on the basis of its size, white yellow markings and smooth sclerites. Males are separated from *reitteri* and several others by the

absence of genal carinae and the sharp angle between the vertiginal and occipital margins. Females may be separated by these characters and the small white-yellow apico-lateral fleck on tergum 1, which is absent in those of *flabellicornis*

Megalodontes phaenicius Lepeletier

(Figs 7, 65, 66)

Tarpa phaenicia Lepeletier, 1823: 15, Konow, 1897. SYNTYPE ♂, Syria (MNHN), [not examined].

Tarpa caucasica André, 1881: 479. SYNTYPE(S) ♀, Caucasus (HNHM?), [not examined]. Synonymised by Konow, 1897.

Megalodontes imperialis Konow, 1897: 5. SYNTYPE ♀, Turkey: Kars, 1860 (Mann) (NHMW), [examined].

Megalodontes kohli Konow, 1897: 6. SYNTYPE ♀, Turkey: Amasia, 1860 (Mann) (NHMW), [examined].

Megalodontes dusmeti Enslin, 1913: 170. SYNTYPE ♀, Spain: Orihuela (Andreu) (ZSMC), [examined].

Megalodontes phoenicius auct., mis-spelling.

Male

Length 9-10 mm; EA 0.95-0.97; A:B 2.6-2.73; B:C 1.67; D:E 0.9-0.95; D:F 1.29-1.36 (2 specimens measured).

Colour: predominately black dorsally, except for terga; laterally and ventrally yellow throughout, except for mesepimeron. Vertiginal yellow, broken medially, contiguous with vertiginal yellow, which is a wide stripe behind the eyes, and contiguous with long, tapering posteriorly, flecks posterior of rear ocelli; face yellow (except below antennal insertions in non-Levantine specimens) and contiguous with yellow between antennal insertions and eye margins, which is strongly produced vertically toward rear ocelli. Mouthparts predominately yellow. Scape yellow, yellow with dorso-lateral black fleck; pedicel brown, marked with yellow at base of inner face and at apex of outer; third antennal segment brown basally, ochraceous apically; flagellum with basal 9 segments ochraceous, apical 6, except terminal, segments testaceous; apical segment dark brown; flabella of segment 3 testaceous basally becoming dark-brown apically, remainder dark-brown. Four yellow flecks on mesoscutum. Lateral yellow flecks on metapostnotum present. Tegula yellow. Mesepisternum yellow and mesepimeron with anterior longitudinal black stripe; metanotum with narrow yellow margin between the cenchri. Wings hyaline-yellow to very slightly fuscous; venation ochraceous to testaceous anteriorly and basally, with the exception of the base of the costal vein, which is yellow to ochraceous; ochraceous posteriorly and apically. Tergum 1 black with large apico-lateral yellow fleck; terga 2-4 black with large apico-lateral yellow fleck, greatly produced medially and only narrowly separated, medially on tergum 4; terga 5-7 yellow band

complete and tergum 8 yellow.

Head Sculpture: punctate with lustrous interspaces between rear ocelli and eyes; closely punctate between anterior ocellus and antennal regions; vertex and occiput punctulate; facial yellow areas smooth, except for setal insertions. Setosity: coating of stout bristles, as in *olivieri*, slightly longer and denser in genal region and denser on lower face. Post-ocellar striae incomplete. Pentagonal area excavated in region of anterior ocellus with shallow trench extending to anterior puncture. Genal carinae present. Malar space wide. Galea slightly elongate; glossa linguiform, downwardly curved and slightly flared apically; paraglossa lamelliform, downwardly curved apically. Antennae 21 segmented, 1 without flabella; pedicel transverse; flabella of third antennal segment as long as the following 11-12 segments.

Thorax Sculpture: closely and coarsely punctate throughout dorsum, with occasional lustrous interspaces; smooth to punctulate at extreme anterior bordering pronotum and in areas marked with yellow; laterally and ventrally smooth, except at setal insertions. Setosity: similar to head, but longer on dorsum and lateral of pronotum, mesepisternum and on pro-pleurae. Pronotal collar collapsing. Hind-coxal apical incision open.

Abdomen Sculpture: smooth dorsally and ventrally. Setosity: tergum 1, laterally of terga 2 and 3 and sterna 1-7 as head, but slightly sparser and shorter; basal plate with coating of short setae. Tergum 8 with V-shaped impression, widening apically. Basal plate curved gradually toward dorsum; without distinct lip; impressed apically; apical margin truncate. Dorsal inner margins of gonostipes gradually divergent from base to three-quarter length and then curved abruptly laterally. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus projecting apically of ventral. Dorsal surface of gonostylus straight and appearing produced into an apical peg, although this is better interpreted as a massive deformation of the ventral surface, since the proportions of gonostylus and gonostipes, dorsally, appear to be in concordance with many other species of megalodontids. Gonostyli with sparse coating of very short hairs; gonomaculae circular. Lateral surface of volsellae straight-sided to mid-length, incut abruptly and slightly angled toward the apico-median of volsellae. Digitus reduced to a triangular and weakly sclerotised projection from apex of volsellae, viewed latero-ventrally curved abruptly from to dorsum to venter (Fig. 7). Cuspis, although much reduced, projecting apically of digitus as a digitiform protuberance from apex of volsellae with a second smaller apico-lateral protuberance. Sclerotisation and form of volsellar sac heavily sclerotised, although less so than in *olivieri* and more rounded. Penis valves, in latero-ventral view, extremely narrow and tapering from mid-length to a fine point apically and curved toward dorsum; viewed dorsally sub-parallel from base to mid-length and tapering to fine point apically; aedeagal apodemes strongly flared apically.

Female

Length 9-11 mm; EA 0.94-0.99; A:B 2.55-2.6; B:C 1.57-1.67; D:E 0.95-1; D:F 1.57 (2 specimens measured)

Colour: slightly more extensively yellow dorsally; extensively marked in black laterally and ventrally. Facial yellow reduced to a fleck between antennal insertions and eyes and a third between the former (most specimens) or produced apico-laterally on frons and broken on face below antennal insertions and between these and malar region giving the appearance of three much larger flecks (Israeli material); clypeal yellow reduced to two large lateral rectangular flecks. Mouthparts as males or black basally becoming brown to testaceous apically. Antennal colour highly variable. Scape, pedicel and third antennal segment without dark markings or testaceous to dark-brown; flagellum and flabellae as males or black throughout. Lateral fleck on metapostnotum present and larger than males (Levantine and Spanish specimens) or absent (Turkish, Bulgarian and Romanian specimens). Mespisternum yellow in dorsal two-thirds or with dorso-posterior yellow fleck extending ventrally; mesepimeron black with small dorsal yellow spot or black; metepisternum with two yellow flecks antero-dorsally and ventrally or black; metepimeron with dorsal yellow stripe or black; propleurae yellow, edged in black or black, metasterna black. Coxae marked black, at least basally, or black. Tergal colour variable but more extensively marked with yellow than males; terga 2-4 with yellow broken medially; terga 5-7 with yellow band complete apically, occasionally broken on tergum 7, but wider or more generally yellow specimens; sterna 2-4 yellow apico-medially, occasionally apico-laterally on tergum 4; terga 5-7 apical yellow band complete, occasionally broken medially on sternum 5, but medially unbroken on sternum 7. Sclerite above sawsheath yellow.

Morphology as males, except for the following.

Head Sculpture: slightly more closely punctulate-punctate on vertex than males, otherwise similar. Setosity: similar density to males but shorter throughout. Antennae 20 segmented, 1 without flabella; flabella of third antennal segment as long as the following 12-13 segments.

Abdomen Setosity: as males, but slightly longer, denser and stouter on sterna.

Material examined: SYNTYPES 1♀ of *imperialis*, 1♀ of *kohli*, 1♀ of *dusmeti* and 7♂, 10♀ (BMNH, IZUI, MHNB, MKRC, MWEC, OLML, TAUI, ZMUM)

Distribution: central and eastern Turkey (Gürün, Konya, Urgup, Vezirkopru, Hakkari), Russia (Kherson, ? Caucasus), Israel (Dovrat, Mishot Rotem), Bulgaria (Black Sea coast), Romania (Hîrsova), Spain (Alicante and Madrid regions).

Comments: May be distinguished from the closely related *olivieri* by the much greater degree of black coloration on the head and by the apical form of the gonostyli. The synonymy of *dusmeti*, known from two females only, from southern Spain, may appear contentious given its highly separate distribution from the remainder of the material.

However, its range of colour, length of third antennal flabella agree well with females from Turkey and Israel (females from Romania and Bulgaria being slightly darker, and the cephalic and antennal ratios (EA 0.96; A:B 2.29, B:C 1.47; DE 1.25; D:F 1.5) are not vastly different from those from *phaenicius*. Its sister species, *olivieri*, has a similar disjunct distribution, with its Moroccan material considerably isolated from the nearest Levantine neighbours. Both may not represent genuine disjunct populations and may be due merely to the non-collection of material from the intervening areas.

Megalodontes quinquecinctus Klug

(Figs 76, 101, 104, 105)

Tarpa quinquecincta Klug, 1824: 193; Konow, 1897. SYNTYPE ♀, Tauria (Pallas) (ZHMB), [examined].

Megalodontes nitidus Maa, 1949: 40. HOLOTYPE ♀, China: Heilungkiang, Chalantun (T.C.Maa) (IZAS), [not examined].

Megalodontes tsunekii Togashi, 1973: 294. Holotype ♀, China: Inner Mongolia, Apaka viii.1939 (K. Tsuneki) (FUUN), [not examined].

Megalodontes apakensis Togashi, 1973: 295. HOLOTYPE ♀, China: Inner Mongolia, Apaka, 29.vii.1939 (K. Tsuneki) (FUUN), [not examined].

Megalodontes quinquecinctus (Klug); Kirby, 1882.

Male

Length 8-11 mm; EA 0.88-0.93; A:B 2.6; B:C 1.67; DE 1.92; D:F 1.44 (2 specimens measured).

Colour: predominately black dorsally; laterally and ventrally predominately yellow. Vertiginal yellow complete and contiguous with genal yellow and with long, and broadening flecks anteriorly. Ocellar triangle marked with yellow spots. Yellow flecks posterior of rear ocelli. Facial yellow complete, produced strongly vertically along eye margin only area immediately below antennal insertions and and along scrobes black. Mouthparts predominately yellow to ochraceous marked brown basally. Scape ochraceous; pedicel ochraceous to testaceous; third antennal segment ochraceous; flagellum ochraceous, apical segment testaceous, flabellae ochraceous basally, becoming testaceous to brown apically. Pronotum yellow except for narrow anterior black ledge. Four yellow flecks on mesoscutum. Tegula yellow. Yellow flecks behind cenchri present. Mes- and metepisterna yellow; mes- and metepimera yellow except for anterior margins. Propleurae and mesosterna yellow, except for darkened margins. All coxae and femora yellow. Wings: slightly fuscous throughout; venation ochraceous to testaceous anteriorly and basally, becoming ochraceous posteriorly and apically; pterostigma marked ochraceous medially. Terga 1-2 black, yellow fleck apico-laterally; terga 3-8 apical yellow band complete. Sterna 1-5 and basal plate yellow; sterna 6-7 yellow, black baso-laterally.

Head Sculpture: sparsely punctulate between rear ocelli and eyes becoming smooth

toward occiput; lower face smooth apart from setal insertions; punctulate-punctate between anterior ocellus and antennal insertions. Setosity: coating of short and stout hairs, about twice the width of the rear ocellus, denser and slightly stouter in lower face. Post-ocellar striae incomplete. Pentagonal area with wide but shallow excavation in region of anterior ocellus extending toward anterior puncture. Genal carinae obsolete, present only as an angle between gena and postgena, not as a distinct carina. Malar space narrow. Galea slightly elongate; glossa parallel-sided, slightly downwardly curved at apex; paraglossa hemitubular, not projecting beyond apex of glossa, slightly downwardly curved at apex. Antennae 16 segmented, 1 without flabella; pedicel oblong; flabella of third antennal segment as long as the following 3-4 segments.

Thorax Sculpture: sparsely punctulate-punctate to punctate on lateral lobes of mesonotum with large lustrous interspaces, sparsely punctulate-punctate anterior of notaulices and on mesoscutellum; laterally and ventrally smooth apart from setal insertions. Setosity: as head, but longer laterally on pronotum, on pro-pleurae and on mesepistemum. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth with very fine and sparse punctulae, dorsally and ventrally. Setosity: as head on tergum 1 and laterally on tergum 2, remainder with short, fine and sparse hyaline setae; ventrally similar to head but slightly shorter and sparser. Tergum 8 with broad impression diverging and becoming obsolete toward apex. Basal plate curved toward dorsum; without lip; apical surface flattened; apical margin slightly convex. Dorsal inner margins of gonostipes diverging gradually from base to three-quarter length and secondarily angled laterally to apex. Dorsal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostipes and gonostylus projecting more anteriorly than ventral. Dorsal surface of gonostylus straight, slightly upwardly curved at apex; gonostyli with coating of short hairs laterally and ventrally, sparse but long hairs dorsally and dorso-laterally; gonomaculae circular. Lateral surface of volsellae rounded. Digitus dorsally concave to slightly beyond mid-length then massively convex and secondarily concave to rounded apex; ventrally virtually straight to mid-length then weakly convex to apex (Fig. 76). Cuspis digitiform; volsellar pocket narrow and asymmetrical apically. Penis valves lateral latero-ventral view slightly convex to mid-length, then concave to three-quarter length and secondarily convex to apex rounded apically, ventrally virtually straight from base to apex; viewed dorsally, divergent from base to mid-length, tapering to apex, appearing slightly constricted basally and apically of mid-length; lateral lobes undeveloped; aedeagal apodemes flared apically.

Female

Length 8-11 mm; EA 0.9-0.92; A:B 2.56-2.58; B:C 1.5-1.7; D:E 2.2-2.25; D:F 1.64 (2 specimens measured)

Colour: predominately dark-brown to black throughout; lateral and ventral yellow coloration strongly reduced. Vertiginal yellow complete and contiguous with genal

yellow; post-ocellar yellow flecks greatly reduced or absent; facial yellow reduced to a large lateral fleck between antennal insertion and eye, produced slightly vertically along eye margin and to a small spot between the antennal insertions and some smaller and almost indistinct spots on the lower face and clypeus. Mouthparts predominately brown, apical palp segments. Scape ochraceous to testaceous; pedicel brown, ringed yellow apically; third antennal segment ochraceous; flagellum ochraceous to testaceous becoming darker toward apex, apical segment brown; basal six flabellae ochraceous to testaceous basally, brown apically, remainder brown to dark-brown. Yellow colouring greatly reduced, particularly on dorsum of pronotum and mesoscutum; laterally and ventrally predominately brown to dark-brown. Two yellow flecks on mesoscutum in axillary region, greatly reduced. Tegula brown basally, testaceous apically. Mesoscutellum brown to dark-brown. Yellow flecks behind cenchri present, although extremely reduced. Mesepisternum brown with small yellow fleck at extreme dorsum. All coxae brown and all femora testaceous basally, becoming ochraceous apically. Terga 1-2 black with small apico-lateral fleck of yellow; terga 3-8 apical yellow band complete. Sternum 2 black; sterna 3-4 black with small yellow spot apico-medially; sterna 5-6 with apical yellow band complete, often indistinct laterally on sternum 5; sternum 7 black with indistinct yellow spot latero-apically. Sclerite above sawsheath yellow suffused with black.

Morphology as males with the exception of the following.

Head Sculpture: punctulate-punctate with lustrous interspaces between rear ocelli and eyes and on lower face, becoming punctulate toward occiput; punctate between anterior ocellus and antennal insertions. Antennae 15 segmented, 1-2 without flabella; pedicel square; flabella of third antennal segment as long as the following 2-3 segments.

Thorax Sculpture: laterally and ventrally punctulate.

Abdomen Setosity: as males, but with tergum 7 sparse coating of hairs, much shorter than on head. Sternum 7 with short but stout hairs apically.

Material examined: SYNTYPE ♀, 5♂, 11♀ (ZHMB, BMNH)

Distribution: China (Manchuria, Inner Mongolia).

Comments: Males may be distinguished from those of *spiraeae* by the predominantly yellow coloration, laterally and ventrally of the thorax, the shorter third antennal flabella and the incomplete post-ocellar striae. Females may be separated from those of *spiraeae* by the finer sculpting between the rear ocelli and eyes, broad band of genal yellow extending in to the malar region and, also, by the shorter third antennal flabella.

Megalodontes reitteri Konow

(Figs 43, 102)

Tarpa reitteri Konow, 1894: 131; Konow, 1897. SYNTYPES ♂,♀, (? Turkey): Caucasus, Araxes valley (DEIC), [examined].

Megalodontes reitteri (Konow); Konow, 1897.

Male

Length 11-13 mm; EA 0.94; A:B 2.67; B:C 1.7; D:E 0.83; D:F 0.77 (1 specimen measured)

Colour: similar to *escalerai*; predominately black, dorsally, on head and thorax; dorsum of abdomen yellow; ventrally yellow throughout. Vertiginal yellow contiguous with genal yellow, which is more extensive, laterally. Yellow flecks, posterior of rear ocelli, widely separated from vertiginal yellow. Facial yellow more extensive than *escalerai*. Mouthparts yellow; galea edged in brown. Scape yellow; pedicel yellow, brown fleck dorsally; third antennal segment and flagellum yellow to ochraceous; flabellae ochraceous. Yellow on pronotum widely broken medially. Four yellow flecks on mesoscutum. Mesoscutellum black. Tegula yellow. Lateral and median yellow flecks on metapostnotum: absent. Mes- and metepisternum and metepimeron yellow throughout. Coxae yellow. Wings very slightly fuscous, except apically; venation yellow, anterior and basally, ochraceous to testaceous posteriorly and apically. Terga 1-2 black, large lateral yellow fleck, extended medially on tergum 2; terga 3-7 yellow band complete, occupying all of sclerite laterally, but only apical one-third to half medially; tergum 8 yellow. Sterna 2-7 yellow.

Head Sculpture: closely punctate between rear ocellus and eye, punctulate toward occiput, punctate-rugulose between anterior ocellus and antennal insertions. Setosity: similar to *escalerai*, but slightly shorter, very sparse between antennal insertion and malar region. Post-ocellar striae incomplete. Pentagonal area slightly excavated in region of anterior ocellus, otherwise flat to anterior puncture. Genal carinae present. Malar space narrow. Galea slightly elongate; glossa elongate, parallel-sided toward and downwardly curved at apex; paraglossa hemi-tubular, slightly shorter than glossa. Antennae 17 segmented, 1 without flabella; pedicel oblong; flabella of third antennal segment as long as the following 6-7 segments.

Thorax Sculpture: closely punctate, punctulate toward anterior of mesonotum. Setosity: similar to *escalerai*, but slightly shorter. Pronotal collar curving. Hind-coxal apical incision open.

Abdomen Sculpture: virtually smooth dorsally and ventrally. Setosity: as head but sparser ventrally; almost bare laterally, except terga 1-3; terga 1 and 2 as head, otherwise with very fine and short setae. Tergum 8 with broad and deep furrow becoming obsolete apically. Basal plate curved more strongly than *escalerai*; without lip; apical surface slightly impressed; apical margin truncate to slightly convex. Dorsal inner margins of gonostipes diverging from base to apex, strongly concave at mid-length and curved abruptly laterally toward apex. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus projecting apically of ventral. Dorsal surface of gonostylus straight with slight upward curvature at apex; gonostyli with sparse coating of

short hairs, denser dorso- and ventro-basally; gonomaculae truncate basally, thus appearing hemi-elliptical. Lateral surface of volsellae rounded. Digitus, in latero-ventral view, dorso- and ventro-basally divergent, strongly convex dorso-medially and then strongly concave to apex, ventrally strongly convex from mid-length to apex (Fig. 102). Cuspis digitiform with apex on a plane with apex of digitus or projecting anteriorly. Penis valves laterally strongly unciform and dorsally slightly divergent from base to beyond mid-length but appearing constricted medially, tapering apically; aedeagal apodemes parallel and rounded apically.

Female

Length 10-11 mm; EA 0.95; A:B 2.94; B:C 1.7; D:E 1.08; D:F 1 (one specimen measured)

Colour: similar to *escalerai* dorsally, but more extensively black ventrally. Differ from males by being more extensively yellow on vertex, longer flecks along striae; facial yellow discontinuous with flecks between antennal insertions and eyes, the latter being produced vertically to be level with anterior ocellus; lower facial colour less extensive than males. Mouthparts dark brown basally, yellow to ochraceous apically. Pedicel ochraceous with brown fleck at base of inner face. Third antennal segment ochraceous; flabellae ochraceous, testaceous apically. Pronotum yellow posteriorly and dorso-laterally but more extensively black than male. Mesoscutellum black, 2 yellow flecks latero-apically. Lateral yellow flecks on metapostnotum present. Mesepisternum yellow in dorsal one-fifth, strongly produced downwards posteriorly; mesepimeron and metepisternum black; metepimeron with dorsal yellow stripe. Pleurae and mesosterna black. Fore- and mid-coxae black; hind-coxae black, yellow laterally and apico-anteriorly. Wings as male, venation testaceous, pterostigma marked ochraceous. Terga 1-7 as males but with apico-lateral yellow flecks larger or more produced medially and with apical yellow bands wider; tergum 8 yellow. Sterna 2-3 black; sternum 4 black, yellow at extreme latero-apices only; sterna 5-7 with yellow band complete, occupying apical two-thirds to three-quarters throughout. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Sculpture: punctate between rear ocelli and eyes, becoming punctulate-punctate toward occiput; punctate-rugulose between anterior ocellus and antennal insertions. Setosity similar to male but much sparser, almost bare between antennal insertion and malar region. Flabella of third antennal segment as long as the following 5-6 segments.

Thorax Sculpture: between notaulices and black region of mesepisternum punctulate, otherwise punctate. Setosity: similar to male but much sparser. Pronotal collar collapsing.

Abdomen Sculpture: smooth ventrally, dorsally with a few very fine and sparse punctulae, otherwise smooth. Setosity: ventrally, terga 1 and 8, lateral margins of

remainder as head, otherwise with a few very sparse and short setae, dorsally.

Material examined: SYNTYPES ♂,♀ and (MWEC, RMNH, ZHMB, ZMUM)

Distribution: Turkey (Amasia, Bulghar Dagh, Agri), Armenia (Dzhervezh).

Comments: Males are separated from those of *eversmanni* and others by the predominance of yellow on the thorax, the yellow coxae, by D:E, the form of the digitus and the parallel-sided aedeagal apodemes. Females are separated from those of *escalerai* by the lesser degree of yellow coloration on the upper face.

Megalodontes skorniakowii (Freymuth)

(Figs 61, 103, 108, 109)

Tarpa skorniakowii Freymuth: 1870: 221; Konow, 1897. SYNTYPE ♀, Uzbekistan: region of Samarkand, 19.iv. (A.P.Fedchenko) (ZMAS), [not examined].

Tarpa lamellata Andre, 1881: 442. SYNTYPE ♂ Uzbekistan: Tashkent (Radoszkowski) (ZMAS), [not examined]. Synonymised by Konow, 1897.

Tarpa victoriosa Jakovlev, 1892: 11. SYNTYPES ♂,♀, Turkestan: Karategin (B. GromB:Czewski) (ZMAS), [not examined]. Synonymised by Konow, 1902.

Megalodontes skorniakowskii (Freymuth); Kirby, 1882 mis-spelling.

Megalodontes skorniakowskyi (Freymuth); Konow, 1897 mis-spelling.

Megalodontes skornjakovii (Freymuth); Klima, 1937 mis-spelling.

Male

Length 9-13 mm; EA 0.95-0.96; A:B 2.2-2.32; B:C 2-2.1; D:E 0.83; D:F 1.35-1.5 (2 specimens measured)

Colour: predominantly black on head, thorax and sterna. All coxae and trochantera black and all trochantelli black or dark brown. A single yellow fleck between antennal insertion and eye. Post-ocellar flecks absent. Antennal segments ochraceous to testaceous, except scape and pedicel which are marked with brown. Flabellae ochraceous, darker ventrally. Mouthparts dark-brown to black. Two axillary yellow flecks on mesonotum extreme apical and apico-lateral margins of tergum 3; all but extreme bases and latero-bases of terga 4-8; apex and lateral margins of basal plate. Anterior of forewings lightly fuscous. Posterior of forewings and entirety of hindwings hyaline to yellow.

Head Sculpture: closely punctate between rear ocelli and eyes becoming closely punctulate-punctate on vertex and toward occiput, coarsely punctate between anterior ocellus and antennal insertions. Setosity: dense covering of long hairs (more than twice as long as rear ocellus), slightly shorter on lower face. Post-ocellar striae incomplete. Pentagonal area deeply excavated. Genal carinae obsolete. Malar space wide. Galea elongate; glossa distinctly longer than galea, slightly downwardly curved apically; slightly flared apically; paraglossa slightly shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 34-37 segmented, 1

without flabella; pedicel square or transverse; flabella of third antennal segment as long as the following 25-27 segments.

Thorax Sculpture: pronotum, mesoscutum and mesepistemum punctate, becoming punctulate in areas marked with yellow and in axillary regions. Remaining lateral sclerites of thorax, coxae and trochantera punctulate. Pleurae smooth or, at most, with a few very sparsely distributed punctulae. Setosity: dense covering of long hairs on dorsal and lateral sclerites of thorax, becoming sparser and slightly shorter on pleurae and femora. Pronotal collar collapsing, ledge narrow. Hind-coxal apical incision closed.

Abdomen Sculpture: terga 2-3 very finely punctate and remainder of abdominal sclerites smooth or, at most, with a few very sparsely distributed punctulae. Setosity: dense covering of long hairs on lateral margins of terga becoming sparser and slightly shorter on remainder of terga of abdomen. Tergum 8, baso-medially, with broad and shallow impression becoming obsolete apically. Basal plate not downwardly curved apically; without lip; apical surface impressed; apical margin slightly convex. Dorsal inner margin of gonostylus widely separated but parallel at base, shallow curvature toward mid-length, sharply angled apically. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostylus and gonostipes projecting more anteriorly than ventral. Dorsal surface of gonostylus curved upwardly from base to median, then appearing notched apically, with sparse dorsal and lateral covering of short hairs; gonomacula rounded basally, in the form of a deformed semi-circle. Lateral surface of volsellae virtually straight. Digitus reduced to a small sagittifom projection (Fig. 108). Cuspis reduced to small antero-lateral protuberance from volsellae. Penis valve massively sagittiform laterally and dorsally; aedeagal apodemes flared apically.

Female

Length 12-14.5 mm; EA: 0.90-0.96; A:B 2.5-2.8; B:C 1.92; D:E 1.13; D:F 1.31 (2 specimens measured)

Colour: as males. Scape yellow, pedicel ochraceous, flagellum ochraceous to testaceous and flabellae darker ventrally. Mouthparts dark-brown to brown but strongly marked ochraceous or testaceous. Tergum 3 with apico-lateral yellow extended medially, tergum 4 with baso-medial black slightly more extensive and with yellow band reduced to apical one-third on terga 5-7 and apical two-thirds on tergum 8. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Sculpture: less coarsely and densely punctate on head and punctulate-punctate on mesepisternum, otherwise similar. Setosity: sparser, more slender and slightly shorter than males. Antennae 25-34 segmented; flabella of third antennal segment as long as the following 19-20 segments.

Abdomen Seventh sternum produced apico-medially, giving the appearance of an irregular pentagon.

Material examined: 6 ♂, 22 ♀ (BMNH, IBBK, IZUI, MHNG, OLML, SMNS, ZMUM

Distribution: Kazakhstan, Kirghizstan, Turkmenistan, Tadzhikistan and Uzbekistan.

