

**Revision of the fossil “mantid” and “ephemerid” species
described by Piton from the Palaeocene of Menat (France)
(Mantodea: Chaeteessidae, Mantidae; Ensifera: Tettigoniodea)**

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**Mantodea, Ensifera, Ephemeroptera, Chaeteessidae, Mantidae, Choeradodinae, Empusidae,
Tettigoniodea, fossil, Palaeocene, France, redescription, biogeography**

Abstract. Some fossil insects from the Palaeocene of Menat (France), described by Piton as Mantodea, but also Ephemeroptera are revised. The presence of the Neotropical mantid family Chaeteessidae in the Palaeocene of France, inferred by Gratshev & Zherikhin, is confirmed. The presence in Menat of the mantid family Empusidae was an error of interpretation. The order Ephemeroptera is represented only by an undescribed nymph. Biogeographic implications are discussed briefly.

INTRODUCTION

Mantodea are very rare in the fossil record. Gratshev & Zherikhin (1993) counted less than two dozen fossil mantids described so far and add that nearly all the taxa need revision. They described several new taxa from the Upper Cretaceous and Oligocene of Siberia and indicated that the fossil genus and species *Arvernineura insignis* Piton, 1940, from the Palaeocene of Menat (Puy-de-Dôme, France), attributed by Piton (1940) to the Ephemeroptera, is a genuine member of Mantodea, Chaeteessidae. The extinct and Recent genera of Chaeteessidae were keyed by Gratshev & Zherikhin (1993) but they could not examine the type specimen of *Arvernineura insignis*, because its location was unknown.

Fortunately, the main part of Piton's collection, including the holotype of *A. insignis* and all other species attributed by Piton to the Mantodea, is now deposited in the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris (MNHN). This material has been examined. Piton's figure of *Arvernineura*, used by Gratshev & Zherikhin for their revision, is incomplete and partly incorrect. The donation of another well-preserved fossil mantid from Menat and the finding of another specimen from the same place, both probably belonging to the same species of the genus *Arvernineura*, provide more information about the genus. Redescriptions of this interesting genus and species and of other fossil Mantodea described by Piton are presented.

Nomenclature of wing venation of the Mantodea and the phylogeny of the Blattoneoptera follows that proposed by Kukalová-Peck (1983) and Kukalová-Peck & Peck (1993) rather than that of Sharov (1962), or Gratshev & Zherikhin (1993).

For the Ensifera: Tettigoniodea, the nomenclature of wing venation follows that of Kukalová-Peck (1983) rather than Sharov (1968). Tables 1 and 2 compare the diverse nomenclatures of the mantid wing venation.

TABLE 1. Nomenclature of forewing venation of the Mantodea.

Giglio-Tos (1927)	Ragge (1955)	Smart (1956)	Sharov (1962)	Beier (1968)	Ramsay (1990)	present designation
veine costale	C	C	C	C	C	C (+ScA)
v. médiastine	Sc	Sc	Sc	Sc	Sc	ScP (-)
v. radiale ant.	R1 (+Rs)	R	R	R	R1 (+Rs)	R+MA (+)
v. radiale post	M	M	MA	M	MA+MP	MP (+)
v. ulnaire ant.	Cu1	Cu1	MP+CuA	Cu1	Cu1 (a+b)	CuA (-/+)
v. ulnaire post	Cu2	Cu2	CuP	Cu2	Cu2	CuP (-)
vena dividens	1A	Pcu	A1	Pcu	PCu	AA1+2 (+)
vena plicata	2A	IV	A2	A	1V	AA3+4 (+)
?	?	?	?	?	2V, 3V, 4V	AP

TABLE 2. Nomenclature of hindwing venation of the Mantodea.

Giglio-Tos (1927)	Ragge (1955)	Smart (1956)	Sharov (1962)	Beier (1968)	present designation
veine costale	C	C	C	C	C (+ScA)
v. médiastine	Sc	Sc	Sc	Sc	ScP
v. radiale ant.	R1	R	R	R	RA
v. radiale méd.	Rs	Rs	Rs	Rs	RP (+MA)
v. radiale post.	M	M	MA	M	MP
v. ulnaire ant.	Cu1	Cu1	MP+CuA	Cu1	CuA
v. ulnaire post.	Cu2	Cu2	CuP	Cu2	CuP
vena dividens	1A	Pcu	A1	A1 (Pcu)	AA3+4
aire anale	2A	2V	A2	A2	AP

Order Mantodea

Family Chaeteessidae Handlirsch, 1925

Archephemeridae Piton, 1940 (synonymised by Gratshev & Zherikhin, 1993).