Comments. A highly distinctive species with its elegant flabellae and one of the few megalodontid species which may be diagnosed on its antennal morphology alone. However, this gives little idea of its proximity to *nitens* and *xanthosomus*, rather than *olivieri* or *phaenicius*, as evidenced by the unsclerotised parapennial sac.

Megalodontes spiraeae (Klug)

(Figs 77, 107, 110)

Tarpa spiraeae Klug, 1824: 188; Konow, 1897; Gussakovskij, 1935. SYNTYPES ♂,♀, Tauria (Pallas) (ZHMB), [examined].

Tarpa pectinicornis Klug, 1824: 194. SYNTYPES ♂, ♀, Russia: Siberia, Barnaul (F.A. v. Gebler) (ZHMB), [examined].

Tarpa ruthena Jakovlev, 1888: 375. SYNTYPE ♀, Russia: Krasnoyarsk (ZMAS), [not examined]. Synonymised by Konow, 1897 (under *pectinicornis*).

Tarpa borealis Jakovlev, 1892: 10. HOLOTYPE ♀, Russia: western Siberia, Irkutsk (ZMAS), [not examined]. Synonymised by Konow, 1897 (under *pectinicornis*).

Megalodontes sibiriensis Rohwer, 1925: 1. HOLOTYPE ♀, Russia: Siberia, Okeanskaya, 15.viii.1923 (T.D.A. Cockerell) (USNM) [examined].

Megalodontes coreensis Takeuchi, 1927: 379. HOLOTYPE ♀, Korea: Mt. Kaya (Y. Hasegawa) (TAKC), [not examined].

Megalodontes spiraeae (Klug); Kirby, 1882.

Male

Length 9-12 mm; EA 0.89-0.91; A:B 2.67; B:C 1.5; D:E 2-2.1; D:F 1.54-1.58 (2 specimens measured).

Colour: predominately dark-brown to black dorsally and laterally; predominately dark brown ventrally except sterna, which are mostly yellow. Vertex black; yellow fleck posterior of rear ocelli absent; occipital yellow complete and contiguous with genal yellow; facial yellow contiguous with markings between antennal insertions and eyes, the latter produced slightly vertically along eye margins. Mouthparts predominately brown, testaceous to ochraceous apically. Scape ochraceous, marked light-brown on upper face; pedicel brown, ringed ochraceous at apex; third antennal segment and flagellum ochraceous; flabellae ochraceous basally, red-brown apically. Postero-dorsal, latero-dorsal and lateral regions of pronotum yellow. Two yellow flecks on mesoscutum. Tegula yellow; humeral sclerite yellow. Two yellow flecks behind cenchri and small yellow marking in between them on the posterior margin of the metanotum. Mesepisternum yellow in dorsal one-quarter but strongly produced downwardly, so that

yellow occupies anterior two-thirds of sclerite; metepisternum marked yellow anteriorly. Fore-coxae light-brown, marked yellow on inner face; mid-coxae brown, marked yellow antero-apically; hind-coxae yellow, marked brown laterally. Fore-femora ochraceous, ringed light-brown basally and with light-brown fleck on upper face; mid- and hind-femora ochraceous. Wings fuscous, less so on hind-wings; venation testaceous to red-brown anteriorly and basally, except for apex of costal vein, which is ochraceous, pterostigma which is ochraceous, yellow basally and with median testaceous fleck. Tergum 1 dark-brown to black; tergum 2 dark-brown to black, very small lateral yellow flecks, tergum 3 dark-brown to black, very small lateral and apico-medial yellow flecks; terga 4-7 with apical yellow band complete; tergum 8 with yellow band complete, produced baso-medially. Sterna 2-7 yellow, brown only basally, more so baso-laterally; basal plate yellow, brown only laterally.

Head Sculpture: punctate between rear ocelli and eyes; punctulate to punctulate-punctate on occiput and vertex; punctate-rugulose between anterior ocellus and antennal insertions; yellow region of face smooth except for setal insertions. Setosity: dense covering of short hairs, longer and denser on lower face. Post-ocellar striae complete. Pentagonal area with very shallow and narrow trench from anterior ocellus to anterior puncture. Genal carinae obsolete, present in the form of a sharp angle between gena and post-gena. Malar space narrow. Galea slightly elongate; glossa flared slightly, slightly downwardly curved at apex; paraglossa hemi-tubular, not projecting beyond apex of glossa, slightly downwardly curved at apex. Antennae 15 segmented, 2 without flabella; pedicel square; flabella of third antennal segment as long as the following 4-5 segments.

Thorax Sculpture: punctate on median regions of mesonotum, including anterior of notaulices and all of mesoscutellum, at perimeter punctulate, becoming smooth at border with pronotum and in axillary regions. Setosity: dense covering of stout hairs, longer on dorso-lateral and lateral regions of pronotum, on pleurae and on mespisternum. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth to very finely and sparsely punctulate dorsally, ventrally smooth. Setosity: tergum 1 and laterally on tergum 2 as head, sterna similar to head but much sparser; remainder with sparse and short hyaline setae. Tergum 8 with broad shallow impression. Basal plate curved toward dorsum; without lip; impressed apically; apical margin truncate to very slightly convex. Dorsal inner margins of gonostipes sub-parallel basally, slightly divergent to two-thirds of its length, sometimes indented at mid-length, then angled abruptly to apex. Dorsal sclerotisation of gonostipes incomplete, a few larger specimens with complete sclerotisation. Dorsal articulation of gonostipes and gonostylus projecting anteriorly of ventral. Dorsal surface of gonostylus straight; gonostyli with coating of short hairs, sparser laterally and apically; gonomaculae deformed circular. Lateral surface of volsellae rounded. Digitus, in latero-ventral view, as *quinquecinctus* but, dorsally not secondarily concave toward apex and, ventrally, slightly

more strongly convex apically (Fig. 77). Cuspis digitiform; apex of volsellar pocket wide and asymmetrical. Penis valves laterally and dorsally as *quinquecinctus* but constrictions at mid-length absent; form of aedeagal apodemes flared apically

Female

Length 9-11 mm; EA 0.86-0.92; A:B 2.25-2.3; B:C 1.55-1.61; D:E 2.11; D:F 1.46 (2 specimens measured)

Colour: as males dorsally, yellow on terga much reduced; ventrally predominately dark-brown throughout, yellow colouring greatly reduced. Occipital yellow as in males. Genal yellow narrower and often not extending the full length of the eye. Flecks between antennal insertions and eye margins reduced to small longitudinal trapezoid or triangular flecks and inter-antennal yellow reduced to small oblong or circular areas. Lower facial yellow reduced to small and irregular spots or flecks or absent. Mouthparts predominately dark-brown, apical palp segments testaceous to red-brown. Scape ochraceous; pedicel brown; third antennal segment brown on upper face, testaceous on lower; flagellum basal three segments as third antennal segment, remainder testaceous to red-brown; flabellae testaceous to red-brown basally, dark-brown apically. Pronotal yellow greatly reduced laterally, less so dorsally. Two yellow flecks on mesoscutum, much smaller than in males and often absent. Yellow flecks behind cenchri present. Tegula yellow, brown basally; humeral sclerite yellow basally, dark-brown apically. Mesepisternum dark-brown, with small yellow fleck dorsally, produced slightly downwards posteriorly; metepisternal yellow absent. Fore- and mid-coxae brown; hind- coxae brown, marked with yellow apico-anteriorly. Fore- and mid-femora ochraceous, ringed brown basally; hind-femora ochraceous. Wings as males, but more hyaline in posterior of both fore- and hindwings. Tergum 1 dark-brown, small yellow spot apico-laterally; tergum 2: dark-brown; terga 4-5 with yellow band complete, occupying apical half of sclerite laterally but only apical one-third medially; tergum 6 black, yellow flecks apico-laterally, extended medially; tergum 7 black, small yellow fleck laterally and extremely narrow yellow apical margin; tergum 8 black, with narrow yellow apical margin. Sternum 1 dark-brown; sternum 2 dark-brown, small yellow fleck apico-medially; sternum 3-4 dark-brown, with narrow yellow apical margin; sterna 5-6 apical yellow band complete, occupying apical one-third of sclerite throughout; sternum 7 black. Sclerite above sawsheath black.

Morphology as males with the exception of the following.

Head Sculpture: closely punctate between rear ocelli and eyes and on lower face; punctate on vertex; punctulate at occiput; punctate-rugulose between anterior ocellus and antennal insertions. Setosity: denser, but shorter hairs than males, except on postgena. Antennae 17 segmented; pedicel transverse.

Abdomen Setosity: as head on tergum 1, laterally on all terga and on sterna; on remainder of terga short hyaline setae interspersed with longer hairs, slightly shorter and finer than those on head and thorax. Seventh sternum: produced strongly apically, but

without two distinct projections, apex truncate and this region wider than half the distance between this and the overlapping sclerite.

Material examined: HOLOTYPE ♀ of *sibiriensis*, SYNTYPES 1♂, 1♀ of *spiraeae*, 1♂, 1♀ of *pectinicornis* and 14♂, 25♀ (BMNH, HNHM, IZAS, ZMUM)

Distribution: Russia (Krasnoyarsk, Irkutsk, Baikal, Nikolayevsk, Ushmin, Primorskii Krai, Vladivostok), China (Manchuria, Mukden, Harbin), North Korea (South Pyongyang).

Comments: The longer third antennal flabella, the complete post-ocellar striae and the greater degree of black coloration on the thrax and sterna separate males of *spiraeae* from those of *quinquecinctus*. Females are distinguished from those of *quinquecinctus* by their coarser punctation between the rear ocelli and eyes and longer third antennal flabellae.

Megalodontes turcicus Mocsáry

(Fig. 49)

Tarpa turcica Mocsáry, 1881: 35. SYNTYPES ♀, Asia Minor (Turkey?) (HNHM), [not examined]. Synonymised by Konow, 1897 (under *pectinicornis*).

Tarpa orientalis Mocsáry, 1881: 34. Syntypes ♀, Turkey: Brussa (J. Pavel) (HNHM), [not examined]. Synonymised by Konow, 1897 (under *pectinicornis*).

Megalodontes turcicus (Mocsáry); Konow 1897.

Male

Length 9-11 mm; EA 0.8-0.83; A:B 2.27-2.8; B:C 1.67-1.83; D:E 1.75-1.82; D:F 1 (2 specimens measured).

Colour: predominately black throughout, white-yellow markings greatly reduced. Occipital white-yellow broken or absent between remnants of post-occipital striae and separated or contiguous with genal yellow. Post-ocellar flecks absent. Facial white-yellow reduced to square or campaniform fleck between antennal insertions and a small oblong or iregular quadriangular fleck between antennal insertions and eye margin. Mouthparts predominately dark-brown to black, apical palp segments lighter. Scape and pedicel black; third antennal segment ochraceous; flagellum ochraceous, apical 7-8 segments ochraceous to testaceous; flabella segment 3 ochraceous basally, testaceous apically, remainder testaceous basally, red-brown apically. Pronotum with large dorso-lateral white-yellow flecks extended medially. Two small white-yellow flecks on mesoscutum in axillary region. Flecks behind cenchri absent. Tegula black; humeral sclerite dark-brown to black. Mesepisternum black, marked white-yellow in dorsal one-sixth, slightly produced downward posteriorly. All coxae black. Fore-femora ringed black in basal one-third, remainder brown becoming ochraceous at apex: mid-femora ringed black in basal one-quarter, remainder brown becoming ochraceous at apex; hind-femora ochraceous, testaceous basally. Wings fuscous anteriorly, slightly fuscous

posteriorly. Venation testaceous basally and anteriorly, ochraceous to testaceous apically and posteriorly; costal vein ochraceous to testaceous; pterostigma ochraceous basally and apically. Terga 1-2 black; tergum 3 black, occasionally with small white-yellow apical fleck; terga 4-7 white-yellow band complete occupying apical half of sclerite laterally, but only apical one-quarter medially; tergum 8 yellow, black basal margin and in median furrow. Sternum 2 black; sternum 3 black, thin apico-medial white-yellow spot; sterna 4-7 black, thin transverse apico-medial white-yellow fleck; basal plate black, yellow to ochraceous band on apical quarter. (One specimen with longitudinal white-yellow fleck medially.)

Head Sculpture: closely and coarsely punctate between rear ocelli and eyes and on face, becoming punctate toward occiput; punctate-rugulose between anterior ocellus and antennal insertions. Scape punctate. Setosity: dense coating of long hairs (more than three times diameter of rear ocellus), slightly sparser on white-yellow markings on face and slightly longer on postgena. Post-ocellar striae incomplete. Pentagonal area with small and shallow excavation in region of anterior ocellus, otherwise planar. Genal carinae present. Malar space narrow. Galea elongate; glossa distinctly longer than galea, slightly downwardly curved apically, parallel-sided; paraglossa slightly shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 18-19 segmented; 3-4 without flabella; pedicel square; flabella of third antennal segment as long as the following 2 segments.

Thorax Sculpture: punctate throughout, except punctulate-punctate mesepimeron. Setosity: as head, slightly shorter anterior of notaulices and longer on propleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth with occasional fine punctulae dorsally, ventrally smooth. Setosity: as head on tergum 1 and laterally on terga 2 and 3; laterally on terga 4-7 as head but shorter; dorsally on terga 2-7 sparse coating of short (less than or equal to diameter of rear ocellus) hairs, tergum 8 and basal plate similar but denser; ventrally as head but much sparser and becoming shorter on apical sterna. Tergum 8 broad, widely separated and shallow impression. Basal plate curved toward apical margin; without lip; apical surface flattened; apical margin concave. Dorsal inner margins of gonostipes widely separated but sub-parallel basally, diverging gradually to mid-length, sharply curving toward apex. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting anteriorly to ventral. Dorsal surface of gonostylus, viewed laterally: straight, upwardly curved in region of gonomaculae; gonostyli with coating of short hairs, slightly longer ventrally; gonomaculae deformed circular. Lateral surface of volsellae rounded. Digitus, dorsally, slightly concave from base to beyond mid-length then massively convex, appearing angled at base of convexity, secondarily slightly concave to apex and rounded apically; ventrally straight to three-quarter length, then slightly convex to apex (Fig. 49). Cuspis digitiform, sub-

clavate apically; volsellar pocket wide. Penis valve, dorsally, divergent basally, sub-parallel to two-thirds its length, then tapering to apex and appearing secondarily constricted between the two; lateral flaps undeveloped; aedeagal apodemes rounded, but not flared apically.

Female

Length 9-11 mm; EA 0.88-0.87; A:B 2.45-2.64; B:C 1.57; D:E 1.67-1.92; D:F 0.95-1.1 (2 specimens measured)

Colour: predominately black, slightly more extensively white-yellow on dorsum of abdomen than males, otherwise white-yellow markings considerably reduced in comparison. White-yellow fleck between antennal insertions slightly larger. Mouthparts as males, but labial palp segments brown to dark-brown throughout. Scape black basally, dark-brown apically; pedicel brown to dark-brown; third antennal segment ochraceous. Two white-yellow flecks in axillary region larger than males. Fore-femora black in basal half to two-thirds; mid-femora black in basal one-third to half. Terga 1-3 black; tergum 8 yellow, black basal margin, enlarged slightly baso-medially. Sterna 2-4 and 7 black; sterna 5-6 black, transverse apico-medial white-yellow fleck; sternum 6 black, transverse apico-medial white-yellow fleck. Sclerite above sawsheath black.

Morphology as males with the exception the following.

Head Setosity: as males, but shorter and denser on lower face and shorter on occiput. Four to five antennal segments without flabella; flabella of third antennal segment as long as following 2-3 segments.

Abdomen Sculpture: finely punctulate dorsally, smooth to finely and very sparsely punctulate ventrally. Setosity: as head on terga 1 and 8, laterally on terga 2 and 3 and on sterna 7, dorsally on terga 2-7 and laterally on terga 4-7 with coating of shorter hairs; remaining sterna as head but sparser.

Material examined: 6♂, 9♀ (BMNH).

Distribution: Turkey (Amasya, Bursa).

Comments: Males of *turcicus* are distinguished form those of *cephalotes* or *Megalodontes* sp.2 by their black scape and longer third antennal flabella and likewise the females from those of *Megalodontes* sp.2 and by the value of A:B.

Megalodontes xanthosomus Zhelochovtsev

(Figs 67, 68, 89, 91)

Megalodontes xanthosomus Zhelochovtsev, 1927: 81; Gussakovskij, 1935; Zhelochovtsev, 1976. SYNTYPE ♀, Russia: Uzbekistan, Charadara, 25.iv.1869 (ZMAS), [not examined].

Megalodontes curticornis Dovnar-Zapolskij, 1930: 92. SYNTYPE(S) ♀. Turkestan, Kisiltshi (A. Gerasimov) (ZMAS), [not examined]. Synonymised by Gussakovskij, 1935 (under *nitens*).

Male

Length 9-10 mm, EA 0.95; A:B 2.2; B:C 1.67; D:E 1.5; D:F 1.5 (1 specimen measured).

Colour: predominately black dorsally; predominantely yellow on terga, laterally and ventrally. Vertiginal yellow, indistinct between post-ocellar striae, contiguous with genal yellow, which is complete, and contiguous with broad and long flecks posterior of rear ocelli. Frons, face and clypeus yellow; face with Y-shaped black mark below antennal insertions. Mouthparts predominately yellow to ochraceous. Scape, pedicel and third antennal segment yellow; flagellum and flabellae ochraceous to testaceous. Mesoscutellum: black, apical border of yellow. Four yellow flecks on mesoscutum; anterior pair sub-divided by notaulices at border with pronotum, thus giving the appearance of six flecks; axillary pair particularly and greatly produced anteriorly. Metanotum with thin margin of yellow between cenchri and marked baso-medially with two yellow flecks. Lateral yellow flecks on metapostnotum present. Indistinct marking of yellow on medio-apical margin of metapostnotum. Mesepistemum yellow; mesepimeron with anterior longitudinal black stripe. Tegula yellow. Wings yellow-hyaline to hyaline apically; venation ochraceous to testaceous anteriorly and basally, becoming yellow to ochraceous posteriorly and apically; pterostigma marked yellow basally. Tergum 1 black, yellow fleck apico-laterally; terga 2-3 black, yellow fleck occupying all of tergite laterally and extended medially; terga 4-7 all with yellow band complete and tergum 8 yellow.

Head Sculpture: sparsely punctulate-punctate between rear ocelli and eyes; remainder smooth, except for setal insertions and punctate scrobal regions and pentagonal area. Setosity: sparse coating of long and stout bristles on upper face and genal region, becoming sparser and slightly shorter on vertex and occiput, but denser on lower face. Post-ocellar striae complete, but very indistinct medially. Pentagonal area with broad triangular but not deep excavation in region of anterior ocellus, flattened toward anterior puncture. Genal carinae present. Malar space wide. Galea slightly elongate; glossa linguiform, downwardly curved and flared apically; paraglossa lamelliform, downwardly curved apically. Antennae 15 segmented, 1 without flabella; pedicel transverse; flabella of third antennal segment: as long as the following 8-9 segments.

Thorax Sculpture: punctate with lustrous interspaces on lateral lobes of mesonotum, sparser and more punctulate-punctate on remainder of dorsum; laterally and ventrally smooth except for setal insertions. Setosity: coating of long and stout bristles, similar to head but slightly longer anterior of notaulices, in axillary regions, on mesepistemum and on pro-pleurae. Pronotal collar collapsing. Hind-coxal apical incision open.

Abdomen Sculpture: smooth dorsally and ventrally. Setosity: tergum 1, laterally on terga 2 and 3 as head, setae slightly longer on basal plate, similar to head on remainder of sterna but much sparser. Tergum 8 slightly flattened medially, but without distinct impression or furrow. Basal plate curving gradually toward dorsum; without lip; strongly

impressed apically; with apical margin truncate. Dorsal inner margins of gonostipes divergent from base to apex, concave medially. Dorsal longitudinal sclerotisation of gonostipes complete. Dorsal articulation of gonostylus and gonostipes projecting marginally more anteriorly than ventral and gonostylus longer than ventral length of gonostipes. Dorsal surface of gonostylus, viewed laterally strongly upwardly curved; gonostyli with coating of fine, short and light hairs; gonomaculae hemi-elliptical and slightly rounded basally. Lateral margin of volsellae divergently angled from base to mid-length and secondarily convergently angled toward apex of volsellae. Digitus reduced to a narrow digitoid projection from anterior of volsellae (Fig. 91). Cuspis reduced to two small protuberances apico-laterally. Penis valve, dorsally, angled and curved toward dorsum, tapering toward apex, more strongly so dorsally, to a point apically (more grossly than in *olivieri*); laterally, basally broad, tapering to mid-length, then sub-parallel and tapering to a point in apical one-third; aedeagal apodemes strongly flared apically

Female

Length 9-10 mm; EA 0.96; A:B: 2.58; B:C 1.58; D:E 1.16; D:F 1.71 (1 specimen measured)

Colour: similar to males. More extensively yellow on face, vertex, occiput and post-genal face below antennal insertions without Y-shaped black marking. Mouthparts yellow or ochraceous to testaceous with yellow markings basally. Pronotum yellow entirely. Anterior pair of mesoscutal flecks, exterior of notaulices greatly extended posteriorly and confluent, albeit narrowly, with enlarged axillary flecks. Mesoscutellum black in basal one-quarter to one-third only. Metanotum marked yellow baso-medially. Metapostnotum with large yellow flecks posterior of cenchri and with baso-medial fleck of yellow. Tergum 1 with larger apico-lateral flecks of yellow; tergum 2 as males; terga 3-6 with apical yellow band complete; terga 7-8 yellow. Sterna 4-5 black baso-medially. Sclerite above sawsheath yellow to ochraceous.

Morphology as males with the exception of the following.

Head Sculpture: sparsely punctulate-punctate on areas marked with black; remainder smooth, except for setal insertions. Setosity: sparse coating of long hairs on upper face, genal region and lower face, becoming sparser and slightly shorter on vertex, occiput and between antennal insertions and eyes. Pentagonal area with elongate triangular but not deep excavation in region of anterior ocellus, flattened toward anterior puncture. Antennae 12-14 segmented, 1 without flabella; pedicel square; flabella third antennal segment as long as the following 7-8 segments.

Thorax Sculpture: punctate with lustrous interspaces on lateral lobes of mesonotum, sparser and more punctulate-punctate on remainder of dorsum; laterally and ventrally smooth except for setal insertions. Setosity: similar to head but slightly longer anterior of notaulices, in axillary regions, on mesepisternum and on pro-pleurae.

Abdomen Sculpture: smooth dorsally and ventrally. Setosity: tergum 1, laterally on

terga 2 and 3 as head, setae slightly longer on basal plate, similar to head on remainder of sterna but much sparser.

Material examined: 3♂, 4♀ (BMNH, ZMAS, ZMUM).

Distribution: Uzbekistan (Chardara, Kisiltshi, Karakum), Turkmenistan (Ashkhabad, Kammadashi).

Comments: Males may be separated from those of *nitens* by the greater D:E value and its extremely long and upwardly curved gonostyli and females by their lower A:B value, shorter third antennal flabella and the great difference in the number of antennal segments.

(The following are descriptions of five, probably new, species. They are un-named and no taxonomic or nomenclatural significance should be attached to their presentation. These will be described and named formally elsewhere.)

Megalodontes sp.1

(Fig. 80)

Male

Length 10 mm; EA 0.9; A:B 2.89; B:C 1.5; D:E 1.58; D:F 1.21 (1 specimen measured)

Colour: predominately black dorsally, laterally and ventrally on head and thorax; predominately yellow on dorsum and venter of abdomen. Occipital yellow discontinuous between occipital remnants of post-ocellar striae, and contiguous with genal yellow. Post-ocellar flecks absent. Facial yellow discontinuous with yellow between antennal insertions and eye margin and also discontinuous with lower facial yellow. Yellow between antennal insertions and eye margin produced vertically along eye margins above line of antennal insertions. Mouthparts predominately dark-brown. Scape yellow; pedicel yellow, ringed brown basally; third antennal segment: yellow; flagellum yellow basally, remainder ochraceous, except apical 4-5 segments which are ochraceous to testaceous; flabellae yellow to ochraceous. Pronotum yellow dorso-laterally. Four yellow flecks on mesoscutum. Tegula yellow. Yellow flecks behind cenchri absent. Mespisternum yellow in dorsal one-third; metepisternum and metepimeron with postero-dorsal yellow fleck. Fore- and mid-coxae black; hind-coxae black, marked yellow apically on inner face. Wings fuscous anteriorly, hyaline to slightly fuscous posteriorly; venation ochraceous to testaceous basally and anteriorly, yellow to ochraceous apically and posteriorly. Terga 1-2 black, with large lateral yellow fleck, extended medially on tergum 2; terga 3-7 with apical yellow band complete; tergum 8 yellow, black margin basally; sterna 2-7 apical yellow band complete; basal plate yellow.

Head Sculpture: closely and coarsely punctate to punctate-rugulose between rear ocellus and eye becoming punctate toward ocellus and on face, except yellow areas which are punctulate-punctate; rugulose between anterior ocellus and antennal insertions.

Setosity: dense coating of long stout bristles (more than three times diameter rear ocellus), slightly shorter and sparser in yellow regions of face. Post-ocellar striae incomplete. Pentagonal area with very slight excavation in region of anterior ocellus, otherwise planar to anterior puncture. Genal carinae present. Malar space narrow. Galea elongate; glossa and paraglossa missing. Antennae 18 segmented, 4 without flabella; pedicel square; flabella of third antennal segment as long as following 1-2 segments.

Thorax Sculpture: closely and coarsely punctate on mesoscutum, becoming punctulate at pronotal margin; laterally and ventrally punctate. Setosity: as head, slightly sparser in yellow markings and slightly longer on pleural sclerites. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: dorsally and ventrally smooth with a few sparse punctulae, except terga 2 and 3 which are punctulate particularly on darker regions. Setosity: tergum 1 and laterally on tergum 2 as head; dorsally on terga 2-8 with short stout black setae; laterally on remainder of terga setae much shorter (equal to the diameter of rear ocellus) and sparser than head; ventrally as head but much sparser, particularly medially. Tergum 8 broad, widely separated and shallow impression. Basal plate curved gradually toward dorsum; without lip; apical surface very slightly impressed; apical margin very slightly concave. Dorsal internal margin of gonostipes diverging gradually from base to apex, curved abruptly apically. Dorsal longitudinal sclerotisation of gonostipes complete. Dorsal and ventral articulations of gonostylus and gonostipes projecting equally apically. Dorsal silhouette of gonostylus, viewed laterally straight but curved upward strongly at apex. Gonomaculae square but rounded at corners. Lateral margins of volsellae rounded. Digitus straight to slightly concave dorsally for three-quarters its length, slightly convex toward apex; ventrally divergent from base in basal one-third; in apical two-thirds convex to apex, giving the digitus a somewhat pointed appearance (Fig. 80). Cuspis digitiform, very broad and long, as long as digitus. Penis valve dorsally sub-parallel in basal two-thirds, appearing constricted between base and median, tapering from median to apex and appearing secondarily constricted between the two; lateral lobes narrow; apices of aedeagal apodemes slightly flared.

Female

Length 12 mm; EA 0.87; A:B 2.33; B:C 1; D:E 1.67; D:F 1.15 (1 specimen measured)

Colour: similar to male, but more extensively marked with yellow dorsally and more extensively black laterally and ventrally. Vertiginal yellow unbroken medially and contiguous with genal yellow and with longitudinal flecks along occipital remants of post-ocellar striae; genal yellow slightly more extensive than male. Facial yellow discontinuous with yellow between antennal insertions and eye margin, yellow between antennal insertions contiguous with that on lower face and clypeus; yellow between antennal insertions and eye margin produced vertically toward rear ocelli and more extensive than male. Pedicel ochraceous; basal three segments of flagellum ochraceous, remainder

ochraceous to testaceous; flabella bases of basal three flabellae ochraceous and ochraceous to testaceous apically, remainder ochraceous to testaceous throughout. Flecks on mesoscutum larger than male. Mespisternum yellow in dorsal quarter produced downwards posteriorly. Metepimeron black. Terga 2-3 black, with large lateral yellow fleck, extended medially, more extensively on tergum 3; terga 4-8 with apical yellow band complete; tergum 8: yellow, black in basal one-quarter. Sternum 2 black; sternum 3 black with transverse yellow fleck apico-medially; sternum 4 black with transverse yellow fleck apico-medially and smaller yellow spot laterally; sterna 5-7 apical yellow band complete, occupying apical half throughout; sternum 7 black, margined yellow apically. Sclerite above sawsheath ochraceous.

Morphology as males with the exception of the following.

Head Setosity: as male, sparser on yellow markings, virtually bare between antennal insertions and malar space. Post-ocellar striae appearing complete. Glossa elongate parallel sided and downwardly curved at apex; paraglossa hemi-tubular and shorter than glossa. Antennae 19 segmented, 4-5 without flabella.

Abdomen Sculpture: finely punctulate on black markings dorsally and ventrally, but much sparser on yellow areas, appearing smooth. Setosity: as head dorsally and laterally on terga, slightly sparser on yellow markings medially; sterna with setae of same length as head on black markings but sparser, on yellow markings shorter and much sparser, except on sternum 7 where the setosity is particularly dense.

Material examined: 2♂, 1♀ (BMNH).

Distribution: Israel (Carmel, Place of Sacrifice).

Comments: The form of the digitus suggests similarities with members of the *flabellicornis*-group. Males possess the flabellicornis facial colour syndrome thus distinguishing them from those of *cephalotes* and *turcicus*. In the key to females it is distinguished from *luteiventris* by the shorter third antennal flabella. One male is missing its head and is badly damaged.

Megalodontes sp.2

(Figs 83, 85, 97)

Male

Length 9-10 mm; EA 0.87-0.92; A:B 2.88-3; B:C 2.67; D:E 1.64-2.2; D:F 0.82-1.05 (2 specimens measured)

Colour: predominately black throughout on head, thorax and dorsum of abdomen; predominately white-yellow on venter of abdomen. Occipital white-yellow continuous (broken medially in one specimen) and contiguous with genal white-yellow. Post-ocellar flecks absent. Facial white-yellow reduced to square to oblong fleck between antennal insertions, a larger trapezoidal fleck between these and eye margin and a transverse band along the lower face and the clypeus (reduced to three smaller tansverse flecks or spots in

one specimen). Yellow between antennal insertions and eye margin produced vertically. Mouthparts predominately black, lighter apically. Scape ochraceous with black fleck on outer surface (absent in one specimen); pedicel, third antennal segment, flagellum and flabella ochraceous. Dorso-lateral and latero-venter of pronotum white-yellow. Two white-yellow flecks on mesoscutum in axillary region. Tegula black basally, white-yellow apically; humeral sclerite white-yellow. Flecks behind cenchri absent. Mespisternum black, with white-yellow fleck on apical one-fifth. All coxae black. Fore-femora black in basal one-third to half, apically testaceous to yellow; mid-femora black in basal one-third, testaceous to ochraceous apically; hind-femora ochraceous. Wings: anterior fuscous, posterior hyaline; venation testaceous anteriorly, ochraceous on costal and median veins and posteriorly. Tergum 1 black; tergum 2 black, with large lateral white-yellow fleck; tergum 3 apical white-yellow band complete or broken medially; terga 4-7 with white-yellow band complete, occupying apical two-thirds of sclerite laterally but only apical half medially; tergum 8 white-yellow, black margin basally. Sternum 2 black with white-yellow apical margin; sterna 3-7 black with white-yellow apical margin, the latter more extensive medially; basal plate white-yellow.

Head Sculpture: very closely and coarsely punctate between rear ocelli and eyes becoming punctate toward occiput; punctate-rugulose between anterior ocellus and antennal insertions. Setosity: dense coating of long hairs (more than three times diameter of rear ocellus), slightly shorter and denser on lower face and clypeus. Post-ocellar striae incomplete. Pentagonal area with wide and shallow excavation extending from anterior ocellus to anterior puncture. Genal carinae present. Malar space narrow. Galea elongate; glossa distinctly longer than galea, slightly downwardly curved apically, parallel-sided; paraglossa slightly shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 19-20 segmented, 4-5 without flabella; pedicel tranverse; flabella of third antennal segment as long as following 1-2 segments.

Thorax Sculpture: punctate to coarsely punctate dorsally, with smooth area medially on lateral lobes of mesonotum, laterally and ventrally punctulate-punctate to punctate. Setosity: as head, but distinctly longer on propleurae. Pronotal collar collapsing. Hind coxal-apical incision closed.

Abdomen Sculpture: punctulate on terga 1 and 2, remainder of terga and all sterna smooth to finely punctulate. Setosity: as head on terga 1 and 2 and on sterna, but much sparser on latter pair; laterally, tergum 8 and basal plate with sparse coating of much shorter hairs (about twice diameter of rear ocellus); remainder dorsally with sparse coating of very short brown setae (less than diameter of rear ocellus). Tergum 8 broad and deep furrow becoming obsolete apically. Basal plate curved gradually toward dorsum, without lip, apical surface flattened, apical margin concave. Dorsal internal margin of gonostipes sub-parallel at extreme base, then diverging gradually to just beyond median and then sharply angled toward apex. Dorsal longitudinal sclerotisation of

gonostipes complete. Dorsal articulation of gonostylus and gonostipes projecting very slightly anteriorly to ventral. Dorsal silhouette of gonostylus, viewed laterally upwardly curved apically; dense coating of long hairs, slightly shorter and sparser apically; gonomaculae elliptical. Lateral surface of volsellae rounded. Digitus broad basally, dorsally slightly concave to beyond mid-length, convex in apical one-third; ventrally straight or marginally concave for basal three-quarters, convex to apex (Fig. 85); cuspis digitiform; volsellar pocket very broad apically. Penis valve, dorsally, sub-parallel in basal half, appearing constricted between base and median, tapering from median to apex and appearing secondarily constricted at apex; lateral flaps undeveloped; laterally as in Fig. 83; aedeagal apodemes slightly flared apically.

Female

Length 9-10mm; EA O.89-0.9; A:B 2.89-3.22; B:C 1.5; D:E 1.9-2; D:F 0.83-0.91 (2 specimens measured)

Colour: predominately black throughout, similar to males but white-yellow markings greatly reduced. Occipital white-yellow discontinuous and contiguous with genal white-yellow.Facial white-yellow reduced to square to oblong fleck between antennal insertions, a trapezoidal fleck between antennal insertions and eye margin, not produced vertically, and a small triangular fleck medially on clypeus. Yellow between antennal insertions and eye margin produced vertically. All antennal segments ochraceous. Dorso-lateral white-yellow on pronotum more extensive medially, lateral white-yellow absent. Two white-yellow flecks on mesoscutum in axillary region, one specimen with anterior pair, thus totalling 4. Tegula black basally, white-yellow apically; humeral sclerite ochraceous. Flecks behind cenchri absent. Mesepisternum black, with white-yellow fleck in dorsal one-fifth, slightly produced downwardly apically. Fore-femora black in basal three-quarters, apically testaceous to yellow; mid-femora black in basal half to two-thirds, testaceous to ochraceous apically; hind-femora ochraceous, ringed black basally. Tergum 2 black, white-yellow spot laterally; tergum 3 black, white-yellow fleck laterally, slightly extended medially. Sternum 2 black; sternum 3 black, transverse white-yellow spot apico-medially; sternum 4 black, transverse white-yellow fleck apico-medially and small spot apico-laterally; sterna 5-6 with white-yellow band complete, occupying apical half of sclerite throughout; sternum 7 black, with a small white-yellow spot apico-laterally. Sclerite above sawsheath black.

Morphology as males with the exception of the following.

Thorax Sculpture: punctate to coarsely punctate dorsally, with smooth area medially on lateral lobes of mesonotum, laterally and ventrally punctulate-punctate to punctate. Setosity: as head, but distinctly longer on propleurae.

Abdomen Sculpture: finely punctulate dorsally, smooth with sparse and fine punctulae ventrally. Setosity: as head on tergum 1 and 8, laterally on terga 2-4, sparser laterally on remainder of terga and ventrally, shorter and sparser dorsally on terga 2-8.

Material examined: 2♂, 2♀ (MKRC)

Distribution: Turkey (Kars).

Comments: Males are distinguished from those of *cephalotes* by the higher B:C value and the form of the digitus and lateral form of the penis valve. Females are separated from those of *turcicus* by the ochraceous scape and the higher A:B value.

Megalodontes sp.3

(Fig. 95)

Male

Length 8-9.5 mm; EA: 0.84; A:B 2.73-3.06; B:C 1.33-1.5; D:E 1.41-1.74; D:F 0.96-1.1 (2 specimens measured).

Colour: similar to *flabellicornis*. Vertiginal yellow broken medially, contiguous with genal yellow but separated from long post-ocellar flecks of yellow. Facial yellow triangular and separated from yellow between antennal insertions and eye margin, the latter in the form of an irregular quadrilateral, wider dorsally than ventrally and produced slightly along eye margin vertically. Mouthparts predominately black, sub-apical palp segments ochraceous to testaceous. Scape yellow, strongly marked with black on dorsal face; pedicel black; third antennal segment and flagellum testaceous; flabella testaceous basally becoming dark-brown apically. Pronotum dorso-laterally and latero-ventrally yellow, the former more widely separated medially than in *flabellicornis*. Four yellow flecks on mesoscutum. Tegulae and humeral sclerites yellow. Yellow flecks behind cenchri absent. Mesepisternum yellow in dorsal one-third, produced downwards strongly posteriorly; metepisternum yellow, bordered with black; metepimeron with dorsal fleck of yellow. Propleurae and mesosterna black. Fore- and mid-coxae black, hind-coxae black but marked strongly with yellow anteriorly and laterally. Fore-femora black on basal three-quarters of outer face and in basal half on inner, remainder yellow; mid-femora black on basal two-thirds of outer face and in basal one-third on inner, remainder yellow; hind-femora ringed black basally and with black fleck on outer face in basal one-third. Wings: weakly fuscous, more hyaline on hind-wing and hyaline apically on fore-wing; venation testaceous to light-brown basally and anteriorly, ochraceous to testaceous apically and posteriorly, pterostigma marked ochraceous basally. Tergum 1 black with apico-lateral yellow spot; tergum 2 black with large apico-alteral yellow flecks; terga 3-7 with apical yellow band complete; tergum 8 yellow; banding generally wider than in *flabellicornis*. Sterna 2-7 yellow, marked black latero-basally; basal plate yellow, black basally.

Head Sculpture: punctulate-punctate or punctate between rear ocellus and eye, becoming smooth to punctulate on vertex and coarsely punctate between anterior ocellus and antennal insertions Setosity: dense coating of long hairs (three times the diameter of rear ocellus), slightly shorter and sparser on facial yellow and longer in post-genal

region. Post-ocellar striae incomplete. Pentagonal area consisting of broad shallow trench extending to anterior puncture. Genal carinae present. Malar space narrow. Galea elongate; glossa distinctly longer than galea, downwardly curved throughout its length, parallel-sided; paraglossa slightly shorter than glossa, downwardly curved apically, between laminar and hemi-cylindrical. Antennae 14-15 segmented, 2 segments without flabella; pedicel square; flabella of third antennal segment as long as the following 4-5 segments.

Thorax Sculpture: mesoscutum sparsely puncate to punctate, becoming punctulate with lustrous interspsaces on lateral lobes, mesepisternum finely punctulate on black areas. Setosity: as head, longer on mesoscutellum and propleurae, slightly shorter on anterior of mesoscutum and on tegulae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: terga 1-2 smooth with fine and occasional punctulae: remainder and sterna smooth. Setosity: as head on tergum 1 and laterally on terga 2-3; shorter and sparser than head laterally on remainder of terga; terga 2-8 with sparse coating of short (about the diameter of rear ocellus) hairs on apical bands of yellow; remainder of terga with short hyaline setae; sterna as head; basal plate with dense coating of shorter hairs. Tergum 8 broad and shallow furrow becoming obsolete apically. Basal plate without lip; apically flattened; apical margin convex. Dorsal silhouette of internal margin of gonostipes angled divergent from base to three-quarter length, weakly concave at mid-length, then curved abruptly laterally to apex. Dorsal longitudinal sclerotisation of gonostipes incomplete. Dorsal articulation of gonostylus and gonostipes projecting more anteriorly than ventral. Dorsal surface of gonostylus, viewed laterally, straight; gonostylus with sparse coating of long hairs; gonomaculae appearing truncate basally, semi-circular apically. Lateral surface of volsellae rounded. Digitus as in *flabellicornis*, slightly convex baso-dorsally and more concave apically (Fig. 95). Cuspis digitiform, volsellar pocket apically wide. Penis valve, dorsally, weakly divergent to beyond mid-length, then tapering gradually to apex, slightly less abruptly so than in *flabellicornis*; laterally, rounded baso-dorsally, virtually straight to rounded apex, ventrally weakly convex to two-thirds centrally length, then concave to apex; aedeagal apodemes parallel-sided and rounded apically.

Female

Length: 8-10 mm; EA 0.85-0.88; A:B 3.18-3.44; B:C 1.31-1.33; D:E 1.56-1.77; D:F 1.15-1.44 (2 specimens measured)

Colour: vertiginal yellow broken medially and contiguous with genal and post-ocellar yellow, all three more extensive than in males. Facial yellow as males but yellow flecks between antennal insertions and eye margin produced vertically and wide dorsally and appearing triangular rather than quadrilateral. Mouthparts as males but palp segments darker. Scape yellow to ochraceous; third antennal segment testaceous, marked black

basally; flagellum testaceous, becoming lighter apically; flabella testaceous basally becoming dark-brown apically. Pronotum as males, latero-ventral yellow absent. Four yellow flecks on mesoscutum, longer and broader than males. Yellow flecks behind cenchri absent. Mesepisternal yellow occupying most of the sclerite dorsally and posteriorly; metepisternum black; metepimeron with narrow dorsal stripe of yellow. All coxae black, hind-coxae with small apico-lateral fleck of yellow. Fore- and mid-femora as males; hind-femora yellow throughout. Wings: anterior fuscous, posterior hyaline to fuscous; venation brown basally and anteriorly, testaceous apically and posteriorly. Terga 1-2 with large apico-lateral spot or fleck; terga 3-8 apical yellow band complete, rarely broken medially on tergum 3. Sterna 2 and 7 black; sterna 3-4 black, small yellow spot apico-medially sterna; 5-6 with apical yellow band complete. Sclerite above sawsheath yellow dorsally, black ventrally.

Morphology as males with the exception of the following.

Head Sculpture: as males, slightly more closely punctate between rear ocelli and eyes. Setosity similar to males but generally shorter (little more than twice diameter of rear ocellus) and sparser; particularly shorter on facial yellow. Pentagonal area broadly excavated but trench not extending to anterior puncture. 2-3 antennal segments without flabella; pedicel oblong.

Thorax Sculpture: punctulate to punctulate-punctate throughout, with large lustrous areas on lateral lobes of mesoscutellum, almost smooth anterior of notaulices. Setosity: as head, but distinctly longer on pronotum, mesoscutellum and propleurae.

Abdomen Sculpture: terga very finely punctulate, sterna smooth. Setosity: as head on tergum 1, laterally on tergum 2 and on sclerite above sawsheath; terga 2-8, on apical yellow band with sparse coating of short hairs (equal to the diameter of rear ocellus), longer and denser on tergum 8; sterna as head, but much sparser.

Material examined: 3♂, 8♀ (BMNH, DEIC, OLML).

Distribution: Turkey (Termessos, Cilic, Hasanbeyli).

Comments: Males are separated from those of *flabellicornis* by the greater de value, the sparsely punctate to punctate mesoscutum and shorter third antennal flabellae. The finer punctation between the rear ocelli and eyes and on the mesoscutum distinguish the females from those of *luteiventris* and *Megalodontes* sp.1.

Megalodontes sp.4

(Figs 23, 75, 90)

Male

Length 9-10 mm; EA 0.92; A:B 2.33; B:C 1.91; D:E 2.92; D:F 1.03 (1 specimen measured)

Colour: predominately black on head and thorax, dorsally and ventrally; predominately yellow on abdomen, dorsally and ventrally. Occipital yellow contiguous

with genal yellow, facial yellow campaniform and separated from yellow fleck between antennal insertion and ocular margin, the latter being produced slightly along the ocular margin. Mouthparts predominately dark brown, sub-apical palp segments and galea testaceous. Scape black, marked with yellow on inner face; pedicel black; third antennal segment dark-brown basally two-thirds, testaceous in apical one-third; flagellum and flabellae testaceous. Pronotum dorso-laterally yellow and (one male) latero-ventrally yellow. Four yellow flecks on mesoscutum. Tegula and humeral sclerite yellow. Mesepisternum black, marked with yellow in dorsal one-third, slightly produced downwards anteriorly. Fore- and mid-coxae black; hind-coxae black, yellow fleck laterally and antero-apically. Fore-femora yellow; ringed with black in basal half to two-thirds; mid-femora yellow, ringed with black in basal one-third to half; hind-femora yellow, ringed black in basal one-sixth, and with ventral fleck of black. Wings: slightly fuscous anteriorly and basally, hyaline posteriorly and apically; venation brown anteriorly and basally, testaceous posteriorly and apically. Tergum 1 black; tergum 2 black with large lateral yellow fleck; terga 3-4 black with large lateral yellow fleck, extended medially; terga 5-6 with apical yellow band complete; terga 7-8 apical yellow band incomplete, narrowly broken medially. Sternum 2 black, marked with yellow laterally; sterna 3-4 yellow band complete, occupying all of sclerite laterally, but only apical half medially; sterna 5 and 7 and basal plate yellow; sternum 6 yellow, black in basal one-quarter.

Head Sculpture: closely punctulate-punctate between rear ocelli and eyes, remainder punctulate, except between anterior ocellus and antennal insertions which is closely punctate. Setosity: dense coating of long black hairs; almost bare between antennal insertion and malar region. Post-ocellar striae incomplete. Pentagonal area slightly excavated near anterior ocellus, otherwise flattened to apical puncture. Genal carinae present, but only distinct in malar region. Malar space narrow. Galea elongate; glossa longer than galea, curved downward apically, parallel-sided; paraglossa hemi-tubular, shorter than glossa. Antennae 15 segmented, 3 without flabella; pedicel transverse; flabella of third antennal segment as long as the following 1-2 segments.

Thorax Sculpture: closely punctulate-punctate on lateral lobes of mesonotum, remainder punctulate, yellow areas smooth. Setosity: as head on pleural sclerites, but sparser dorsally and laterally, particularly so on regions marked with yellow. Pronotal collar collapsing. Hind coxal-apical incision closed.

Abdomen Sculpture: smooth to very finely and sparsely punctulate dorsally, ventrally similar but with fewer punctulae. Setosity: as head laterally, dorsum of terga 1 and 2 and dorso-median of tergum 3, ventrally as head but much sparser; remainder with sparse covering of shorter hairs. Tergum 8 with broad and deep furrow, becoming obsolete apically. Basal plate curved gradually toward apex; without lip; apical surface slightly impressed; apical margin slightly convex. Dorsal inner margins of gonostipes

parallel basally, widely divergent to three-quarter length and secondarily curved laterally to apex. Dorsal sclerotisation of gonostipes complete. Dorsal articulation of gonostipes and gonostylus projecting more anteriorly than ventral. Dorsal surface of gonostylus straight; gonostyli with sparse coating of long hairs, becoming slightly shorter apically; gonomaculae large appearing truncate basally and semi-circular. Lateral surface of volsellae rounded. Digitus, in latero-ventral view, with inner face longer than outer, slightly curved toward outer apically, outer face concave basally, then concave to apex (Fig. 75). Cuspis digitiform; volsellar pocket very wide apically. Penis valves, dorsally mitriform, similar to *gratiosus* but lateral lobes less well developed although more so than in *bucephalus* and *capitalatus*; laterally, shallow curvature on baso-dorsal surface, dorsally weakly concave to strongly rounded apex, ventrally angled downwards from base to mid-length then weakly angled or convex to apex; aedeagal apodemes slightly flared apically.

Female

Length 7.5-9.5 mm; EA 0.94; A:B 2.33; B:C 1.62; D:E 2.13; D:F 1.14 (1 specimen measured)

Colour: yellow predominant only on dorsum of abdomen; remainder predominately black. Occipital and post-ocellar yellow more extensive; facial yellow as males, but not produced along ocular margin. Scape yellow; third antennal segment testaceous; flagellum testaceous; flabellae testaceous to red-brown, becoming darker at apices. Dorso-lateral yellow on pronotum more extensive medially, reduced or absent latero-ventrally. Four yellow flecks on mesoscutum. Mesoscutellum black. Yellow flecks behind cenchri present or absent. Mesepisternum black with yellow fleck on dorsal one-third, strongly produced downwardly posteriorly. Fore-femora yellow, ringed with black in basal one-third to half; mid-femora yellow, ringed with black in basal one-quarter to one-third; hind-femora yellow. Terga 1-4 as males, lateral yellow flecks more extended medially on tergum 4; terga 5-8 with apical yellow band complete. Sterna 2-3 black; sternum 4 black, very small yellow fleck apico-laterally; sterna 5-6 incomplete yellow band, regularly broken in apical one-third of sclerite; sternum 7 black, lateral yellow fleck. Sclerite above sawsheath yellow.

Morphology as males with the exception of the following.

Head Setosity: coating of long black hairs, slightly shorter than males; almost bare between antennal insertion and malar region. Pentagonal area similar to males, but excavation slightly more elongate anteriorly. Antennae 14 segmented, 2-3 without flabella; pedicel square or transverse.

Thorax Sculpture: similar to head, punctulae more widely spaced and with lustrous interspaces.

Abdomen Sculpture: appearing smooth with very fine and sparse punctulae dorsally and ventrally. Setosity: dorsally much shorter and sparser than on head or thorax; laterally

as head; ventrally hairs slightly shorter and sparser than on head.

Material examined: 2♂, 1♀ (INRA

Distribution: Morocco (Imouzzer, Baiet Ahoua).

Comments: The presence of the genal carina in the malar region only, the higher D:E value and the complete dorsal sclerotisation of the dorsal surface of the gonostipes distinguish the males of the new species from those of *gratiosus*. The shorter third antennal flabella the lower D:F value separate the females from those of *gratiosus*

Megalodontes sp.5

(Figs 79, 96, 98, 99)

Male

Length 11-12 mm; EA 0.88-89; A:B 3-3.1; B:C 1.43-1.5; D:E 2; D:F 0.92 (2 specimens measured).

Colour: predominately black on head and thorax, dorsally and ventrally; predominately yellow laterally on thorax and dorsally and ventrally on abdomen. Occipital yellow broken medially but contiguous with genal yellow. Post-ocellar flecks present, but greatly reduced (one specimen); absent (the second). Face immediately below antennal insertions black; facial yellow contiguous with yellow between antennal insertions and eye margin; yellow between antennal insertions and eye margin strongly produced vertically. Mandibles yellow to ochraceous, teeth brown to red-brown. Mouthparts predominately dark-brown, palp segments predominately yellow. Scape yellow, black fleck on upper face; pedicel ochraceous, brown on upper face; third antennal segment ochraceous; flagellum ochraceous, apical 5 segments testaceous to red-brown; flabellae ochraceous becoming testaceous apically. Pronotum dorso-laterally yellow, medially black, laterally yellow edged in black; two yellow flecks on mesoscutum in axillary region (much larger than *fabricii*); tegula yellow; humeral sclerite yellow to ochraceous. Yellow flecks behind cenchri absent. Mesepisternum yellow in dorsal two-thirds to three-quarters; mespimeron with longitudinal yellow stripe posteriorly, metepisternum with longitudinal yellow stripe anteriorly; metepimeron marked yellow dorsally and dorso-posteriorly. Propleurae yellow, edged in black; meso- and metasterna black. Fore-coxae ochraceous, brown longitudinal stripe medially; mid-coxae black, marked yellow apically on outer and inner faces; hind-coxae yellow, marked black basally. Fore-femora ringed brown basally, testaceous becoming yellow-ochraceous apically; mid-femora marked brown basally, testaceous becoming yellow-ochraceous apically; hind-femora ochraceous. Wings fuscous throughout, except for hyaline apices. Venation testaceous basally and anteriorly, ochraceous to testaceous apically and posteriorly; costal vein ochraceous to testaceous; pterostigma marked ochraceous basally and apically. Tergum 1 black, yellow spot laterally; terga 2-3 black, yellow fleck apico-laterally, extended medially; terga 4-7 with apical yellow band complete; tergum 8 yellow,

narrow longitudinal black stripe medially. Sterna 2-7 yellow, black laterally and baso-medially; basal plate yellow.

Head Sculpture: punctate between rear ocelli and eyes and below antennal insertions becoming punctulate with lustrous interspaces toward occiput; closely and coarsely punctate to punctate-rugulose between anterior ocellus and antennal insertions. Setosity: coating of long hairs (more than twice diameter of rear ocellus), sparser on yellow regions of face and absent between antennal insertions and malar region, denser and slightly longer on postgena. Post-ocellar striae incomplete. Pentagonal area with broad and very shallow excavation between anterior ocellus and anterior puncture, appearing planar on casual inspection. Genal carinae present, only distinct in malar region, remainder present as angle between gena and postgena. Malar space narrow. Galea elongate; glossa distinctly longer than galea, slightly downwardly curved apically, parallel-sided; paraglossa shorter than glossa, slightly downwardly curved apically, between laminar and hemi-cylindrical. Antennae 21-23 segmented, 7-9 without flabella; pedicel square; flabella of third antennal segment as long as the following 1-2 segments.

Thorax Sculpture: punctate with lustrous interspaces on lateral lobes of mesonotum, anterior of notaulices punctate becoming smooth at border with pronotum; mesoscutellum closely punctate; laterally and ventrally smooth on yellow markings except for setal insertions, otherwise punctulate. Setosity: as head but distinctly longer on dorsum of pronotum and on pleurae. Pronotal collar collapsing. Hind-coxal apical incision closed.

Abdomen Sculpture: smooth with a few fine punctulae, dorsally, ventrally smooth. Setosity: as head on tergum 1 and laterally on terga 2 and 3; laterally on terga 4-7 as head but shorter; dorsally on terga 2-7 sparse coating of short (less than or equal to diameter of rear ocellus) hairs, tergum 8 and basal plate similar but denser; ventrally as head but much sparser and becoming shorter on apical sterna. Tergum 8 with broad, widely separated and shallow impression. Basal plate curved strongly toward dorsum; without lip; apical surface flattened; apical margin convex. Dorsal internal margin of gonostipes sub-parallel basally, sharply angled apico-laterally from median. Dorsal longitudinal sclerotisation of gonostipes complete. Dorsal surface of gonostylus, viewed laterally, straight, curved upwards in region of gonomaculae. Dorsal articulation of gonostylus and gonostipes projecting anteriorly to ventral; gonostyli with sparse coating of long and dark hairs interspersed with shorter, finer and lighter hairs; gonomaculae in the shape of a deformed circle projecting basally or deformed ellipse apically rounded. Lateral surface of volsellae rounded. Digitus broad basally, dorso-basally straight or marginally concave to mid-length then convex to apex (much less so than in *fabricii*), ventrally straight or marginally concave in basal one-third then curving dorsally to apex (Fig. 79). Cuspis digitiform, sub-clavate apically, apex of volsellar pocket wide. Penis valve, dorsally, sub-parallel in basal half, appearing constricted between base and median, tapering from median to apex;

lateral flaps undeveloped; aedeagal apodemes strongly flared apically.