The study of Gratshev & Zherikhin (1993) has increased greatly our knowledge of the palaeontological record of the Chaeteessidae. It was known by three living neotropical species only and there was no direct evidence that it was not a purely neotropical group. After the discovery of many fossil taxa from the Cretaceous and Oligocene of Asia and the reinterpretation of *Arvernineura* as a Chaeteessidae, it appears that this family has a more complex history and broader occurrence.

The type-genus is *Chaeteessa* Burmeister, 1838. The type-species of *Chaeteessa* is *C. filata* Burmeister, 1838 and the genus contains two other Recent neotropical species: *C. valida* (Perty, 1833) and *C. caudata* Saussure, 1871, all known from Brazil and Guyana.

Genus *Arvernineura* Piton, 1940

TYPE SPECIES: *Arvernineura insignis* Piton, 1940, monobasic.

Arvernineura insignis Piton, 1940

Arvernineura insignis Piton, 1940: 146–147, Fig. 22.

Arvernineura insignis: Gratshev & Zherikhin, 1993: 149–150.

HOLOTYPE. Specimen MNHN-LP-R.07020 (specimen 715, coll. Piton).
OTHER SPECIMENS. MNHN-LP-R.10427 (coll. Olivier), MNHN-LP-R.10428 (coll. Nel). Laboratoire de
Paléontologie du Muséum national d'Histoire naturelle de Paris.
TYPE LOCALITY. Menat, Puy-de-Dôme, France.
TYPE STRATA. Palaeocene, palaeolake, fossil Maar, spongeform-diatom rock.

PRESENTATION OF THE FOSSILS

Holotype R.07020. The main part of a forewing with the base and the apex missing, the anal area is apart from the rest of the wing.

Specimen R.10427. A thorax with the two forewings and the right hindwing attached. The right forewing is nearly complete but only the base of the left is preserved. The hindwing is very poorly preserved. The spines of the fore femora and tibiae are visible.

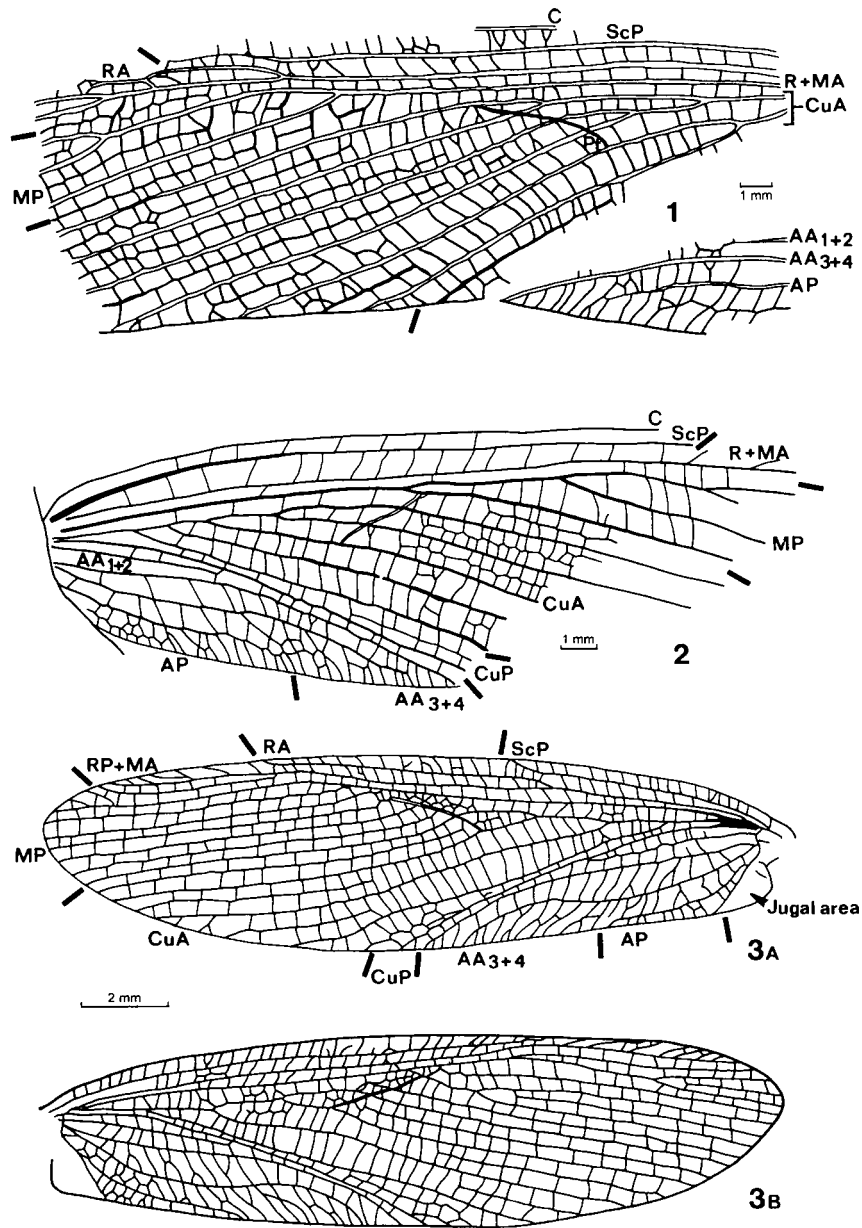
Specimen R.10428. The part and counterpart of a forewing and a poorly preserved hindwing folded together. The spines of the fore femora and tibiae are clearly preserved.