Female

Length 11-12 mm; EA 0.88-0.9; A:B 2.82-3.3; B:C 1.43-1.57; D:E 1.83-2; D:F 1-1.1 (2 specimens measured)

Colour: similar to males, dorsally, slightly more extensive yellow colouring of mesonotum; laterally and ventrally yellow colouring greatly reduced in comparison. Genal yellow similar to males but reduced in malar region. Post-ocellar yellow absent. Facial yellow greatly reduced to large square fleck between antennal insertions and to a large oblong or longitudinally trapezoidal yellow fleck between antennal insertions and eye margin produced vertically along eye margin. Mandibles ochraceous basally, testaceous to red-brown apically, teeth red-brown to brown. Scape yellow, ochraceous to testaceous fleck on upper surface; pedicel brown basally, testaceous apically; flagellum ochraceous, apical 1-2 segments testaceous to red-brown; flabella ochraceous, flabellae of segments 4-10 testaceous to red-brown apically. Pronotal yellow reduced slightly dorso-medially and considerably laterally. Four yellow flecks on mesoscutum, axillary pair larger. Yellow flecks behind cenchri absent. Mesepisternum black, marked yellow in dorsal one-fifth, slightly produced downward posteriorly; metepimeron occasionally with narrow dorsal yellow fleck. Fore- and mid-coxae black; hind-coxae black, yellow fleck apico-anteriorly. Fore-femora ringed black basally, black flecks basally extending to median, on inner face, and three-quarters, on outer; mid-femora ringed black basally, black fleck basally extending to apical three-quarters on outer face; hind-femora ochraceous. Wings anterior fuscous, posterior hyaline to slightly fuscous. Terga 1-2 black, large yellow spot apico-laterally: tergum 8 yellow. Sternum 2 black; sterna 3-4 black, small transverse medio-apical yellow fleck; sterna 5-6 with apical yellow band complete, occupying apical two-thirds of sclerite medially, tapering laterally towards apex; sternum 7 black, with small apico-lateral yellow fleck and extremely narrow yellow apical margin. Sclerite above sawsheath black.

Morphology as males with the exception of the following.

Head Setosity: dense coating of short setae (barely longer than diameter of rear ocellus) throughout; longer setae (twice diameter of rear ocellus) on postgena; generally shorter than males throughout. Antennae 20-21 segmented, 7-8 without flabella.

Thorax Sculpture: similar to males, but with larger lustrous interspaces on lateral lobes of mesonotum and punctulate anterior of notaulices becoming smooth at border with pronotum: mespisternum and propleurae punctulate-punctate; remaining sclerites laterally and ventrally smooth to finely punctulate with lustrous interspaces. Setosity: as head, longer on mesoscutellum and mesepisternum; as males on pleurae.

Abdomen Sculpture: finely punctulate dorsally, smooth to finely and very sparsely punctulate ventrally Setosity: as head on terga 1 and 8, laterally on terga 2 and 3 and on sterna 7, dorsally on terga 2-7 and laterally on terga 4-7 with coating of shorter hairs;

remaining sterna as head but sparser.

Material examined: 2♂, 2♀ (MWEC).

Distribution: Turkey (Konya, Asiat).

Comments: Males are separated from those of *fabricii* by their possession of the cephalotes syndrome of facial coloration, higher A:B and lower B:C values. The facial coloration also distinguishes the females from those of *fabricii*.

Species Inquirendae

For several nominal species of Megalodontidae the types were unavailable for examination or lost and the original descriptions and/or material identified as these nominal species were examined, where available and dissections were made of male genitalia, where possible. The majority of these nominal species exist in their type series only and dissection was not always possible. A problem was noted that many of the names are distinguished from each other by the most subtle differences of cephalic and thoracic sculpture, colour of antennal segments and flabellae and by colour patterns of the abdomen. All these characters have been discussed in the character assessment and have been found wanting as a suitable method for distinguishing between species. This is particularly so of the nominal species possessing genitalia similar to the type of plagiocephalus or cephalotes (as here defined) and for this reason, until a more satisfactory method (e.g. using alternative characters, morphometrics and/or biological data) may be found for distinguishing between these nominal species, they are placed, temporarily, in species inquirendae.

Megalodontes anatolicus Mocsáry, 1883: 8; Konow, 1897. SYNTYPES ♂,♀, Turkey: Brussa (E. Merkl) (HNHM), [not examined].

No material available for examination. Placed as a synonym of *flabellicornis* by Konow (1897) but its description suggests it is closer to the females examined under *exornatus* below, particularly the dorsally darkened scape, tergum 1 black and tergum 3 with lateral yellow flecks of the female. *M. flabellicornis* has its scape yellow entirely ochraceous but without darker markings, tergum 1 marked with yellow flecks apico-laterally and tergum 3 with apical yellow margin complete.

Megalodontes aquilus Konow, 1902b: 1; Gussakovskij, 1935. SYNTYPE ♀, Transcaucasia (N.Kokuvew) (DEIC), [examined].

No males available for dissection. The syntype female is very similar to material identified as *flabellatus* and is discussed under this species.

Megalodontes eversmanni Gussakovskij, 1935: 210, nec Freymuth 1870. SYNTYPES ♀,

Russia: Orenburg, Ural'sk, Crimea (ZMAS), [not examined].

Name pre-occupied by *T.eversmanni* Frejmut' 1870. See under *M. scythicus* Zhelochovtsev.

Tarpa exornata Zaddach, 1865: 199; Konow 1897, 1902a; Gussakovskij (1935). SYNTYPE(S) ♀. Europe (ZKON), [type lost or destroyed].

Megalodontes exornatus (Zaddach), Kirby 1882.

Two females (from Bulgaria and Turkey) have been examined which agree well with the original description and the redescriptions by Konow (1897, 1902a) and Gussakovskij (1935). The length of the third antennal flabella was slightly shorter of the Bulgarian specimen was slightly shorter (as long as the 3-4 following segments) than the 4-5 stated by Gussakovskij. No males available for examination. Colour syndromes and D:E suggest that the specimens belong to a, probably good, species with affinities to *flabellicornis* and *Megalodontes* sp.3. A neotype for *exornatus* is being selected (Taeger, pers. comm.).

Tarpa flabellata Eversmann, 1847: 57. SYNTYPE(S) ♀, Russia: Orenburg, vi. (ZMAS) [not examined].

An apparently enigmatic species to judge from its previous systematic placement. Konow (1902) thought it synonymous with *pectinicornis* Klug (= *spiraeae* Klug) and this was followed by Gussakovskij (1935). Material compared with Eversmann's original description suggests that it is unrelated to *spiraeae* and that its digitus and its overall colour pattern suggests similarities with *plagiocephalotes*. Zhelochovtsev (1988) does not cite *flabellatus* or *aquilus* from the European part of the USSR, preferring to cite the closely related, possibly synonymic, *nigritegulis*. The descriptions of all three cite the two basal antennal segments as black and give similar tergal colour patterns (terga 1 and 3 marked white yellow, tergum 2 black, tergum 4 with broad yellow hind margin, terga 5-8 with narrow yellow or white yellow margins). The main differences between these nominal species appears to be size and distribution. Konow (1902b) states *aquilus* as 8-9mm and nigritegulis (1904) as 11mm. Eversmann cites the distribution of *flabellatus* as the province of Orenburg; Konow (1902b) states Transcaucasia for aquilus and Gussakovskij states 'Zakavkaz'ya (=Trancaucasia) (Lagodekhi) and Zhelochovtsev states the central and eastern regions of the European part of the USSR, western Siberia and northern Kazakhstan for *nigritegulis*. All three species are similar to the type of *plagiocephalus* in their overall colour pattern and digitus. It is noteworthy that the eastern distribution of *plagiocephalus*, as given by Zhelochovtsev corresponds with that cited for *nigritegulis*.

Tarpa flavicornis Klug, 1824: 192; Konow, 1897. SYNTYPE ♂, Germany (ZHMB),

[examined].

Klug's description states the type locality as Germany, yet all material referable to his type specimen is from the Transcaucasus or Turkey. Its colour pattern is similar to that of *cephalotes* but its penis valve is similar laterally and dorsally to *fabricii* and its digitus is similar to form 3 (e.g. as in *jucundus* or *flabellicornis*). The syntype requires dissection to establish its true identity. Both Gussakovskij (1935) and Zhelochovtsev (1988) state an extremely widespread distribution for *flavicornis*, extending from the southern European part of the USSR (Podol'sk, Sarepta), Crimea (Zhigulei), northern Caucasus (Terskaya oblast), Transcaucasus, Turkish Armenia, Turkmenistan (Kopet-Dag) to northern Iran (Tabriz).

Tarpa klugii Leach, 1817: 131; Konow, 1902. SYNTYPES ♀, Germany and England: (BMNH), [1 examined].

Type specimen does not agree well with its brief description, particularly in relation to the punctation or the yellow markings. Type bears the labels 'Type H.T.', B.M. TYPE HYM. I.14', 'klugii', 'spissicornis' 'Leach coll. type of klugii', B.M. TYPE HYM. Tarpa Klugii'. However, the type agrees well with other females identified as *klugii* [e.g. from central Switzerland (NMLS) and northern Italy (IZUB)]. However, their associated males possess genitalia similar to the type of *plagiocephalus*. Leach cites *M. klugii* as being found in England, near Bristol, but this is dubious (Perkins 1923, 1928).

Megalodontes medius Konow, 1897: 9; Gussakovskij, 1935. SYNTYPES 3♀♀, Turkey: Amasia, 1860 (Mann) (NHMW) [examined]; Turkey: Amasia (DEIC) [examined]; Russia: Novorossisk DEIC), [examined].

The syntypes agree well with Konow's description. A male from Turkey (BMNH) was dissected and its genitalia were found to be similar to those of *cephalotes* from Geneva, which it resembles strongly in terms of its yellow coloration and punctation. Again, both Gussakovskij (1935) and Zhelochovtsev (1988) state a widespread distribution for *medius* extending from the Ukraine (Starobel'skoye, Kharkhov region), Crimea, northern Caucasus (Novorossiisk, Gelendzhik) and Turkey (Amasya, Brussa).

Tarpa mocsáryi André, 1881: 480. SYNTYPE(S) ♂, Hungary (HNHB), [type lost?].
Megalodontes mocsáryi (André); Konow, 1897 (as a synonym of *M. exornatus*).

No material available for examination. Its description is virtually identical with that of *M. exornatus*.

Megalodontes mundus Konow, 1904: 228-229; Gussakovskij, 1935. SYNTYPE ♀, Spain: Los Moulinos (R.G.Mercet.) (DEIC), [examined].

One male examined and dissected and compared with the female syntype. Larger,

more extensively coloured in yellow and more coarsely punctate than most specimens. Similar to *cephalotes* in colour patttem but more coarsely sculpted on head and mesonotum. Both sexes possess yellow flecks behind the cenchri, unknown in other species related to *cephalotes*. The male digitus is similar to that of the type of *plagiocephalus*.

Megalodontes nigritegulis Konow, 1904: 229; Gussakovskij, 1935. SYNTYPES ♂,♀, Russia, Lower Ural mountains (DEIC), [examined].

Comments as for *aquilus*.

Tarpa panzeri Leach, 1817: 132. Syntypes 1♂, 2♀♀, Germany and England (BMNH), [examined].

Megalodontes panzeri (Leach); Kirby, 1862.

Leach states both male and 2 female syntypes in his description. The type locality is listed as Germany and he cites the presence of *panzeri* in England, near Plymouth (see Perkins, 1923, 1928). The male has not been found, but the female syntypes bear the following labels, the first 'panzeri', 'cephalotes', 'LECTOTYPE' and 'B.M. TYPE HYM 1.838 panzeri' and the second 'cephalotes', 'Stephens Coll. 1853-46'. Both syntypes are similar to material of *cephalotes* from the Geneva Basin, as is other non-typic material. However, the associated males possess genitalia that appear closer to *plagiocephalus*.

Tarpa plagiocephala Fabricius, 1804: 20. Syntype ♂, Austria: (Megerle) (NHMW), [examined].

Megalodontes plagiocephalus (Fabricius); Kirby 1882.

The type agrees, for the most part, with Fabricius' very brief description, although its citation of an entirely yellow tergum 1 is incorrect. The form of the digitus is radically different from that of *cephalotes* (as defined here) and much closer to that of *turcicus* (Fig. 49). In many keys (e.g. Chevin, 1987) it is distinguished from *cephalotes* primarily by its possession of a small lustrous area on the lateral lobes of the mesoscutum (uniformly punctate, although not closely so in *cephalotes*); antennae reddish with scape and pedicel brown or black; scape sometimes yellow but with at least a small brown or black line below (scape yellow to ochraceous pedicel testaceous to brown, flagellum and flabellae; tegulae completely black, rarely with small yellow spot in the middle (yellow); second tergite entirely black, sometimes with a yellow fleck apico-laterally, but then always smaller than the flecks on first tergite (terga 1-3 with apico-lateral flecks, tergum 2 occasionally black throughout); yellow apical stripes on tergites five and six narrower than those on the seventh and eight tergites, these occasionally interrupted medially in males (terga 4-8 with apical yellow band complete, widest on tergum 4).

A more suitable distinction between *plagiocephalus* and *cephalotes* needs to found,

as the current is most unsatisfactory and requires the the reinterpretation of all the species names where the males possess the same form of genitalia as *plagiocephalus*. Material referable to *plagiocephalus* has been recorded from northern Spain, southern Italy and Tunisia (!) to the Caucasus and northern Kazakhstan (see also comments under *flabellatus*).

Megalodontes (Megalodontes) scythicus Zhelochovtsev (in Skarlato 1988): 33. Replacement name for *M. eversmanni* Gussakovskij 1935, nec Freymuth 1870.

No males available for examination. Three females from Russia and Armenia examined, one without antennae. One female with flabella of third antennal segment much shorter than the fourth segment and the other with flabella as long as the fourth segment. In his description of *eversmanni*, Gussakovskij cites its distribution as the eastern part of the European part of the USSR (Orenburg and Ural'sk) and the Crimea, but the origin of the syntypes is not certain. Zhelochovtsev gives the distribution as the southern European USSR, from Odessa to Ural'sk, but does not indicate how much material was examined.

Tarpa spissicornis Klug, 1824: 187. SYNTYPES ♂,♀, Germany: Ebersdorff (Grimm) (ZHMB), [examined].

Megalodontes spissicornis (Klug); Kirby 1882.

Colour pattern of female syntype similar to that of *cephalotes* but genitalia, particularly the digitus, of the male syntype appearing similar to *plagiocephalus*.

Megalodontes xanthocerus Gussakovskij, 1935: 211. SYNTYPES ♂,♀ Algeria or southern France (!) (ZMAS), [not examined].

Material referable to Gussakovskij's description was obtained from France, dissected and found to be similar to the type of *plagiocephalus*, although the broad apical yellow bands of the terga are closer to those found on material identified as *mundus*.

Clada Pic, 1918: 12. Nomen nudum.

Tarpa sulphurea, Lucas, 1848: 344. Nomen nudum.

Biology

Remarkably little is known about the biology of Megalodontidae. Host records are sparse and many of the citations of megalodontid hosts have been culled from those of Stritt (1937), although this is not always stated. Hosts or host-plants are defined as the larval food-plants and adult food-plants are those from which the adults gather nectar or pollen. None of the examined specimens possessed host data.

Stritt (1937) collecting in Germany, cited *klugii* (= ? *cephalotes*, as defined above)

as developing on sermountain (*Laserpitium latifolium* L.), masterworts (*Peucedanum cervaria* (L.) Lapeyr.) and the moon-carrot, *Seseli libanotis* (L.) Koch. Benson (1961) collecting at altitudes of more than 1750m in Valais, also cites *klugii* on *Laserpitium* spp.), later confirmed by Pschorn-Walcher, based upon studies in Austria, (1990) as being *L. latifolium* and *L. siler* L. Stritt (1937) cited *Peucedanum alsaticum* L. as the host of *plagiocephalus* (see species inquirendae). Studies in the Geneva basin did not reveal any larvae but all of the material collected (of *M. cephalotes*) was taken in areas dominated by or immediately next to masses of *P. cervaria.*

Verzhutskii (1973, 1981) cites *Sphallerocarpus gracilis* (Bess.) K. Pol. (Apiaceae) as a host-plant of *spiraeae* and, in the earlier paper, mentions the collection of about 50 larvae, from an area of $1m^2$, in August and September 1971, stating between 2-3 larvae per host plant.

Based upon observations of central Asian and eastern Palaearctic species, Gussakovskij (1935), Zhelochovtsev (1976) and Ermolenko (1984) state the genera *Ruta* and *Haplophyllum* (both Rutaceae) as host-plants. Gussakovskij cites *H. hirsutum* Regel and Schmalh. as the host-plant for *skorniakowii*, *Ruta* and *Haplophyllum* as hosts for *nitens* and Ermolenko illustrates *kohli* (= *phaenicius*) ovipositing on *H. suaveolens* (DC) G. Don fil. and its egg. According to Lorenz and Krauss (1957), based upon observations in Germany, the Megalodontidae are univoltine.

According Pschorn-Walcher (1990) the cream-white eggs of *klugii* are abundant on the underside of leaves of *L. latifolium* and *L. siler*, laid in a slit which appeared to pinch the chorion of the egg's underside. The average egg size was 2 mm. Young larvae, emerging from an egg cluster, fed gregariously in a fragile web covering the surface of the leaflet on the underside of the leaflet, at first, then inside the leaflet or on the leaf's edge. Older larvae dispersed and fed individually or in small groups in silken tubes of a light brown colour. This feeding habit is similar to that of larval Pamphiliidae.

Like the pamphiliids, megalodontids have five larval instars, in contrast to the usual four or, sometimes, three instars, prevalent in other groups of sawflies, such as Tenthredinoidea. The first larval instar of *M. klugii* is 4-5mm in length and the fifth about 20-24 mm (Pschorn-Walcher, 1990). Mature larvae and prepupae leave the food-plant and over-winter underground as pupae. Placing mature larvae of *M. klugii* in a bucket of sand proved an effecting method for rearing megalodontids, since 200 adults emerged from more than 300 mature larvae (Pschorn-Walcher, 1990).

Most of the records for *klugii* suggest the adults are flying in late June through to early August, but collecting in the Geneva Basin recorded adults from the first week of June. Material of species from very arid areas in the Levant and the Maghreb, such as *olivieri*, *phaenicius* and *escalerai* have been taken much earlier, in late March and early April, due to the much earlier spring and summer seasons in these areas. Others are taken much later, e.g. *spiraeae* from late June to the end of August, a probable consequence of

the very late spring and relatively short summer seasons in the Siberian, Mongolian and Manchurian regions. Observations on the Geneva populations suggested that much of the adult flight activity and feeding was dependent upon the flowering of their food-plants, noted to be *Ranunculus repens* L. (Ranunculaceae) and *Tripleurospermum inodorum* (L.) Schultz-Bip. (Asteraceae), with the first males being taken a few days before the first females. Before the adult food-plants were open, no activity was observed and less than 10 individuals were collected after the inflorescences had wilted. During this period, no adults were noted upon the adjacent *P. cervaria*, since these remained as ground level leaves, having not yet developed the aerial stems and umbels. Adults have been collected from the heads of *R. repens* and *T. inodorum* and various Euphorbiaceae (Else; Guichard, pers. comm.), suggesting that the megalodontids prefer feeding from open flowers, whose nectaries may easily be robbed. Adults appeared very sluggish and rather ponderous on the wing and, thus, were caught easily, although the reverse was reported from collecting in the southern Urals (Bashkiria) (Taeger, pers. comm.) which suggested that some species are rapid flyers. Additional records of adult food-plants include Apiaceae and Asteraceae, in general (Verzhutskii, 1966), *Thapsia* and *Peucedanum* (for *merceti*) (Ceballos, 1941) (all Apiaceae), *Haplophyllum tuberculatum* (Benson, 1955) (Rutaceae) and *Buphthalmum salicifolium* (for *klugii*) (Pschorn-Walcher, 1990) and *Leucanthemum* (Blank, 1993) (for *flabellicornis*) (both Asteraceae). Collecting widely in the Alps and Pyrénées in 1988 and 1989, Lacourt (1994) recorded *klugii* from *Jasione perennis* (Campanulaceae) (blue flowers); *Ranunculus bulbosus* (Ranunculaceae), *Scabiosa columbaria* (blue flowers), *Knautia arvensis* (blue flowers) (both Dipsacaceae); *Biscutella laevigata* (Cruciferae) (pale yellow flowers) and from various Asteraceae.

Records of parasitoids being recorded or emerging from megalodontids are unknown except for Pschorn-Walcher's (1990) note that two adult *Ctenopelma* sp. (Ichneumonidae: Ctenopelmatinae) emerged during rearing experiments in Austria.

Cladistic analysis

Background. Previous classifications of Megalodontidae have been based upon differences between species, rather than shared-derived characters. These included potentially artificial groupings and are not testable. In order to detect phylogenetic relationships within Megalodontidae cladistic methodology, as derived by Hennig (1950), is employed. It attempts to to demonstrate phylogenetic relationships by using synapomorphies (shared-derived characters). The main problem in applying cladistic analysis is the appraisal of conflicting evidence and much of the previous work upon Megalodontidae suggests that, indeed, there is a high degree of such conflicting evidence. The principle of phylogenetic systematics or cladistics is that a classification should reflect phylogenetic relationships based upon common ancestry. Groups that are not strictly monophyletic are rejected as uninformative. This monophyly is discovered by the search

for synapomorphies. Paraphyletic (i.e. where one or more of the descendents of the ancestral species is excluded) or polyphyletic (i.e. where the common ancestor is placed in another taxon) groupings are of no interest as they will give no information upon the relationships within Megalodontidae and how characters have become modified by descent. Another problem is the detection of and distinction between genuine synapomorphy (i.e. homologous characters) and homoplasy (i.e. analogous characters, reductions and reversals).

Hennig's original approach was to search for characters which appeared convincing and powerful; the subsequent grouping of species with these characters, and the search for more to support the grouping and the production of a single cladogram, which would be used as the basis for a scheme of argumentation (Argumentationsschema). However, where there is a large amount of conflict between characters, it becomes impossible to illustrate this in a single cladogram and it was decided that parsimony should be used to decide which of the postulated solutions would be the most probable. This and the manipulation of large data sets may easily be calculated by the use of computer-based algorithms such as PAUP or Hennig86.

Techniques. In the analysis of phylogenetic relationships between taxa of Megalodontidae, the selection of characters was based upon the character assessment above. The raison d'être was to test potential synapomorphies within the Megalodontidae, i.e. the selection of characters which are likely to be shared and uniquely derived. Using the character assessment, the following thirty eight (22 binary and 16 multistate) were selected to detect the relationships within Megalodontidae:

1. lateral form of galea: swollen (0); elongate (1);
2. form of glossa: barely longer than galea, distinctly flared and strongly downwardly curved (0); longer than galea, distinctly flared and strongly downwardly curved (1); much longer than galea, slightly flared and slightly downwardly curved (2); much longer than galea, parallel sided and slightly downwardly curved (3);
3. malar space: wide (0); narrow (1);
4. genal carinae: present (0); obsolete (1); absent (2);
5. antennal segments without flabellae: less than 7 (0); 7 or more (1);
6. pentagonal area: excavated with trench (0); planar (1);
7. post-ocellar striae: incomplete (0); complete (1):
8. teeth of tarsal claws: proximal (0); widely separated (1);
9. pronotum laterally: collapsing (0); curving (1);
10. basal plate: prominent lip (0); remnant of lip (1); lip absent (2);
11. basal plate: apically impressed (0); apically flattened or rounded (1);
12. dorsal sclerotisation of gonostipes: complete (0); incomplete (1);
13. dorsal surface of gonostylus: curved (0); straight (1); curved strongly apically (2); peg-shaped apically (3);

14. digitus and cuspis: projecting strongly from volsellae (0); atrophied (1);
15. lateral margin of volsellae: rounded (0); straight (1);
16. form of digitus: form 1 (0); form 2 (1); form 3 (2); form 4 (3); form 5 (4); form 6 (5); form 7 (6); atrophied protruberance (7).
17. form of cuspis: not projecting apically of digitus (0); projecting apically of digitus (1);
18. form of penis valve, laterally: form 1 (0); form 2 (1); form 3 (2) form 4 (3); form 5 (4); form 6 (5); form 7 (6)
19. form of penis valve, dorsally: lateral lobes unenlarged (0); lateral lobes wider than maximum width of penis valve (1); lateral lobes massively enlarged (2);
20. sclerotised apical volsellar sac: absent (0); present (1);
21. aedeagal apodemes: flared (0); parallel-sided and rounded apically (1);
22. apical margin of basal plate: convex (0); truncate or concave (1);
23. articulation of gonostipes and gonostylus: dorsal articulation projecting more apically than ventral (0); dorsal and ventral articulations projecting equally apically (1);
24. length of gonostylus: much shorter than ventral length of gonostipes (0); equal to or slightly longer than ventral length of gonostipes (1);
25. male eighth tergum: with medial furrow (0); semi-circular or hemi-elliptical impression or tergum folded downwardly apically (1); flattened (2);
26. vertiginal colour syndrome: olivieri (0); flabellicornis (1); bucephalus (2); cephalotes (3);
27. male facial colour syndrome: olivieri (0); flabellicornis (1); cephalotes (2); fabricii (3);
28. male lateral and ventral colouring: entirely yellow (0); propleurae yellow, mesosterna black (1); yellow area on mesepisternum large, propleurae black (2); predominately black, yellow area on mesepisternum small or absent (3);
29. female leg colour: all yellow or, at most, with very small areas of black at base of fore-legs (0); black basally, hind femur predominately yellow or ochraceous (1); predominately black with distinct white markings (2);
30. head sculpture: smooth to finely punctulate (0); sparsely punctate with lustrous interspaces (1); closely punctate, lustrous in between (2); closely and coarsely punctate or puncate-rugulose (3);
31. mesepisternal sculpture: as cephalic sculpture or finer (0); coarser than cephalic sculpture (1);
32. mesoscutal sculpture: smooth with occasional punctulae (0); many punctulae or punctae with small smooth and lustrous areas (1); coarsely punctate (2);
33. flabella of third antennal segment: as long as the following seven segments or more (0); longer than the following 2 segments, but less than the following seven segments (1); as long as the following 1-2 segments (2); not longer than the following (i.e. fourth) segment;

34. flabella of fourth antennal segment: less than 1.5 times longer than flabella on third antennal segment (0); 1.5 times longer than flabella on third antennal segment (1);
35. form of third antennal segment: transeverse (0); square (1); about 1.5 times longer than broad (2); twice as long as broad or longer (3);
36. scrobal region: shallow, without pit behind antennal insertions (0); deep and with pit behind antennal insertions (1);
37.vertex and occipital region: rounded (0); strongly angled (1) and
38. hind coxal apical incision: open (0), closed (1).

A data matrix was prepared and the characters coded. Character polarity was based, initially, on an examination of members of the supposed sister-group, the Pamphiliidae (the genera *Acantholyda* and *Pamphilius* being examined). However, polararisation of many of the characters posed a great problem, particularly those derived from the antennal flabellae, colour syndromes and male genitalia, since these were absent or of a completely different form in the sister group, with the result that 22 of 38 characters were scored with a '?' (A full discussion of these is within the character assessment.) Characters were also polarised using an outgroup based upon a hypothetical ancestor, in which all the character states are assumed to be plesiomorphic (termed a dummy outgroup), and this outgroup is included in the matrix shown in table 2. Thus, two series of analyses were peformed using the PAUP3.1 algorithm (Swofford, 1989) (a heuristic search without any of the characters being ordered or weighted and without the use of constraint groups): one, using an outgroup derived from Pamphiliidae and the second using the dummy.

Discussion. The first analysis revealed the following: tree length = 193, consistency index (CI) excluding uninformative characters: 0.372, retention index (RI): 0.6 and homoplasy index (HI): 622, with 174 trees being saved. No characters were supported as synapomorphies and, with the exception of characters 8 (the form of the tarsal claws in *kuznetzovi*) and 37 (the form of the vertex and occipital region in *parvus*), all were considered as homoplasies. The synapomorphies for Megalodontidae (discussed above) were not mapped onto any of the trees. A consensus tree is shown in Fig. 138.

In the first set of analyses, using Pamphiliidae, *judaicus* is considered as the sister-species of the remainder of the Megalodontidae on the bases of the closed hind-coxal apical incision, the mesepisternal sculpture being coarser than that of the head, the virtual absence of cephalic sculpture, legs black with white markings, the lateral lobes of the penis valve being wider than the latter's maximum width, the absence of genal carinae and the narrow malar space (characters 38, 31, 30, 29, 19, 4 and 3 - all homoplasies).

A grouping of *kuznetzovi+levaillantii+merceti* is supported by characters 9 (the 'curving' lateral form of the pronotum) and 10 (the prominent lip at the apex of the basal plate). This is considered a sister-group of the remaining 27 megalodontids since these, and *judaicus* retain the symplesiomorphic swollen form of the galea (character 1), which is only slightly shorter than the glossa (character 2), the latter being distinctly flared and

downwardly curved apically. The remaining megalodontids all share an elongate galea which is shorter than the glossa.

The clade of *phaenicius*+(*nitens*+*olivieri*+*xanthosomus*) is supported by characters 14, (the atrophication of the digitus), 15 (the straight lateral margin of the volsellae), 16 (the form of the atropied digitus) and 33 (the length of the third antennal flabella). *M. phaenicius* is considered as the sister species to the three others on the bases of its apically peg-shaped the gonostylus and its 'collapsing' pronotal collar. The unique form of the gonostylus (character 13, state 2) may better be considered as an autapomorphy for this species, since its placement treats the presence of a sclerotised apical volsellar sac (character 20, state 1) as a homoplasy rather than a putative synapomorphy for *phaenicius*+*olivieri*. This clade is considered as a sister-group for the remaining 23 megalodontids.

Four species, *spiraeae*, *quinquecinctus*, *interruptus* and *jucundus* are treated as successively-nested sister species of the remaining 19 species, all of which are in a largely unresolved polychotomy. All 23 species possess closed incisions on the hind-coxae (with the exception of *escalerai*) and dorsal articulations of the gonostipes and gonostylus which project more apically than the ventral (with the exceptions of spp. 1 and 2). The deep scrobal region with pit behind the antennal insertions (character 36, state 1), thought to be a possible synapomorphy for *spiraeae*, *quinquecinctus*, *interruptus* and *parvus*, is not supported as such, since this last is placed in a clade of sp.3+*parvus*+*flabellicornis* which is supported by the incomplete dorsal sclerotisation of gonostipes (character 12, state 1). *M. jucundus* is treated as a sister species to the polychotomy on the basis of its long glossa, which is slightly flared and slightly downwardly curved toward the apex (character 2, state 2) and its coarsely punctate mesoscutal sculpture (character 32, state 2).

Within the polychotomy a clade of sp.2+*fabricii*+(*turcicus*+*cephalotes*) is supported by form 7 of the digitus (character 16) and form 6 of the penis valve (character 18), laterally. Species pairs of *bucephalus*+*lacourti* are supported by character 28 (the flabellicornis syndrome of the facial colour) and characters 7, 18 and 33; that of *turcicus* and *cephalotes* is supported by the same characters and that of *gratiosus* and *capitalatus* by the flabellicornis facial colour syndrome.

The placement of *skorniakowii* appears enigmatic since it suggests that several characters, including the atrophication of the digitus and cuspis (character 14), the lateral margin of the volsellae (character 15) and the highly deformed penis valve (character 18) are homoplasies, rather than synapomorphies for a clade containing *skorniakowii*+*phaenicius*+*nitens*+*olivieri*+*xanthosomus*. However, it appears that the placement of *skorniakowii* is sensisitve to character 30 (head sculpture). Of these five species, only *skorniakowii* possesses closely and coarsely punctate to punctate-rugulose cephalic sculpture, a character its shares with several members of the polychotomy, e.g.

fabricii, *gratiosus*, *lacourti*, *luteiventris*, *reitteri* and *turcicus*.

Slightly higher indices were scored for the multistate genitalic characters 16 and 18 (0.7 and 0.778) than the colour syndromes (the highest being 0.667 for characters 25 and 29), but these were not significant. However, it should be noted that none of these genitalic characters or colour syndromes was scored for Pamphiliidae and, certainly, more information is needed upon the outgroup characters to bring about improvement in the resolution of the cladograms.

Using the dummy outgroup only 4 trees were saved, each with 191 steps; CI, excluding uninformative characters: 0.382, RI: 0.607 and HI: 624, all slightly higher than with the pamphiliid outgroup, but not significantly so. A consensus tree is shown in Fig. 139. Characters 6, 8, 14, 15, 20 and 37 are worthy of discussion. The widely separated form of the teeth of the tarsal claws (of *kuznetzovi*) and the strongly angled nature of the vertex and occipital region (of *parvus*) are considered as autapomorphies (characters 8 and 37 respectively). The planar form of the pentagonal area (character 6, state 1) is considered to be a synapomorphy for *interruptus*+*jucundus*+(the polychotomy). This character was scored as a '?' using the Pamphiliidae outgroup and is treated as a homoplasy rather than as a synapomorphy.

The atrophication of the digitus and cuspis and the straight lateral margins of the volselluae (characters 14 and 15, respectively) are considered as synapomorphies. Thus and in contrast with the analysis using Pamphiliidae, *skorniakowii* is placed as the sister-species of *olivieri*+*phaenicius*+ *nitens*+*xanthosomus*. Like the first analysis, the sclerotised apical volsellar sac (character 20) is treated as a homoplasy, rather than a potential synapomorphy.

A clade of *levaillantii*+(*merceti*+*kuznetzovi*) is considered to be a sister-group of *judaicus*+(the remainder of Megalodontidae) and the bases of the curving pronotum (character 9, state 1), the straight dorsal suface of the gonostylus (character 13, state 1, although this was not scored for *levaillantii*), the cuspis projecting apically of the digitus (character 17, state 1), the dorsal and ventral articulations of the gonostipes and gonostylus projecting equally apically (character 23, state 1), the semi-circular or hemi-elliptical impression on the eighth tergum (character 25, state 1) and the mesoscutum with many punctulae or punctae with small smooth and lustrous areas (character 32, state 1), all homoplasies.

Within the polychotomy, the Iberian and Maghrebian species *gratiosus*+*capitalatus*+sp.4+(*lacourti*+*bucephalus*) are considered as a sister-clade to one consisting of sp.1+(sp.2+*fabricii*+(*turcicus*+*cephalotes*)). The former is supported the distorted form of the digitus (character 16, state 3), the digitoid lateral form of the penis valve (character 18, state 0), the wide lateral lobes of the penis valve (character 19, state 1) and the flabellicornis facial colour syndrome (character 27, state 1), all homoplasies. The latter is supported by the complete dorsal sclerotisation of the gonostipes (character

12, state 0) and the truncate or concave apical margin of the basal plate (character 22, state 1).

Other than characters 6, 8, 14, 15, 20 and 37, the remaining 32 exhibited a high degree of homoplasy and some reversal. Of the 16 bipolar characters, none were significantly different in their character indices from the values scored using the Pamphiliidae outgroup. Comparisons between the 16 multistate characters revealed several interesting differences between the character types and between the analyses. In this analysis, higher character indices were noted for the form of the digitus and the lateral form of the penis valve than for any of the colour syndromes, all of which had lower consistency indices than the analysis using the pamphiliid outgroup. Characters 16 and 18 did not undergo reversal in either analyses, but reversal was noted for colour syndrome characters 27, 28 and 29 in both analyses.

The importance of the male genitalic characters to the topology of the consensus tree was demonstrated when two further sets of analyses were perfomed. In the first, characters associated with the male genitalia were eliminated from the heuristic search. The latter retained more than 2000 trees and the computed consensus (not shown) revealed a wholly unresolved polychotomy. This importance was examined further by a second heuristic search in which the multistate characters 16 (the form of the digitus) and 18 (the lateral form of the penis valve) were omitted. After more than 42 hours the search was terminated with more than 2200 trees retained. Using the retained trees, a consensus cladogram, composed of 169 steps was computed and is shown in Fig. 140. Whilst the base of the tree remains the same, 23 species are included in the polychotomy which, with the exceptions of the species pairs of *bucephalus+lacourti*, *capitalatus+gratiosus* and *turcicus+cephalotes* (all determined, primarily, by colour syndrome characters), is wholly unresolved.

Both analyses have their inherent problems. The polarisation of characters with Pamphiliidae as an outgroup is unsatisfactory because of the large number of characters which cannot be scored in the outgroup. Introducing scores in the outgroup (= dummy outgroup) produced fewer and slightly shorter trees, with a slightly higher consistency index but a considerably different topology. It is obvious that more material is required, particularly information upon larvae and biochemical data, to construct a more sound database in order to resolve some of the many contradictions and conflicts that have been observed in the analysis based purely on adult morphology. The use of more and varied outgroups, particularly members of Xyelidae and Siricoidea are likely to provide a stronger basis for comparing the characters observed in the Megalodontidae.

Previous concepts of the placement of species within Megalodontidae have been highly subjective, with the possible exception of the *bucephalus* group (based upon their colour patterns and relative geographic isolation) and the *phaenicius* group (based upon their antennal flabellae). Interpretation of the cladograms suggests that there is no

evidence for dividing the genus into monophyletic groups which are well supported. Separation of megalodontids into different genera, for example, the placement of *judaicus* in *Tristactus*, *fabricii* in *Melanopus* and *levaillantii* in the subgenus *Forficulotarpa* is not supported by any of the cladograms. At present the characters are not sufficiently powerful to enable a decision to be made upon the precise generic classification within Megalodontidae and, therefore, for reasons of practicality and expediency, it is decided that all pre-existing generic and subgeneric names be synonymised under *Megalodontes*.

Biogeography

Biogeographical relationships may be investigated by various means, depending upon the context of its study. For example, ecological biogeographers will study the distributions of animals and plants using population studies and ecological methods. Within the present context, one of historical biogeography, it is intended to investigate historical explanations for the composition of extant faunas. The precepts of historical biogeographical analysis are subtly different from those in taxic analysis. In the latter, the presence of absence of a character, be it morphological or biochemical, is simply that but, in the former, the presence or absence of a species from any particular area may be accounted for in several ways: 1) the species was not present but immigrated; 2) the species was present but emigrated; 3) the presence or absence of the species both past and present; 4) the species was present but became extinct or 5) the species is present but has yet to be discovered. However, the concept that the extant presence of species in an area is due to their historical presence and that their diversification has been caused by the diversification of that area can be used as a working hypothesis which can be tested and falsified. This concept is significant and has been chosen by cladistic biogeographers who are interested in the study of area interrelationships.

The most significant dvelopments in the application of cladistic methodology to the study of biogeopraphy came with the reinterpretation of Leon Croizat's (1964) panbiogeographic ideas, by presenting vicariance rather than dispersal models which suggested the appearance of barriers fragmenting the former ranges of ancestral taxa (e.g. Nelson, 1974, 1978; Rosen, 1975, 1978). Rather than a 'vacuum' theory of biogeography, whereby certain areas were considered to be devoid of taxa, waiting passively to be colonised from other source areas with no relation to historical events, disjunct distributions could exist because of vicariant events. Ancestors originally occurred in areas where the modern taxa are present today, or the taxa observed today evolved in situ and the patterns observedwere due to earth and biotic history being one and the same. However, it is probable that dispersal and vicariant patterns cannot necessarily be resolved decisively from one another. When examining a particular pattern of distribution, the main criterion is whether it conforms to a general pattern of area relationships shown by other groups of taxa occurring in the same areas. Like the use of

three-taxon statements in cladistic taxonomy, cladistic biogeography uses three-area statements as the most basic units for expressing area relationships, with area cladograms indicating the relative recency of common ancestral biotas.

The rationale for applying systematic theory to biogeography is based on the idea that phylogenetic reconstructions are essential precursors for historical interpretation. By replacing taxa with areas, the principles of congruence and synapomorphy can applied with the same rigour. Area cladograms are produced by substituting for taxa the areas in which they occur (Rosen, 1975; Platnick and Nelson, 1978)

Within Megalodontidae, the consensus tree derived from the Pamphiliidae outgroup will form the basis of the analysis and discussion. The specific names on the consensus tree were substituted with their known distributions (Fig. 141). Given the generally unresolved nature of the consensus tree, the presence of widespread taxa (e.g. *eversmanni*, *fabricii*, *olivieri* and *phaenicius*) and the means of eliminating ambiguity caused by them (e.g. Nelson and Platnick, 1981; Page, 1989) will detract but little from the discussion.

No overall pattern was observed from the consensus tree, but sister-areas defined include the Levantine/Irano-Turanic region as the sister-area of the remainder of the Palaearctic, with Central Asia+Algeria+central Spain as a nested sister-area. Sister-area pairings of the western Rif (Morocco)+south-eastern Iberia is supported (based upon *lacourti+bucephalus*) and south-western and central Spain+southern Spain (based upon *capitalatus+gratiosus*), although the latter is rather uninformative. Ignoring the widespread species, sister-area pairings of northern and central Turkey+north-eastern Turkey (based upon *fabricii*+sp.2) and central Asia: lowland desert+ south-eastern Turkey (based upon *parvus*+sp.3). The relationship of the eastern Palaearctic to the remainder of the Palaearctic is unclear since the three species found east of the Urals, *interruptus*, *quinquecinctus* and *spiraeae* are all widespread and are shown as sister-species of the polychotomy. It is noteworthy that the majority of these areas are classified as temperate desert, semi-desert or or Mediterranean semi-arid (West, 1975) and it is suggested that the Megalodontidae originated in these habitats and that they are a group of semi-arid area specialists whose distributions appear to have become fragmented, in a vicariant sense. Given the relative youth of the family (about 70 mya), it is unlikely that the present distributions are the result of any of the great Palaearctic orogeneses, these having occurred many millions of years before and it would appear that more subtle vicariant events have shaped the extant distributions. Again, the unresolved nature of the taxic cladogram and, thus, the area cladogram precludes any hypothesis of overall relationships of areas, particularly within the polychotomy. An additional problem of investigating area interrelationships within the Palaearctic is that discussion of these is dependent upon the definition of areas of endemism, be they based upon political or historical boundaries or ecological or biogeographic zones. The first two are artificial in

zoological terms, and thus uninformative, and the two last are based heavily on floras, which do correspond with the distribution of Megalodontidae. Therefore, there is no simple or straightforward solution for Palaearctic floras and faunas, such as exists for their Gondwanan counterparts. Semi- or temperate desert faunas are probably flexible entities, which may move about easily with changing conditions and this means that is difficult to use them as a system for examining historical interrelationships between areas.

Conclusion

The re-examination of adult morphology showed that there is no single character which is useful for defining species and that combinations of characters were necessary to separate them. These combinations were of antennal morphology and dimensions, colour syndromes and mouthpart and male genitalic morphology. Many characters used previously, were useful to a certain extent, but were not found to be powerful enough for defining species. However, even with the newly-defined characters, particularly those from the male genitalia, these were not sufficiently diagnostic to be used alone and, within the updated key to males, again combinations are used.

It is shown that there was a high degree of conflict and contradiction within and between the use of both previously-used and newly-defined characters them. Their uncertain and unclear value was certain to be the cause of the unresolved nature of the taxon cladograms, which was compounded by the unsatisfactory situation of their comparison with Pamphiliidae and subsequent scoring for the data matrix. Certainly, other appraoches are needed to supplement and/or redefine these characters.

At a taxonomic level, due to the paucity or unavailability of adequante amounts of material for study, the definition of several nominal species (mostly those species putatively related to *cephalotes* and *flabellicornis*) could not be resolved and are listed under species inquirendae. The status of the majority of these should be re-examined, particularly with more material, preferably from a single population, and dissection of the type specimens.

At the systematic and nomenclatorial levels, before any well-defined basal groupings can be supported, it is not useful to retain previous generic and subgeneric divisions of Megalodontidae and, therefore, all pre-existing names are synonymised under *Megalodontes*. In particular, in a situation where less than 50 specific names (i.e. even allowing for the validation of all the names considered species inquirendae) exist. there is no need, let alone a sound basis, for subdivision of the family, certainly when this is compared with some of the extremely speciose genera within the sawflies and the Apocrita [e.g. *Tenthredo* (Tenthredinidae of Tenthredinoidea) and *Anagyrus* (Encyrtidae of Chalcidoidea)].

Based upon the lack of clarity within the taxic cladogram, it follows that the corresponding cladistic biogeographic analysis is slightly vague. However there are well-

supported sister groups of Levantine/Irano-Turanic+(central Asian: lowland desert+Mediterranean Algeria+central Spain) and the remainder of the Palaearctic and of Morocco and south-eastern Iberia.

The biology of Megalodontidae remains something of an enigma. Apart form the host-plant records culled from the literature (two genera of Rutaceae and four of Apiaceae) for four species, no new information was forthcoming, either from material or from field work in the Geneva Basin, upon the remaining 27. In both consensus trees, species feeding upon Apiaceae were in the same, albeit unresolved, clade. However, again, it was not possible to derive any general pattern, particularly with reference to species feeding upon Rutaceae. For example, in Fig. 139 rutaceous feeders are shown in a single clade and apiaceous feeders are in another, whereas in Fig. 138 they are divided between two clades. Therefore, it will be necessary to have far greater information about host-plant relationships between species. For example, the extent of feeding on Rutaceae and Apiaceae within the family, the host-specificity of species and whether larval Megalodontidae feed on plants outside of the above mentioned families are all unknown.

The value of the male genitalia and associated sclerites in the identification and systematic placement of sawflies has long been underestimated by symphytologists, despite the existence of several high-quality syntheses [particularly those of Snodgrass (1941) and Ross (1945)] and, all but, dismissed by workers on Apocrita (except for those studying a few groups within Apidae and Pompilidae). For example: ".... but on the whole the form of the male genitalia is less useful for species recognition in the Hymenoptera than it is in the other major orders." (Gauld and Bolton, 1988: 77). The evidence from this study of Megalodontidae, admittedly a very small taxon, is very much to the contrary and to paraphrase Richards (1977: 48), all of the sawflies "would no doubt repay study from this point of view."

Summary

The systematics and taxonomy of the Megalodontidae were revised using modern systematic approaches based upon character assessment and, thus, it represents possibly the first time that a group of sawflies has been subjected to such treatment. Adult morphology is re-examined and revised, in lieu of redefining species and discovering characters which are putative synonyms for discovering phylogenetic relationships.

The analysis of variation within a single population was investigated by the search for and collection of a large quantity of specimens within the Geneva Basin, an area from where Megalodontidae had been collected in latter half of the last and the first half of this century and from where the putative host plants had been recorded. The collection of more than 110 individuals (here identified as *Megalodontes cephalotes*) from two sites, represents possibly the largest sampling of a single population. This and the study of eleven other species formed the basis for the character assessment and the acceptance or

rejection of many of the characters used in species definitions, key construction and the analysis of phylogenetic relationships.

The value of characters newly-derived from the mouthparts and from the male genitalia is emphasised, particularly in species definition and, to a lesser extent, in cladistic analysis, although these were not decisive. A comparative table of male genitalic characters was made and is appended. Twenty one characters, mostly of colour, were rejected from the analysis and, of these, only 6 were used sparingly during key construction. General colour patterns of head and thorax considered more informative and eight 'syndromes' were noted and these proved useful in key construction. Their precise value in the cladistic analysis must be queried since it was not possible to associate with, consistency, head and thoracic colour syndromes. Five, previously used, structural characters are rejected and five retained. Twenty-one, previously unused, morphological characters were defined. In addition, five useful and, often, diagnostic sets of ratios, based upon the vertiginal and antennal morphology are defined for each species.

In the present study, the family is considered to consist of a single genus, *Megalodontes*, and thirty one species. Five generic or subgeneric level names and 11 specific names are placed in synonymy with *Megalodontes* and a sixth is considered to be a nomen nudum. .

During the construction of keys to adults and the cladistic analysis, it was necessary to use complexes of characters, rather than singletons, since no single character was found to be powerful enough for either purpose. Thus, it was difficult to define synapomorphies for demonstrating phylogenetic relationships, with the result that there was much conflict and contradiction between these characters. For the analysis of phylogenetic relationships, 38 potential synapomorphies (15 from the head, including 2 of colour, 7 from the thorax, including 2 of colour, and 16 from the abdomen, all from the male genitalia or associated sclerites) were selected and analysed using PAUP3.1 and 2 outgroups, one based upon comparison with the Pamphiliidae and the second a dummy (based on a hypothetical ancestor). Polarising the former was problematic since many of the characters scored for Megalodontidae were not recorded within Pamphiliidae, with the result that 22 of the 38 characters in the outgroup were scored as '?' Both sets of analyses gave slightly different results and, after comparing the consensus trees of both, the following clades are supported by both:

(*kuznetzovi+merceti+levaillantii*);

phaenicius+(*olivieri+xanthosomus+nitens*);

(*bucephalus+lacourti*) and

(*turcicus+cephalotes*).

Basally, the cladograms are not particularly well-supported and, for this reason, a general system of classification cannot be derived and for practical and expedient reasons all generic and subgeneric names are synonymised under *Megalodontes*.

The family is considered to monophyletic on the basis of their unique form of lamellate digitus in association with a large digitifom cuspis and their flabellate antennae. The sister-group relationship with Pamphiliidae is retained on the basis of the unique ventral closure of the head capsule in the post-genal area, thus forming three apertures in the venter of the head capsule, one for each of the mandibles and a third for the mouthparts. These characters separate Megalodontidae+Pamphiliidae from other families of sawflies where larval abdominal legs are absent (i.e. Xiphydriidae, Siricidae and Anaxyelidae).

Details upon the biology of the Megalodontidae remain scattered and no new data upon the extent of feeding upon Rutaceae, Apiaceae or outside of these families and host-plant specificity (i.e. monophagy, oligophagy or polyphagy) could be obtained. In a strict sense, the family as a whole must be considered polyphagous, but this cannot be confirmed for individual species. The limited biogeographic information that could be derived from the consensus cladogram suggested that the family are semi-arid area specialists and that vicariant events are responsible for the current distribution of species.

Résumé

La systématique et la taxonomie des Megalodontidés ont été revisées au moyen d'approches modernes faisant appel à l'évaluation des caractères et il est possible, de ce fait, qu'il s'agisse de la première étude de ce genre concernant un groupe de Symphytes. La morphologie des adultes a été examinée à nouveau et révisée, dans le but de redéfinir les espèces et de découvrir de nouveaux caractères utiles à l'étude des relations phylogénétiques entre celles-ci.

L'analyse des variations au sein d'une population fut effectuée par la récolte d'un grand nombre de spécimens dans le Bassin Genevois, une région où les Megalodontidés ont été récoltés depuis la deuxième moitié du XIXe siècle, ainsi que pendant la première moitié de ce siècle, et où l'identité de leurs plantes-hôtes supposées, a été rapportée. La récolte de plus de 110 individus (identifiés ici comme *Megalodontes cephalotes*) en deux endroits différents représente possiblement le plus grand échantillon connu provenant d'une seule population. Ceci et l'étude de onze autres espèces formèrent la base pour l'évaluation des caractères ainsi que pour l'acceptation ou réjection de certains d'entre eux utilisés dans la définition des espèces, la construction des clés et l'analyse phylogénétique.

La valeur de certains caractères nouvellement étudiés concernant les pièces buccales et les genitalia mâles est soulignée, particulièrement pour la définition des espèces, et, dans une moindre mesure, pour l'analyse cladistique, bien qu'ils ne furent pas décisifs dans ce cas. Une table comparative des genitalia mâles a été élaborée et ajoutée. Vingt-et-un caractères, principalement en rapport avec la coloration, furent rejetés de l'analyse, et, de ceux-ci, seuls six furent utilisés, avec parcimonie, pour l'édification

des clés. Les différents types principaux de coloration de la tête et du thorax considérés comme plus informatifs et huit "syndromes" furent notés et se révelèrent utiles pour l'élaboration des clés. Leur valeur pour l'analyse cladistique est douteuse car il fut impossible d'associer de manière satisfaisante les types de coloration de la tête et du thorax. Cinq caractères structuraux de la tête, déjà utilisés auparavant, ont été rejetés, et cinq autres retenus. Vingt-et-un caractères morphologiques, jamais utilisés auparavant, ont été définis. de plus, cinq ensembles de rapports, qui se révelèrent utiles, furent définis pour chaque espèce, basés sur la morphologie des antennes et du vertex.

Dans cette étude, la famille est considérée comme étant constituée d'un genre unique, *Megalodontes,* et de trente-et-une espèces. Cinq noms génériques ou sub-génériques et onze noms spécifiques sont placés en synonymie avec *Megalodontes* et un sixième est considéré comme un nomen nudum.

Pendant la construction des clés et l'analyse cladistique, il fut nécessaire d'utiliser des complexes de caractères plutôt que des caractères isolés, car aucun caractère seul n'était assez puissant pour servir à l'un ou l'autre de ces objectifs. Ainsi, il fut difficile de définir des synapomorphies pour démontrer des relations phylogénétiques, ce qui résultait en un certain taux de conflit entre ces caractères. Pour l'analyse des relations phylogénétiques, 38 synapomorphies potentielles (15 de la tête, dont deux concernant la coloration, 7 du thorax, dont deux en rapport avec la coloration, et 16 de l'abdomen, toutes concernant les genitalia mâles et les sclérites associés) furent séléctionnées et analysées avec PAUP 3.1 et deux groupes externes furent choisis, un groupe basé sur une comparaison avec les Pamphilidés et le deuxième hypothétique. Le codage de ce premier fut problématique car beaucoup de caractères relevés chez les Megalodontidés n'avaient pas d'équivalent chez les Pamphilidés, ce qui résulta dans le fait que 22 des 38 caractères du groupe externe furent codés avec un point d'interrogation. Les deux ensembles d'analyse donnèrent des résultats légèrement différents, et, après comparaison des arbres consensus des deux, les clades suivants se trouvèrent supportés dans les deux cas:

kuznetzovi+merceti+levaillantii;
phaenicius+(olivieri+xanthosomus+nitens);
(*bucephalus+lacourti*) et
(*turcicus+cephalotes*).

Les cladogrammes sont mal supportés en leur base et, pour cette raison, un système général de classification ne peut pas en être dérivé. Pour des raisons de commodités, tous les noms de genres et de sous-genres ont donc été synonymisés avec *Megalodontes*.

La famille est considérée comme monophylétique sur la base de la forme unique du digitus lamellé associé avec un important cuspis digitiforme et des antennes flabellées. La relation de groupe-frère avec les Pamphilidés est retenue sur la base de l'unique fermeture ventrale de la capsule céphalique dans la région post-génale, formant ainsi trois

ouvertures dans la face ventrale de la capsule céphalique, une pour chacune des mandibules et une troisième pour les autres pièces buccales. Ces caractères séparent les Mégalodontidés+Pamphilidés d'autres familles de symphytes dont les larves n'ont pas de pattes abdominales (p. ex. Xiphydriidés, Siricidés et Anaxyélidés).

Les détails sur la biologie des Megalodontidés sont rares et aucune nouvelle donnée sur l'étendue de l'herbivorie sur les Rutacées, Apiacées ou sur d'autres familles, et sur la spécificité envers les plantes-hôtes (p.ex. monophagie, oligophagie ou polyphagie) n'a pu être obtenue. Au sens strict, la famille doit globalement être considérée comme polyphage, mais il ne peut pas être déduit des cladogrammes que la famille est constituée de spécialistes de régions semi-arides et que des évènements de vicariance sont responsables de la distribution actuelle des espèces.

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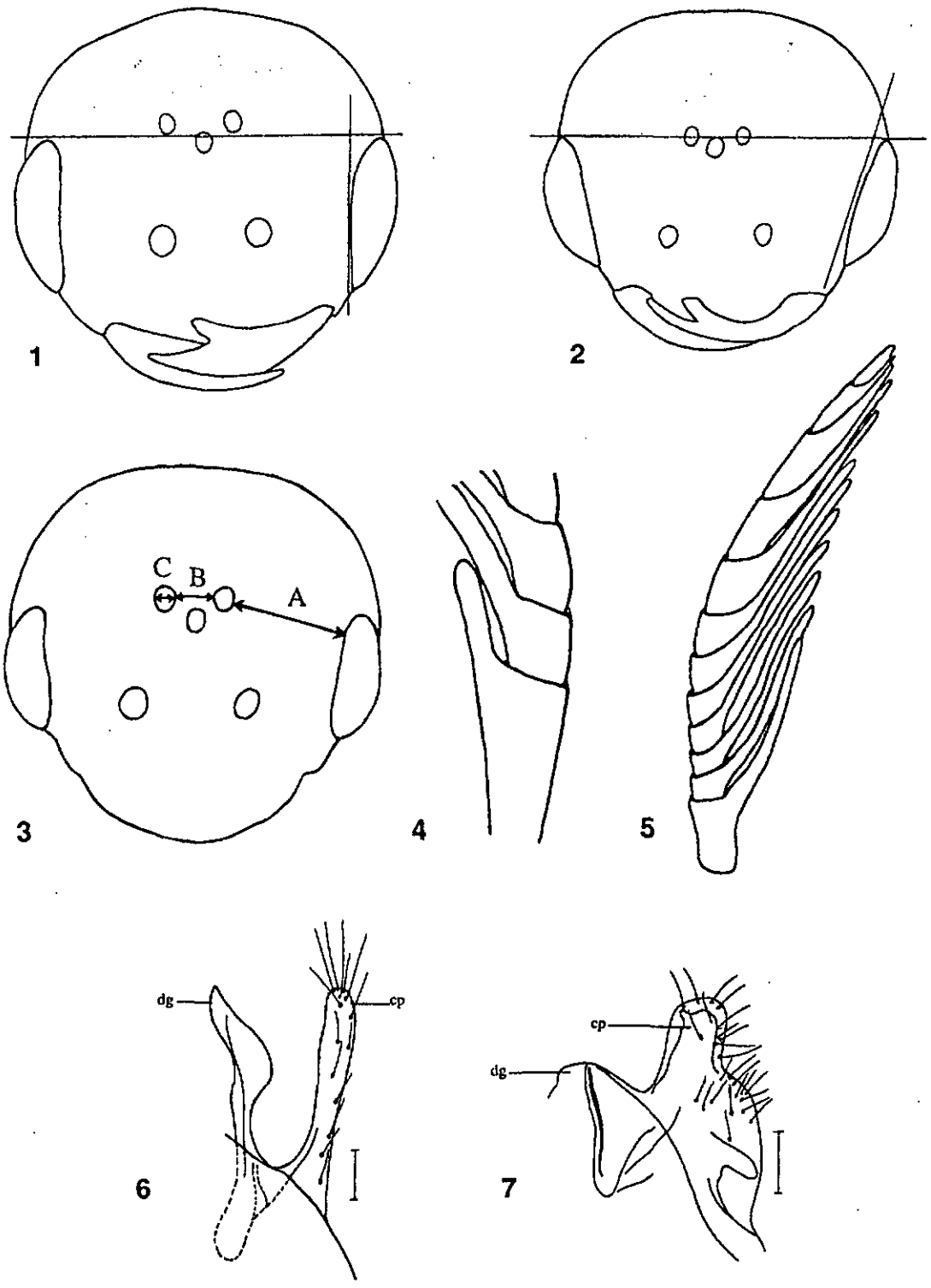
Table 1. Comparative terminology of male genitalia

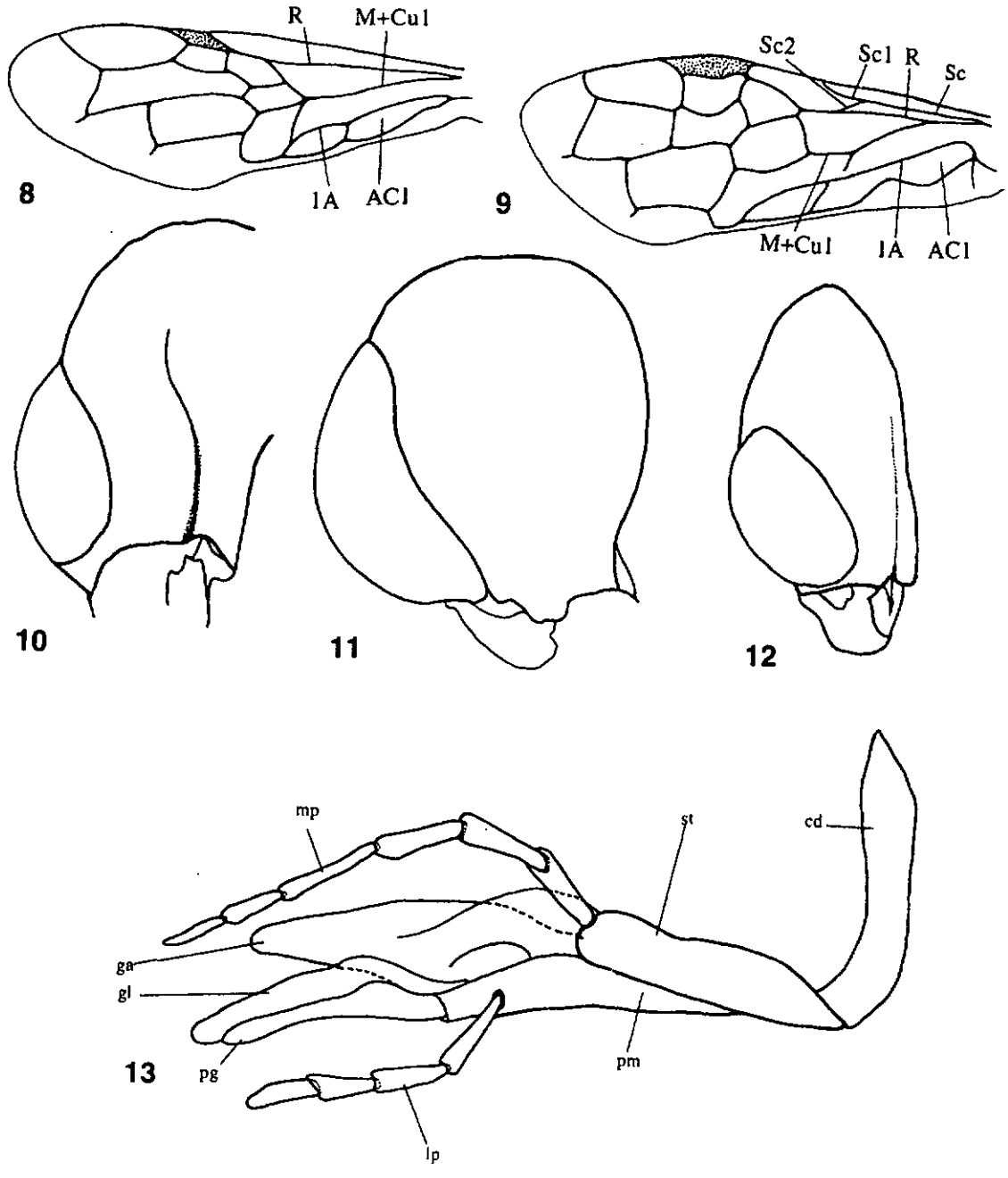
Snodgrass (1941)	Ross (1945)	Smith (1970)	Gauld & Bolton (1988)	present work
basal ring	gonocardo	gonobase	basal ring	gonocardo
basiparameres	gonostipes	gonocoxite 9	parameres	gonostipes
parameres	harpes	gonostyli	parameres	gonostyli
cupping disks	gonomaculae	cupping discs	cupping discs	gonomaculae
parapenial lobes	parapenial lobes	parapenial lobes	parapenial lobes	parapenial lobes
volsellae	volsellae	volsellae	volsellae	volsellae
digitus	distivolsella	digitus	gonolacina	digitus
cuspis	apiceps	cuspis	distivolsella	cuspis
aedeagus	penis valves	gonapophysis 9	aedeagus	penis valves
apodema	valvura	ventral ramus	undefined	aedeagal
aedeagalis		and rhachis		apodemes

Table 2. Data set for Megalodontidae species

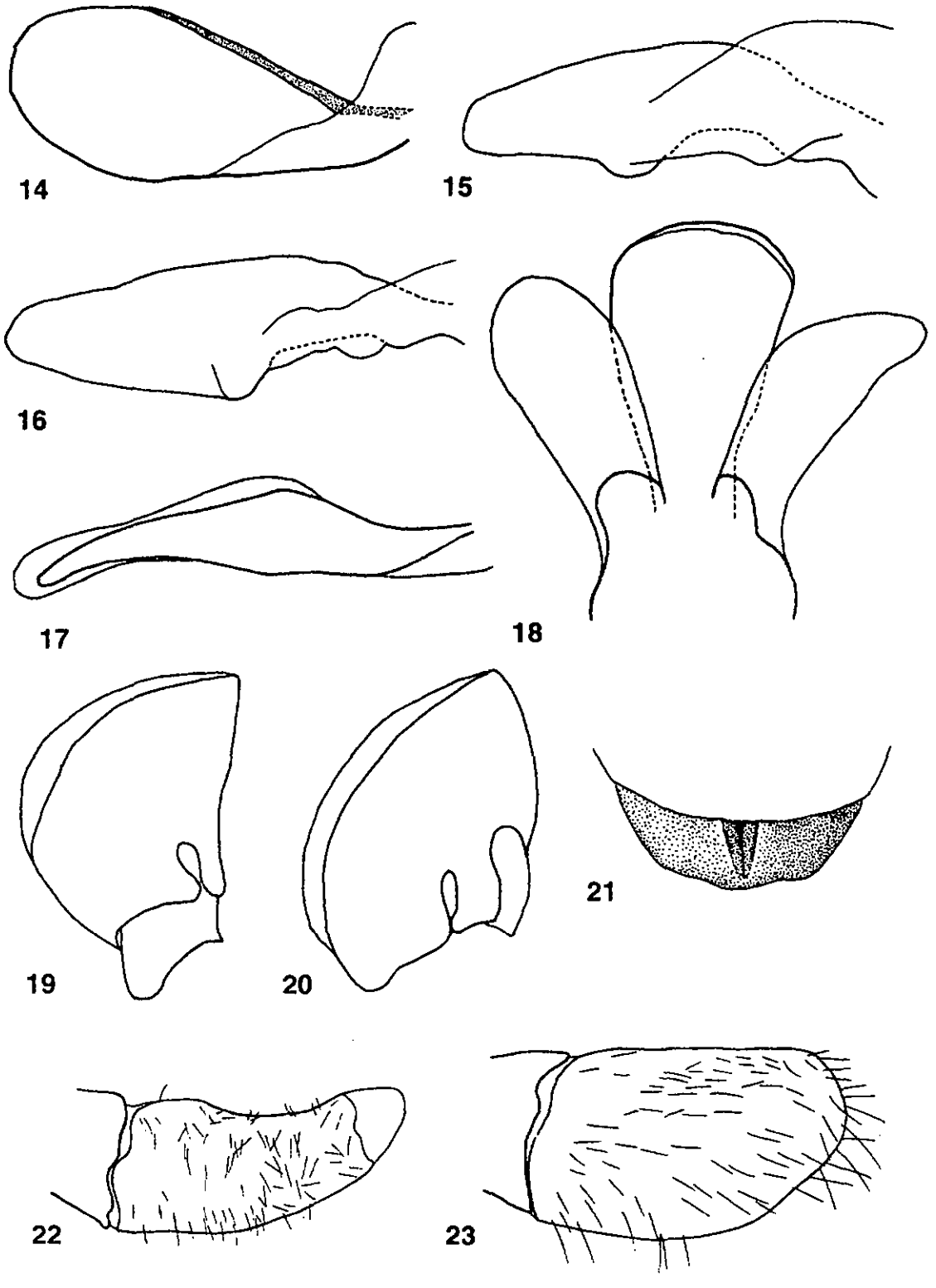
	12345 67890 12345 67890 12345 67890 12345 678
	1 2 3
bucephalus	13110 11002 00100 30410 00000 21012 01313 001
capitalatus	13100 10002 11100 30010 0?000 21212 01213 001
cephalotes	13100 10002 11100 61500 11000 32312 02313 001
escalerai	13100 10002 10100 10100 00000 11102 02002 000
eversmanni	13100 10002 10000 10100 00000 12302 01002 001
fabricii	13101 10002 01000 60500 00000 33313 01313 001
flabellicornis	13100 10002 01100 20200 00000 12211 01002 001
gratiosus	13100 10002 11100 30020 00000 21213 01213 001
interruptus	13110 10002 11100 40300 00000 32303 01?03 101
jucundus	12100 10002 11100 20300 00000 10003 00001 001
judaicus	00110 00002 00000 41010 00101 10320 10003 001
kuznetzovi	00000 00110 00100 01000 00101 00001 01002 000
lacourti	13100 11010 00200 30400 00000 ?1103 02303 001
levaillantii	0?000 00010 0???? ????? ?0??1 ?00?0 01213 000
luteiventris	13100 10002 11100 20200 00000 12113 02002 001
merceti	00000 00010 00200 01000 00101 10001 01003 000
nitens	11100 00011 00111 70600 01102 00000 10102 000
olivieri	11010 00012 11111 70601 01100 00000 00101 000
parvus	11120 00002 01100 20100 10000 12210 00001 111
phaenicius	11000 00002 00311 70601 00100 10001 01101 000
quinquecinctus	13110 00002 11100 40300 00000 ?0001 00003 101
reitteri	13100 100?2 00100 11100 1?000 10003 01002 001
skorniakowii	13010 00002 00011 70770 00000 ?2213 02100 001
spiraeae	11010 01002 0?100 40300 0?000 30102 01003 101
turcicus	13100 10002 11100 50500 11000 32313 02213 001
xanthosomus	01000 01001 00211 70600 01112 00001 01102 001
sp.1	13100 10002 00100 20200 01100 22213 01213 001
sp.2	13100 10002 10000 60200 01110 32313 01212 001
sp.3	13100 10002 11100 20200 10000 11211 01002 001
sp.4	13110 10002 00100 30020 00000 22112 02213 001
sp.5	13111 10002 10100 60200 00000 ?2112 02202 001
outgroup (dummy)	00000 00000 00000 00000 00000 00000 00000 000
outgroup (Pamph.)	00000 ?00?? 0?00? ?0?00 00010 ?0301 00??3 ?00



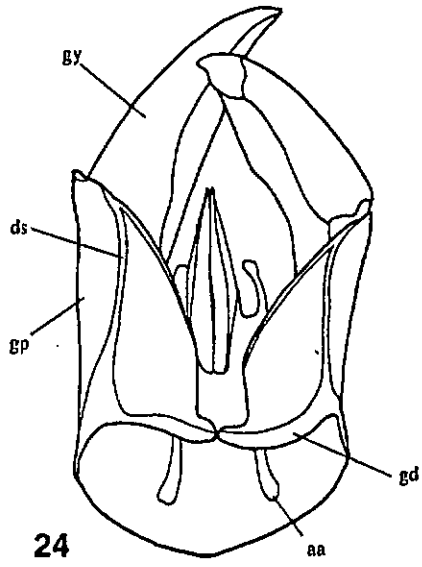
FIGS 1-7. 1: Eye angle straight or vertical. 2: Eye angle inclined or convergent. 3: Vertex of head showing distances A, B, C. 4: *levaillantii*; third antennal segment and basal flagellar segments. 5: *kuznetzovi*; antenna, except scape and pedicel. 6: *cephalotes*; digitus (dg) and cuspis (cp). 7: *phaenicius*; digitus (dg) and cuspis (cp).

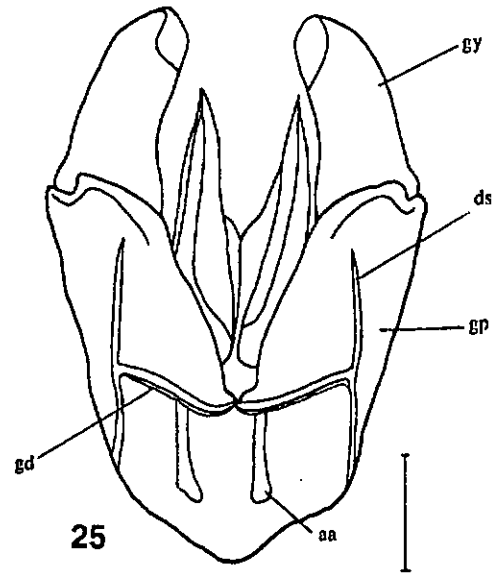


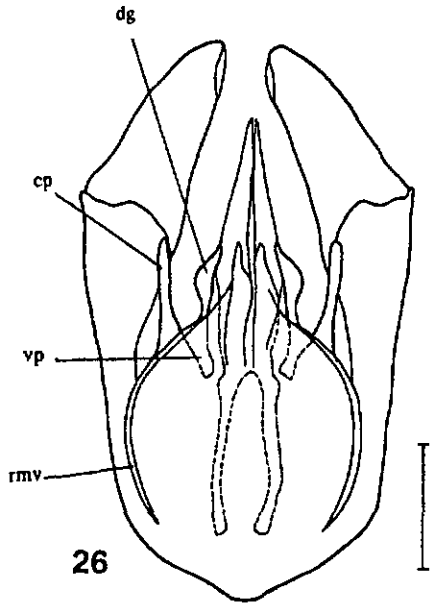
FIGS 8-13. 8. *Megalodontes* sp.; left forewing. 9. *Pamphilius* sp.; left forewing. 10: Genal carina present. 11: Genal carina absent. 12: Genal carina obsolete. 13. *flabellicornis*; mouthparts laterally.

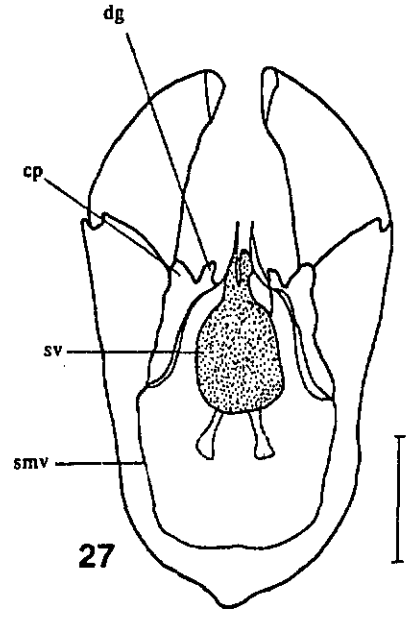


FIGS 14-23. 14: Galea swollen. 15: Galea slightly elongate. 16: Galea elongate. 17: Glossa and paraglossa slightly downwardly curved apically. 18: *merceti*; apex of prementum, glossa and paraglossae viewed ventrally. 19: Hind-coxal apical incision open. 20: Hind-coxal apical incision closed. 21. *luteiventris*; tergum 8 dorsally. 22: *merceti*; gonostylus. 23. *Megalodontes* sp.n.4; gonostylus.

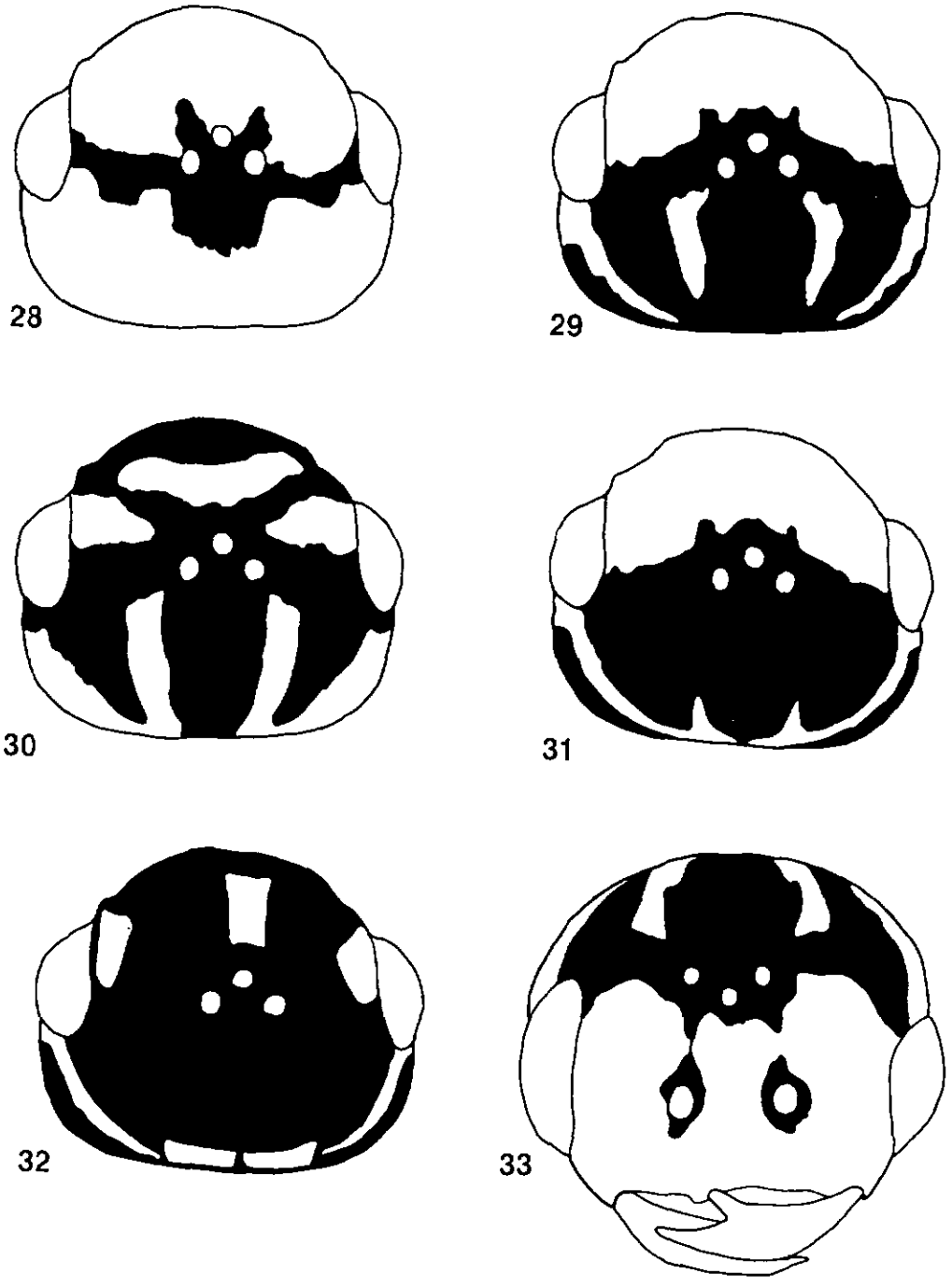




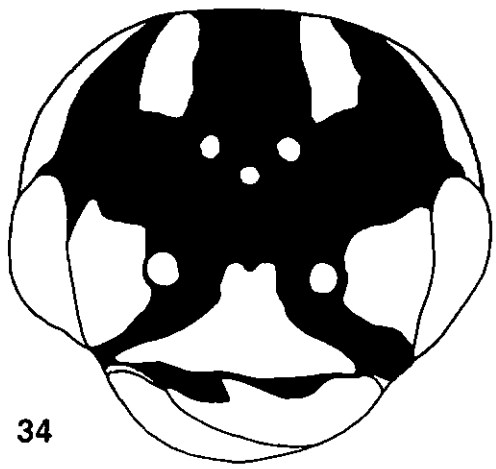




FIGS 24-27. Male genitalia. 24. *merceti*; dorsal. 25: *capitalatus*; dorsal. 26: *cephalotes*; ventral. 27: *olivieri*; ventral. (Legends in text under 'Morphological terminology'.)



FIGS 28-33. Colour syndromes. 28: olivieri; vertex. 29: flabellicornis; vertex. 30: flabellicornis; vertex (variant). 31: bucephalus; vertex. 32: cephalotes: vertex. 33: olivieri; facial.



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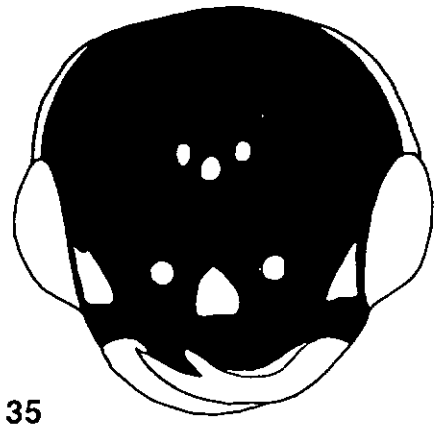

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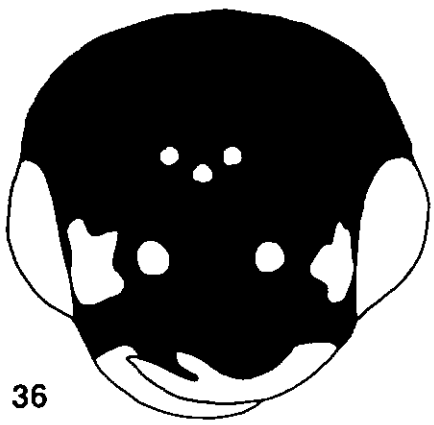

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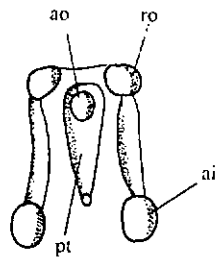

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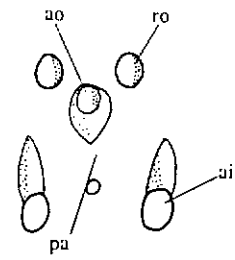

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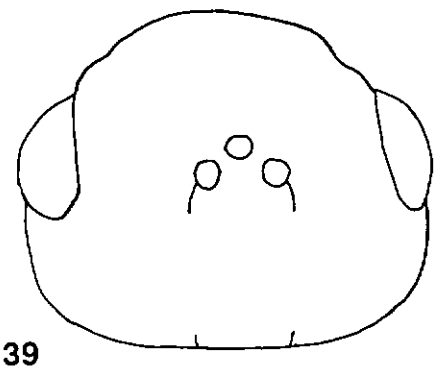

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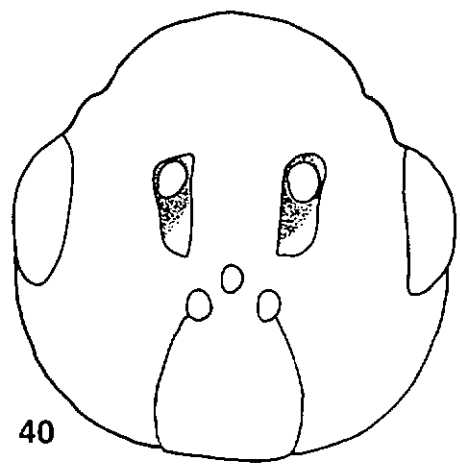
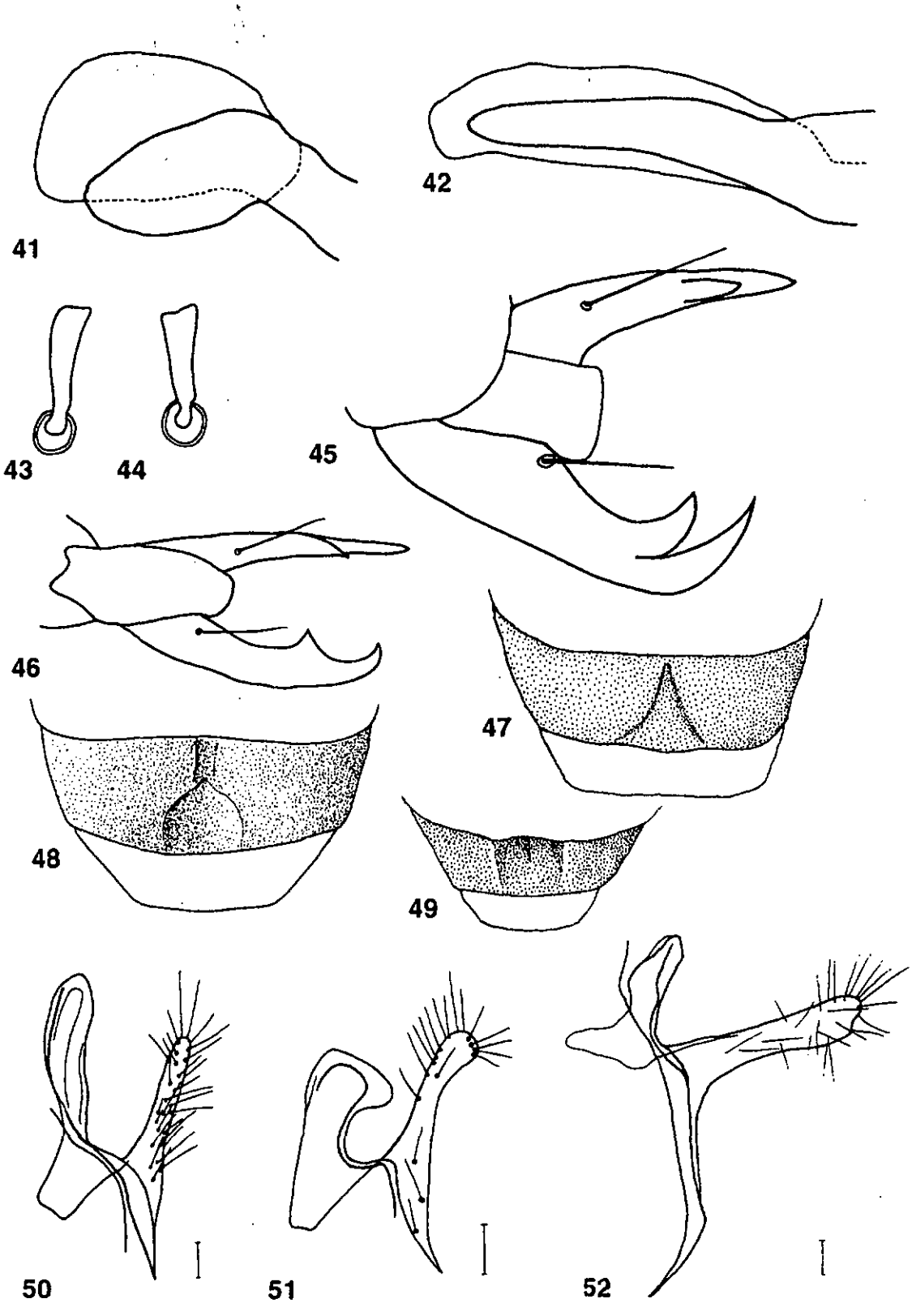
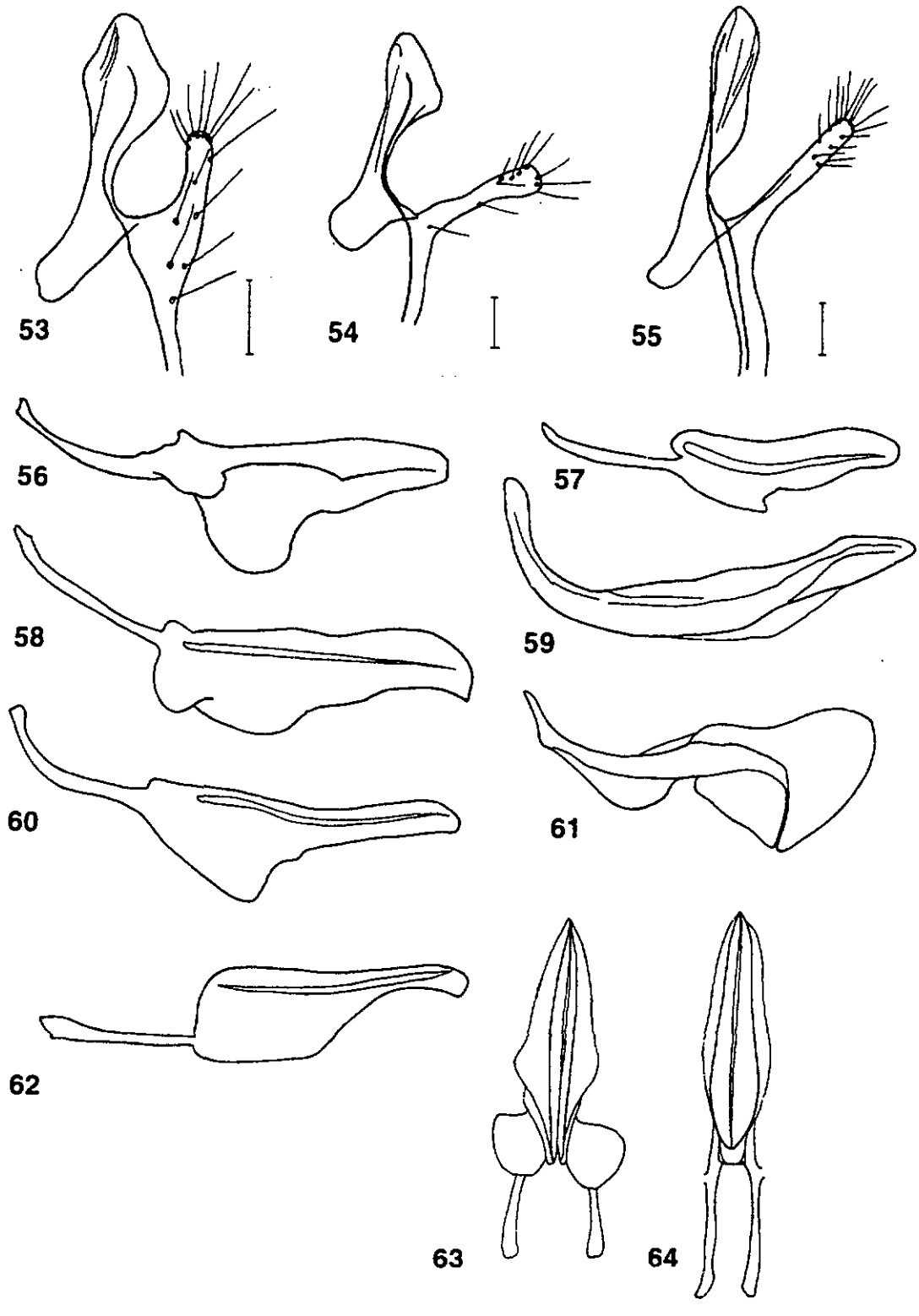


40

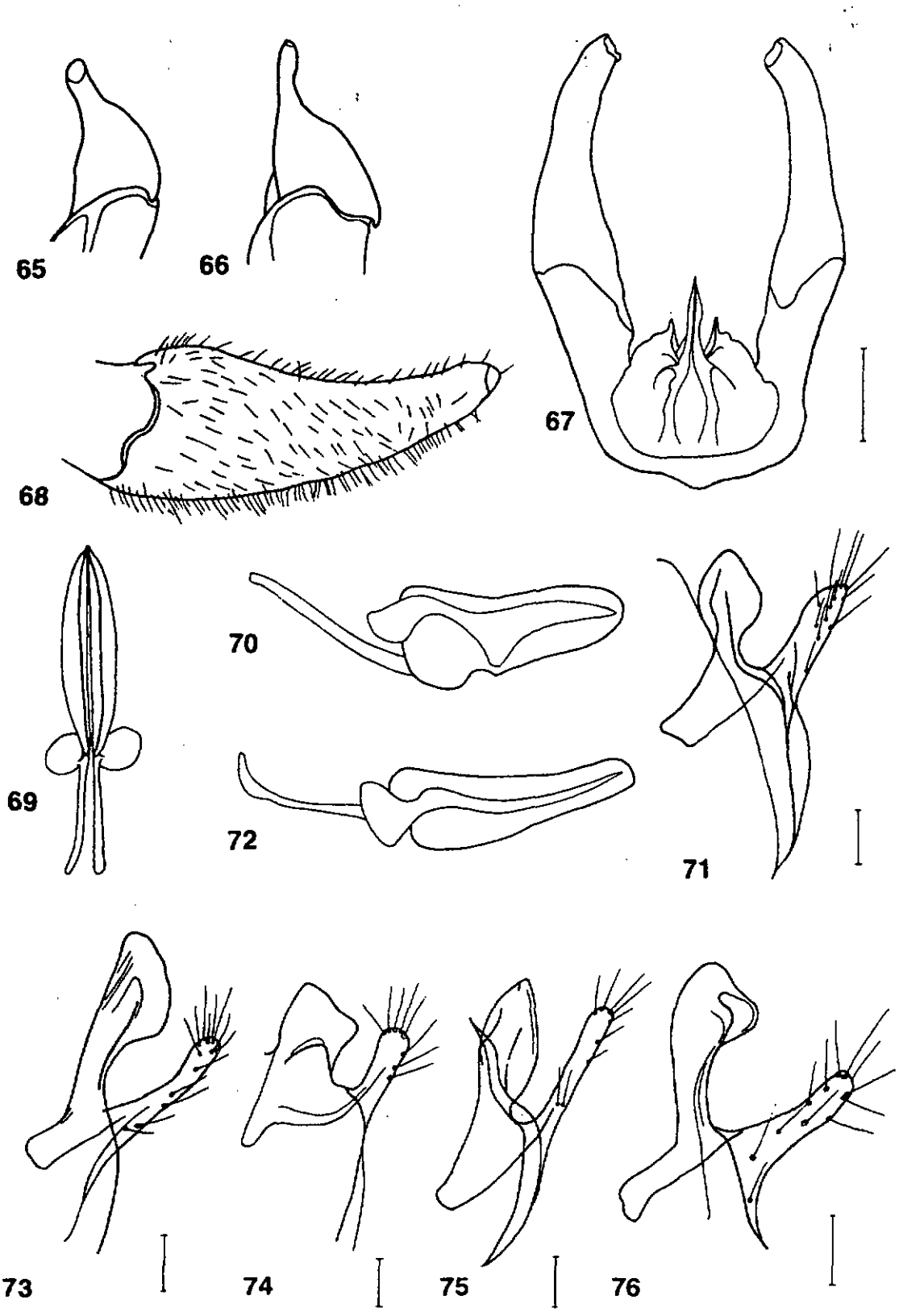
FIGS 34-40. 34: Facial colour syndrome; flabellicornis. 35: Facial colour syndrome; cephalotes. 36: Facial colour syndrome; fabricii. 37: Pentagonal area with trench. 38: Pentagonal area planar. 39: Post-ocellar striae incomplete. 40. Post-ocellar striae complete.



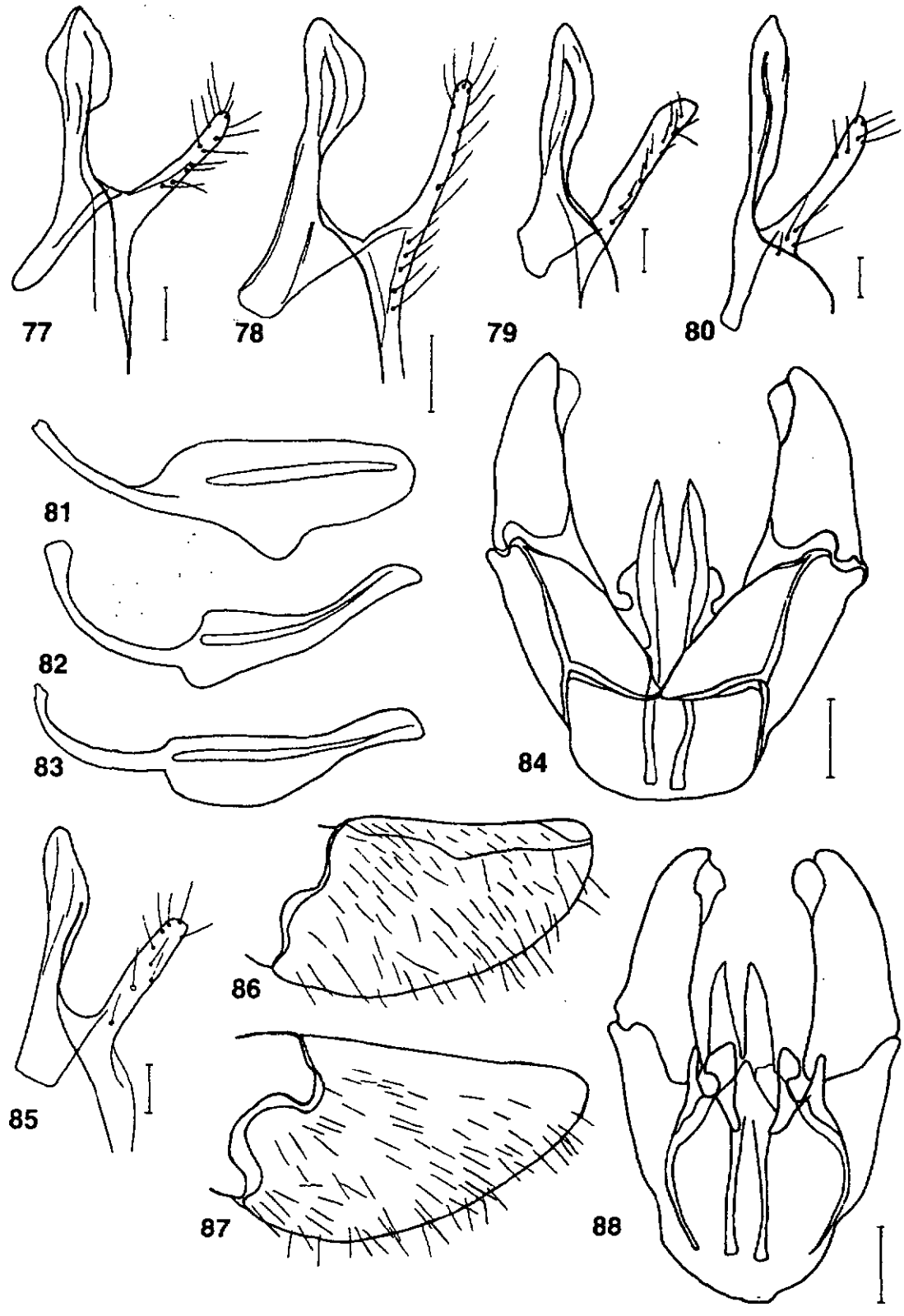
FIGS 41-52. 41: Glossa and paraglossa strongly swollen. 42: Glossa and paraglossa elongate. 43: *reitteri*; scape. 44: *eversmanni*: scape. 45: Teeth of tarsal claws proximal. 46: Teeth of tarsal claws widely separated. 47-49: male tergum 8, viewed dorsally. 47: *kuznetzovi*. 48: *merceti*. 49: *turcicus*. 50-52: digitus and cuspis. 50: *eversmanni*. 51: *bucephalus*. 52: *kuznetzovi*.



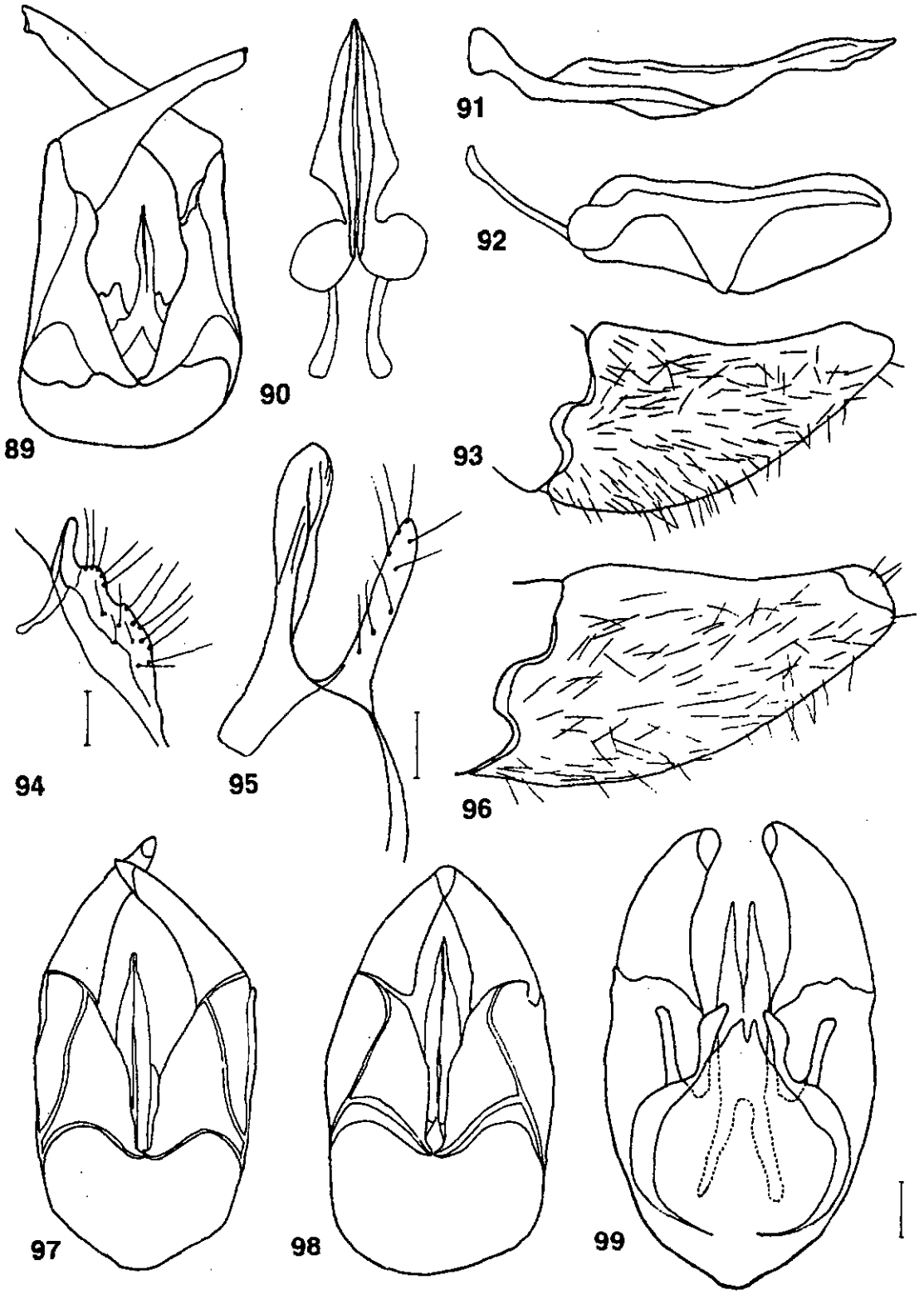
FIGS 53-64. 53-55: Digitus and cuspis. 53: *interruptus*. 54: *turcicus*. 55: *jucundus*. 56-61: Penis valve in lateral view. 56: *kuznetzovi*. 57: *cephalotes*. 58: *eversmanni*. 59: *nitens*. 60: *jucundus*. 61: *skorniakowii*. 62: *bucephalus*. 63-64: Penis valves in dorsal view. 63: *capitalatus*. 64: *bucephalus*.



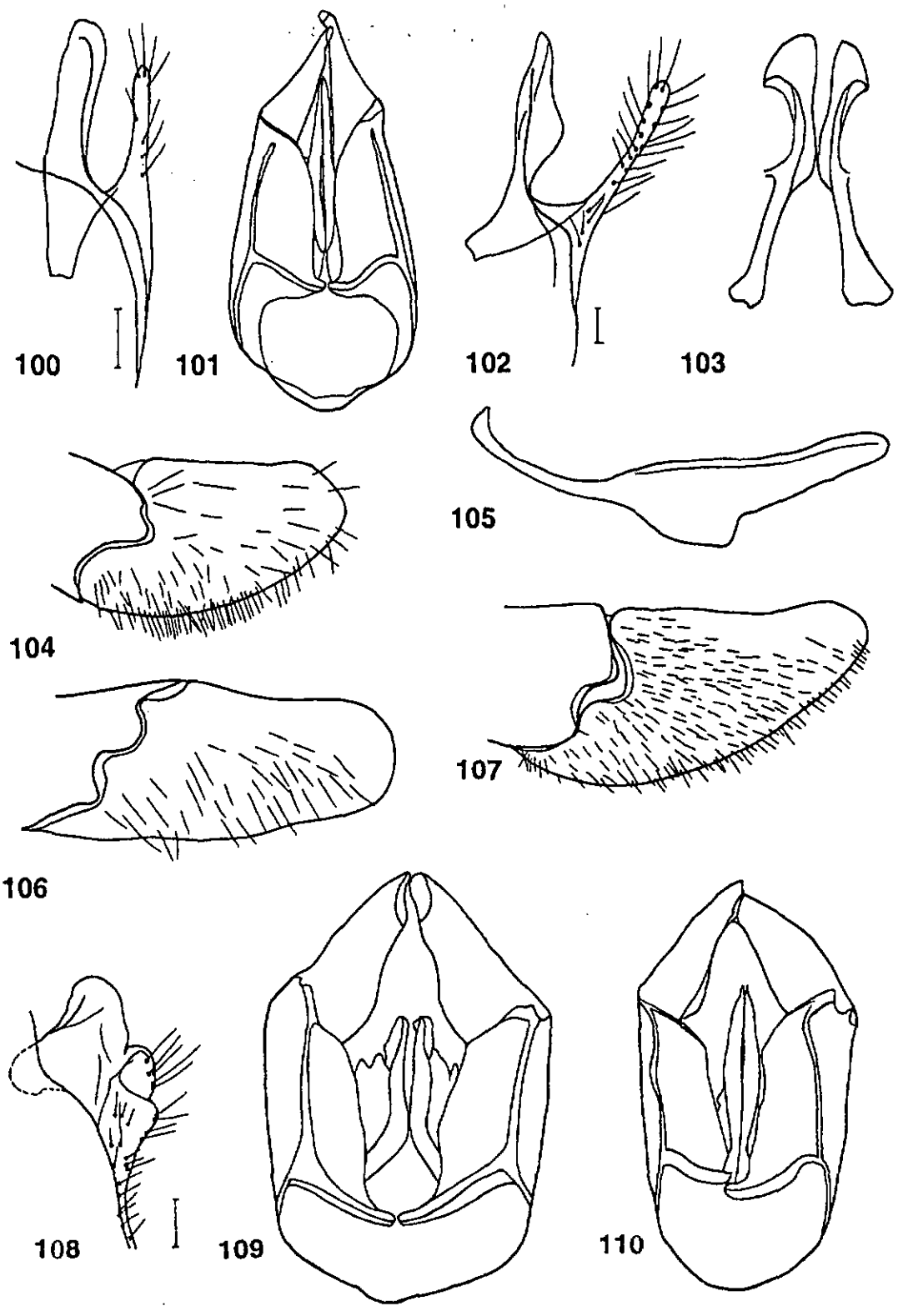
FIGS 65-76. 65 and 66: *phaenicius*; gonostylus, dorsally and laterally, respectively. 67-68: *xanthosomus*. 67: Genitalia ventrally. 68: Gonostylus laterally. 69: *lacourti*; penis valves and aedeagal apodemes dorsally. 70-71: *capitalatus*. 70: Penis valve in lateral view. 71: Digitus and cuspis. 72-73: *lacourti*. 72: Penis valve in lateral view. 73: Digitus and cuspis. 74-76: Digitus and cuspis. 74: *gratiosus*. 75: *Megalodontes* sp.4. 76: *quinquecinctus*.



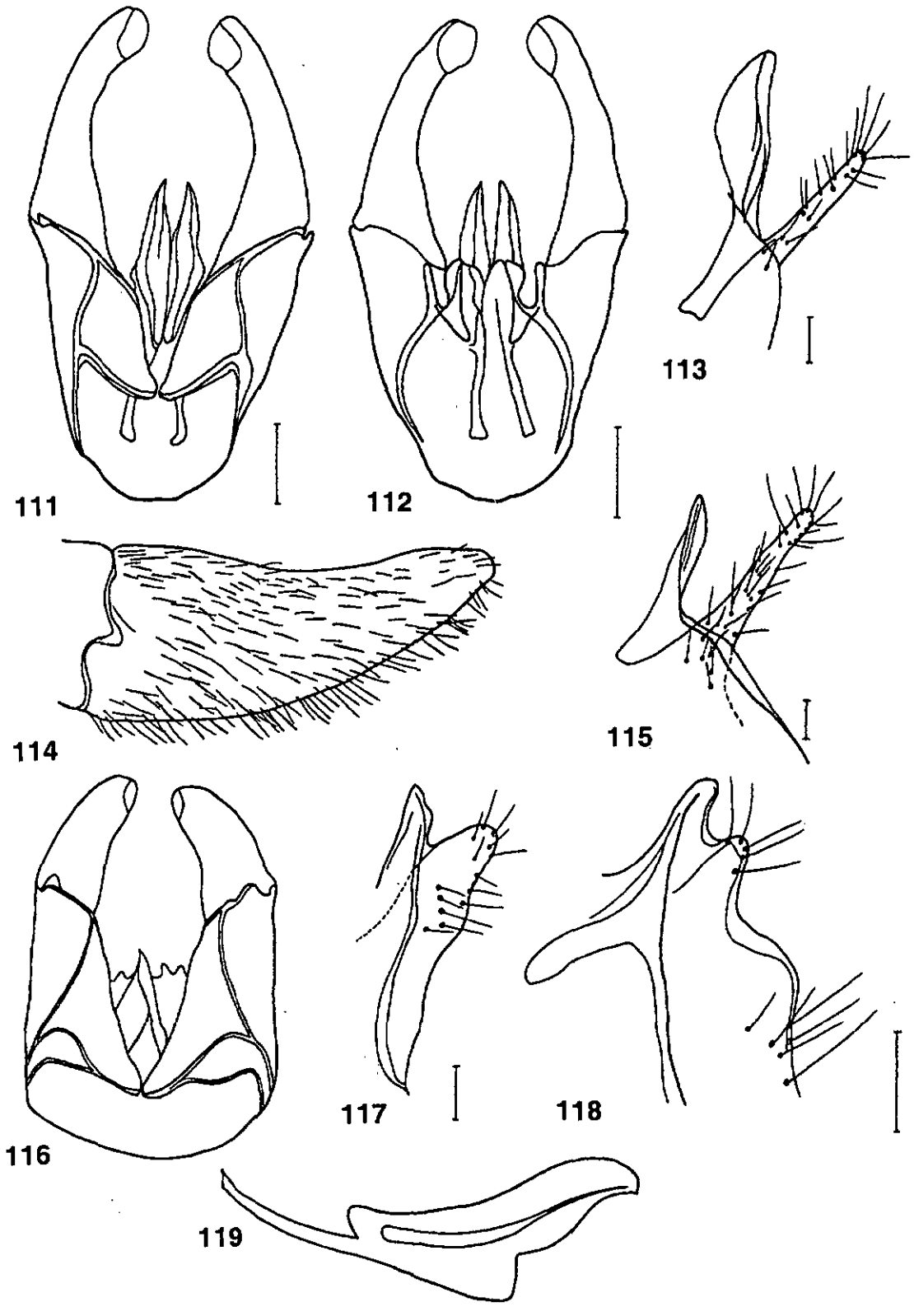
FIGS 77-88. 77-80: Digitus and cuspis. 77: *spiraeae*. 78: *fabricii*. 79: *Megalodontes* sp.n.5. 80. *Megalodontes* sp.1. 81-83: Penis valve in lateral view. 81: *fabricii*. 82: *Megalodontes* sp.5. 83: *Megalodontes* sp.n.2. 84: *bucephalus*; genitalia in dorsal view. 85: *Megalodontes* sp.2; digitus and cuspis. 86-87: Gonostylus. 86: *capitalatus*. 87: *cephalotes*. 88: *bucephalus*; genitalia in ventral view.



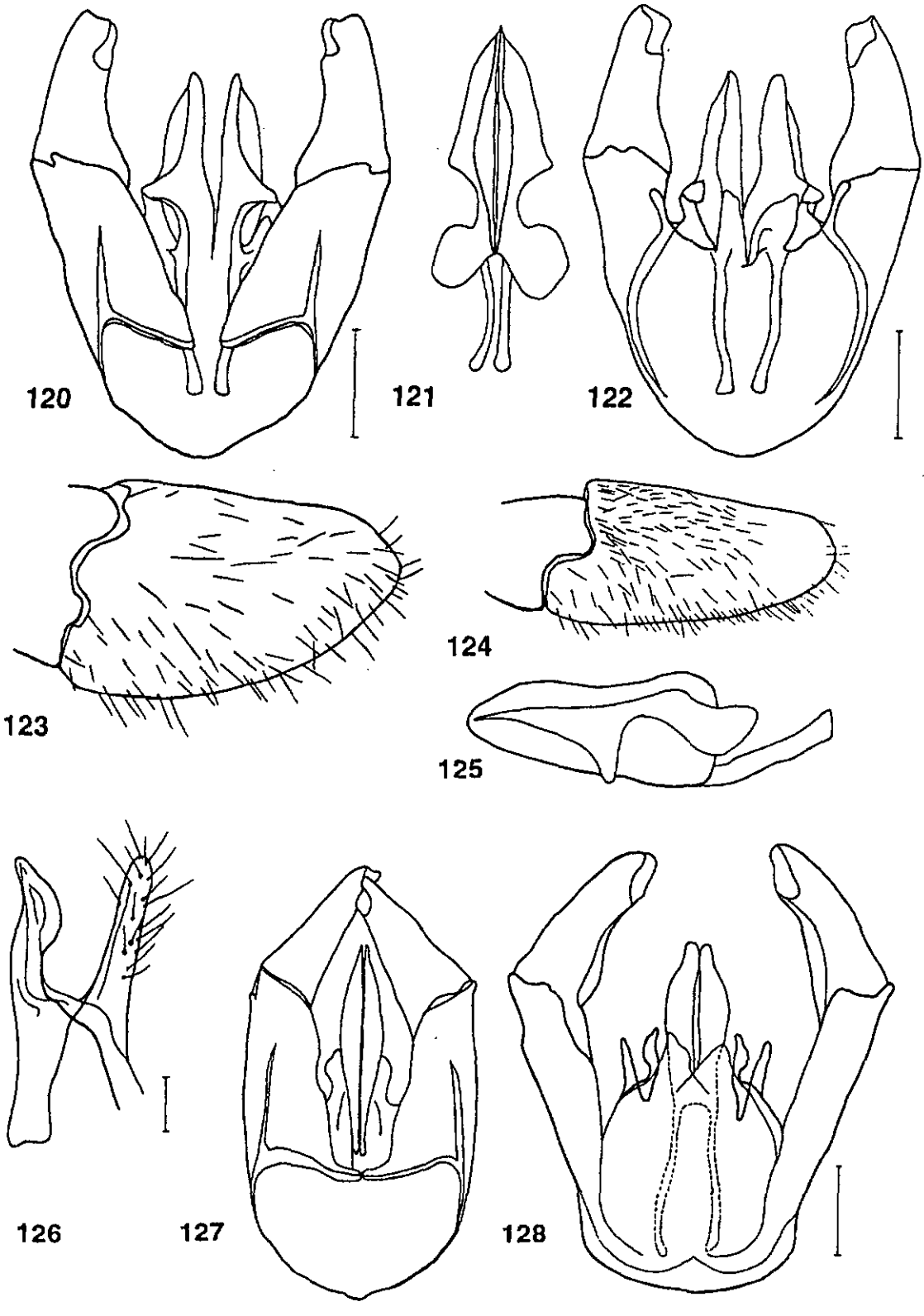
Figs 89-99. 89: *xanthosomus*; genitalia in dorsal view. 90: *Megalodontes* sp.4; penis valves in dorsal view. 91-92: Penis valve in lateral view. 91: *xanthosomus*. 92: *Megalodontes* sp.4. 93: *Megalodontes* sp.2; gonostylus. 94-95: Digitus and cuspis. 94: *xanthosomus*. 95: *Megalodontes* sp.3. 96: *Megalodontes* sp.5; gonostylus. 97-98. Genitalia in dorsal view. 97: *Megalodontes* sp.2. 98: *Megalodontes* sp.5. 99: *Megalodontes* sp.5; genitalia in ventral view.



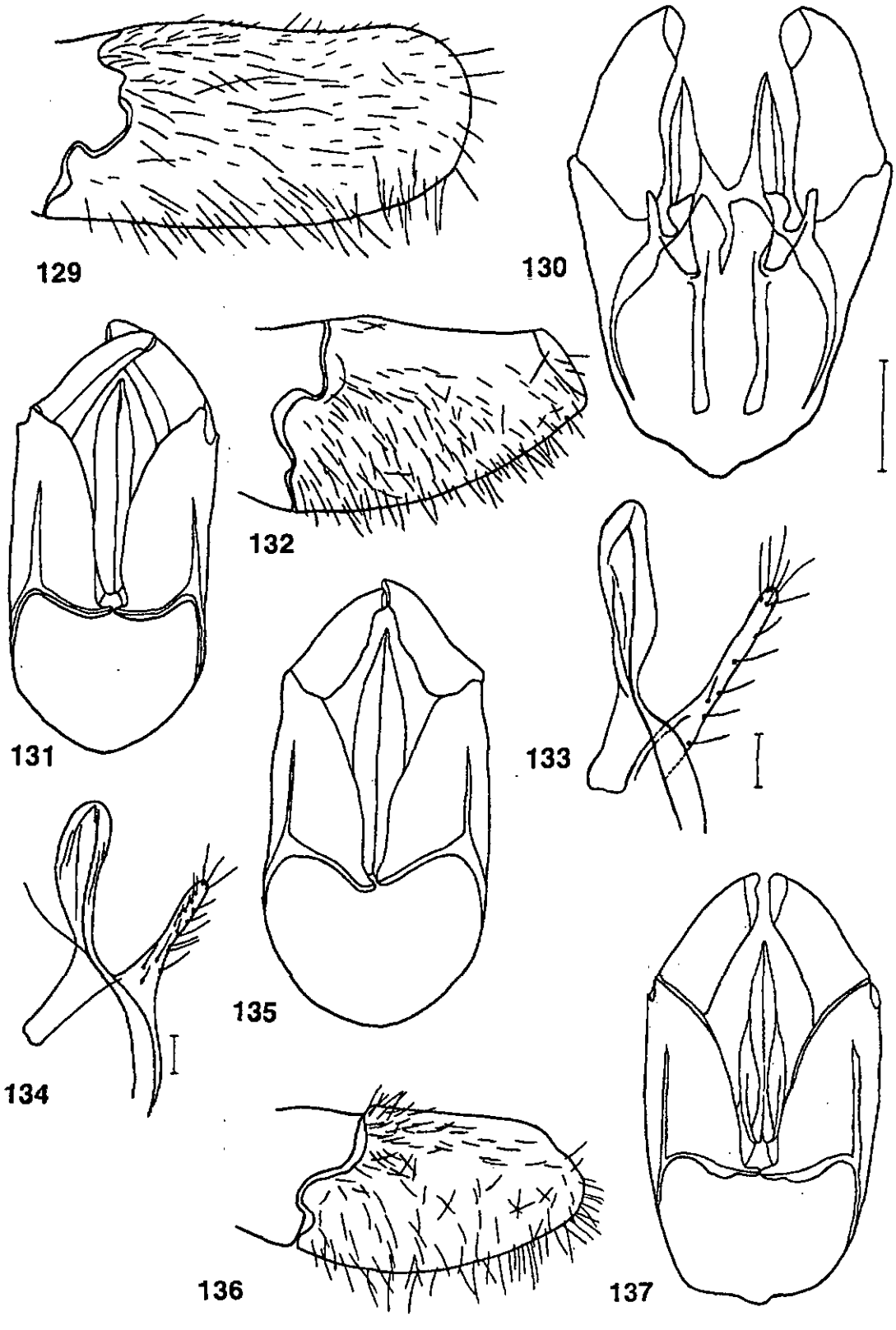
FIGS 100-110. 100: *parvus*; digitus and cuspis. 101: *quinquecinctus*; genitalia in dorsal view. 102: *reitteri*; digitus and cuspis. 103: *skorniakowii*; penis valves in dorsal view. 104-105: *quinquecinctus*. 104: Gonostylus. 105: Penis valve in lateral view. 106: *skorniakowii*; gonostylus. 107. *spiraeae*: gonostylus. 108-109: *skorniakowii*. 108: Digitus and cuspis. 109: Genitalia in dorsal view. 110: *spiraeae*; genitalia in dorsal view.



FIGS 111-119. 111-112: *lacourti*; genitalia. 111: Dorsal view. 112: Ventral view. 113: *luteiventris*; digitus and cuspis. 114: *lacourti*; gonostylus. 115: *merceti*; digitus and cuspis. 116: *nitens*; genitalia in dorsal view. 117-118: Digitus and cuspis. 117: *olivieri*. 118: *nitens*. 119: *parvus*; penis valve in lateral view.



FIGS 120-128. 120-123: *gratiosus*. 120: Genitalia in dorsal view. 121: Penis valves in dorsal view. 122: Genitalia in ventral view. 123: Gonostylus. 124: *interruptus*; gonostylus. 125: *gratiosus*; penis valve in lateral view. 126: *judaicus*; digitus and cuspis. 127-128: Genitalia in dorsal view. 127: *interruptus*. 128: *judaicus*.



FIGS 129-137. 129: *bucephalus*; gonostylus. 130: *capitalatus*; genitalia in ventral view. 131: *cephalotes*; genitalia in dorsal view. 132: *fabricii*; gonostylus. 133-134: Digitus and cuspis. 133: *flabellicornis*. 134: *escalerai*. 135-136: *flabellicornis*. 135: Genitalia in dorsal view. 136: Gonostylus. 137: *fabricii*; genitalia in dorsal view.

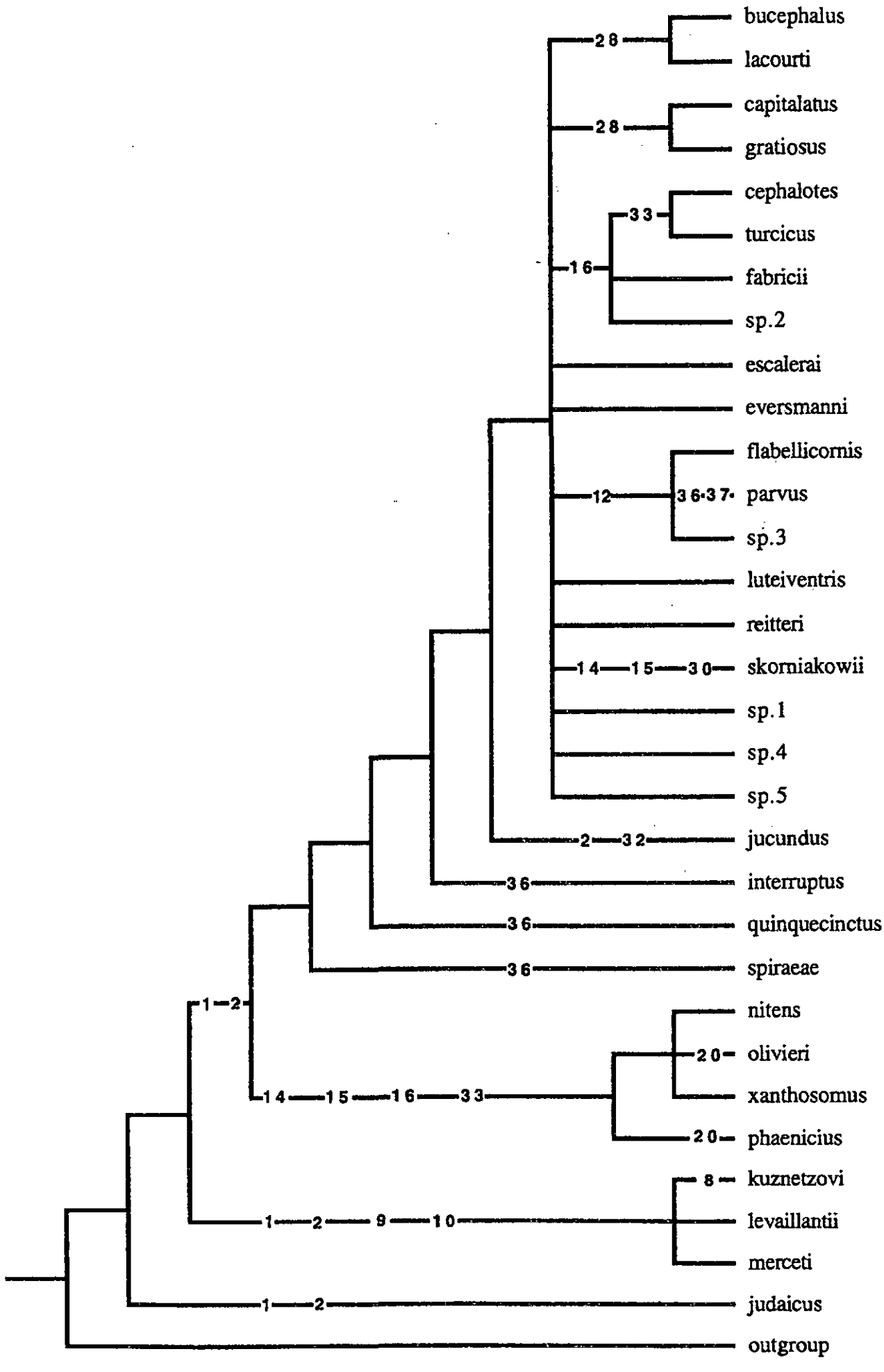


FIG. 138. Cladogram of Megalodontidae (Pamphiliidae outgroup). (Numbers refer to characters discussed in text.)

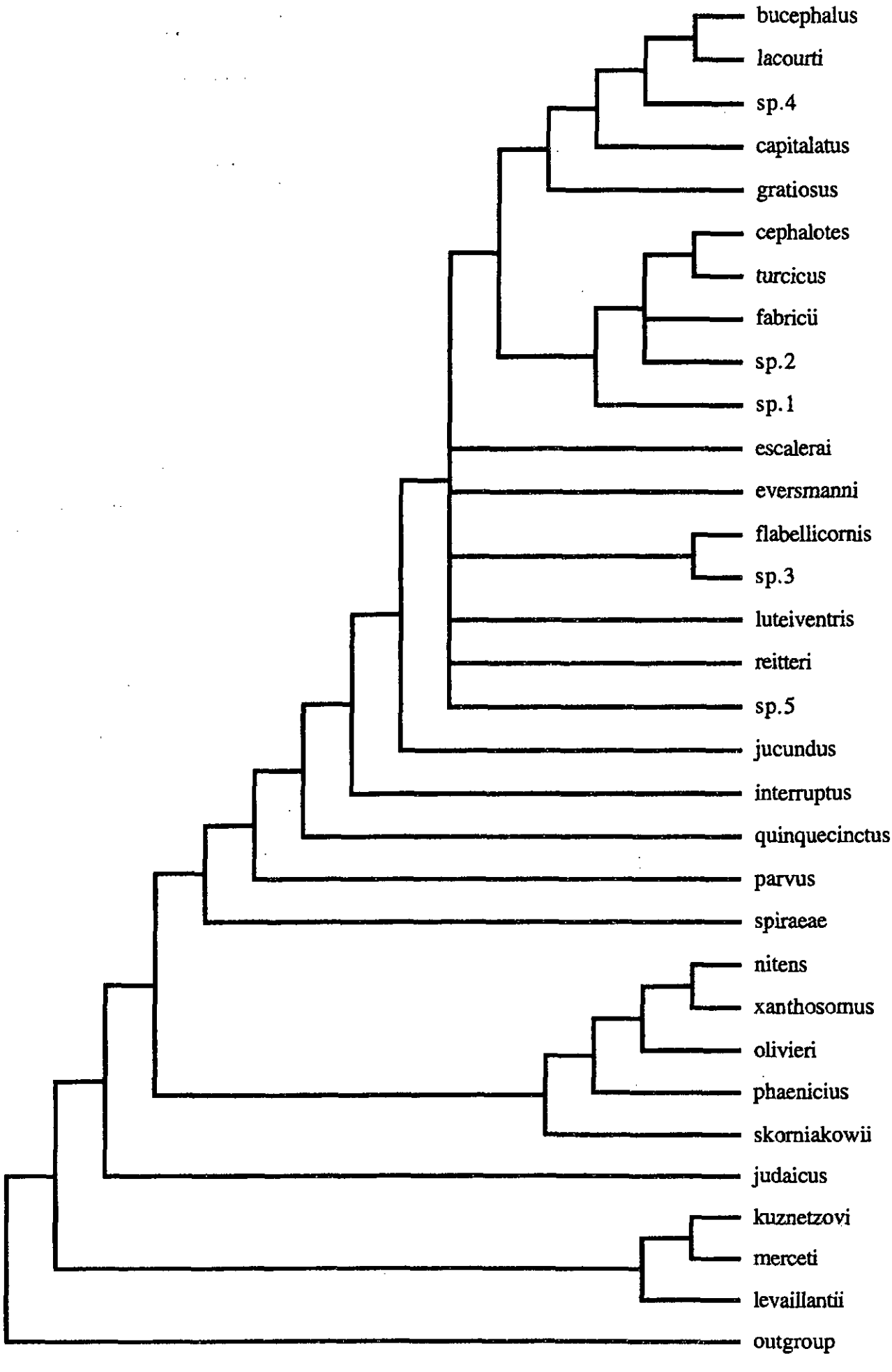


FIG. 139. Cladogram of Megalodontidae ('dummy' outgroup).

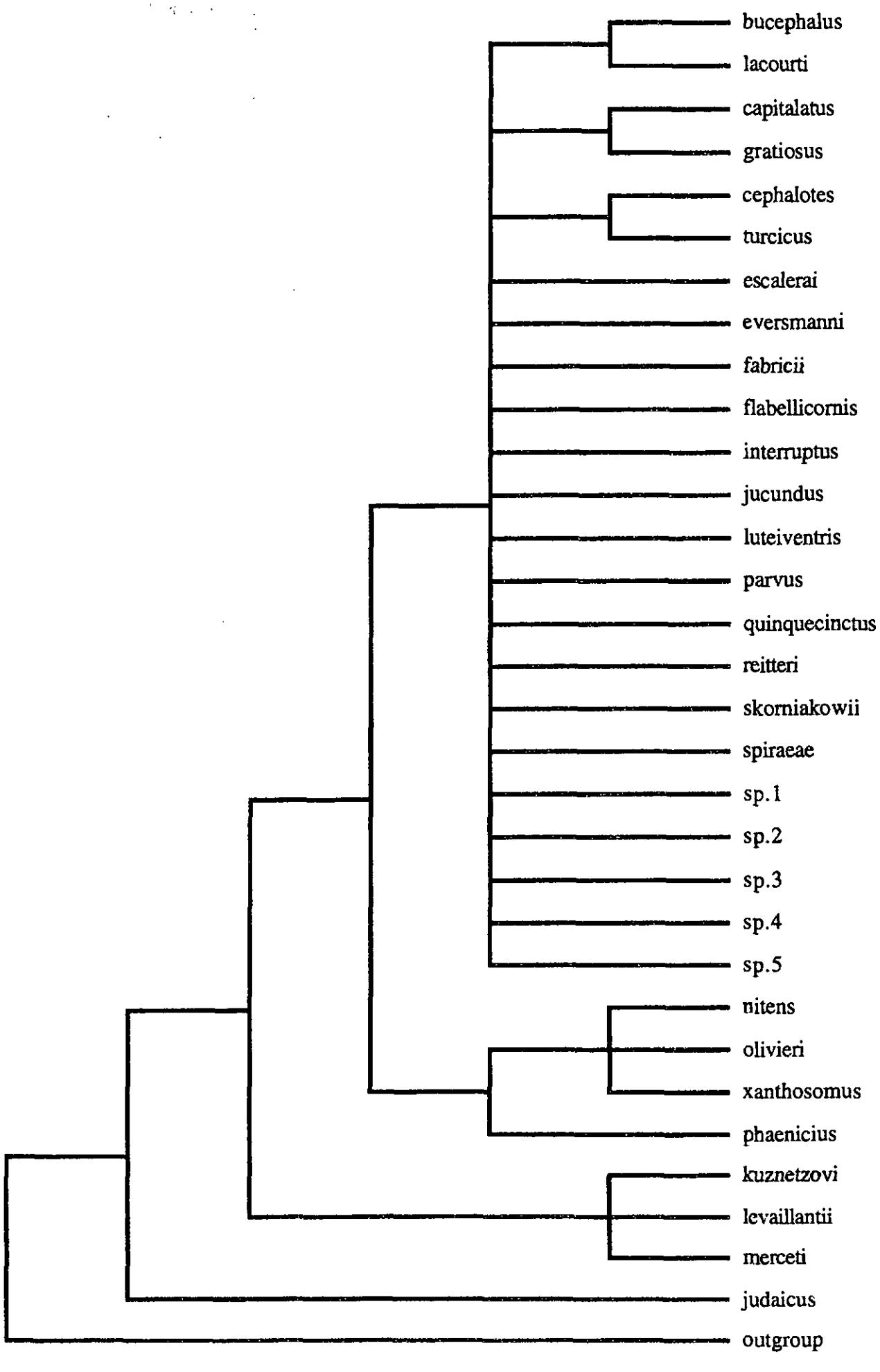


FIG. 140. Cladogram of Megalodontidae (Pamphiliidae outgroup) with characters 16 and 18 removed.

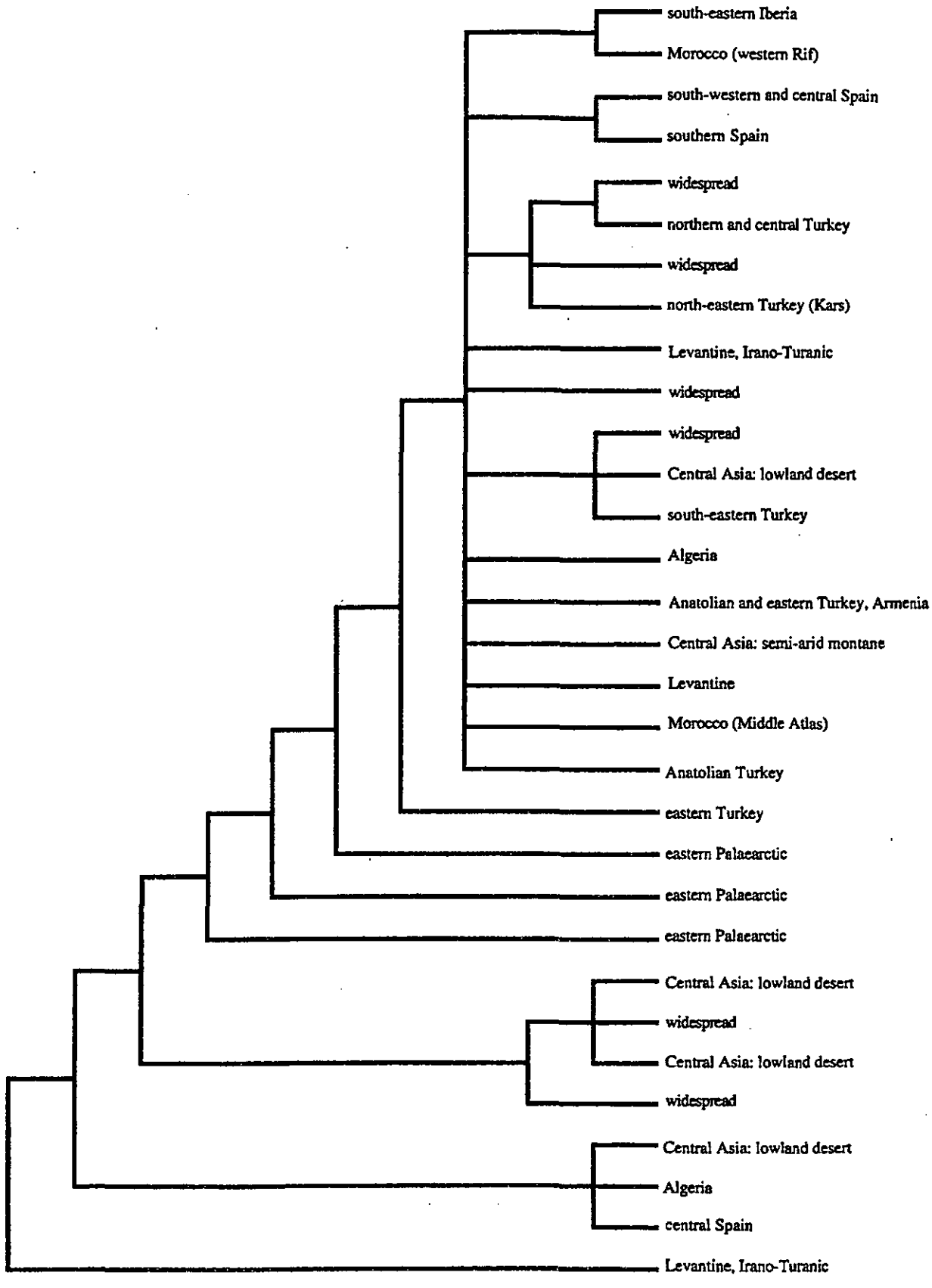


FIG. 141. Area cladogram of Megalodontidae (Pamphiliidae outgroup).