REDESCRIPTION

Holotype R.07020 (Fig. 1). Forewing. Costal area narrow (width, 0.6 mm), as wide as the subcostal area (width, 0.6 mm). The costal area is not preserved basally. There are many intercalary veins between the main longitudinal veins of the medial and cubital areas. Some of the crossveins are nearly as strong as the longitudinal veins. ScP is a long straight vein, ending about 12 mm before the wing apex. ScP does not send off strong branches but there are many crossveins between ScP and C. R+MA presents four branches in its distal part, the first one RA appears a little proximal (1.5 mm) to the level of the end of ScP. MP presents three apical branches. CuA presents six branches. There is the same special elongate bracing structure in the area between the branches of CuA and MA as in Recent *Chaeteessa* spp., which is a pseudovein due to the alignment and reinforcement of some crossveins in that region of the wing. The vein CuP is destroyed because the wing is broken around the anal area. The apex of vein AA1+2 (A1 sensu Sharov, 1962) is preserved but its base is missing. This vein is never fused with CuP and it only arrives at 6.7 mm to wing margin (in a direction parallel to AA3+4). The veins AA3+4 and AP are well-developed. There are three complete parallel veins in the anal area reaching wing margin.

Length of the preserved part of the wing, 23 mm. Probable length of the wing, 30 mm; width of the wing, 8 mm. Estimated length/width ratio of the wing, 3.75.

Specimen R.10427 (Fig. 2). Forewing. Costal area narrow (width, 0.6 mm), almost as wide as the subcostal area (width, 0.7 mm). The costal area is not widened basally. There are many intercalary veins between the main longitudinal veins of the medial and cubital areas. ScP is a long straight vein, ending about 10 mm before the wing apex. ScP does not send off strong branches but there are many crossveins between ScP and C. RP+MA is fused with RA. R+MA presents two (or more) short branches in its distal part, the first appearing a little before the level of the end of ScP. MP divides into four long branches. CuA presents five branches. There is the same oblique bracing structure as in the holotype. The vein CuP is long, parallel with the first branch of CuA. The vein AA1+2 (A1 sensu Sharov, 1962) is well-preserved, 5.5 mm long. This vein is never fused with CuP. AA3 and AA4 branches run in parallel. AA4 is forked distally. AP is well-developed and parallel with AA4.



Figs 1–3. 1 – wing of specimen MNHN-LP-R.07020, holotype, *Arvernineura insignis* Piton, 1940, Menat, Puy-de-Dôme, France, Palaeocene; 2 – wing of Specimen MNHN-LP-R.10427, *Arvernineura insignis* Piton, 1940, Menat, Puy-de-Dôme, France, Palaeocene; 3 – *Chaeteessa valida* (Perty, 1833), Recent specimen in the collection of the Laboratoire d'Entomologie, Muséum national d'Histoire naturelle de Paris, coll. Le Moulton – Chopard, 1919, female, French Guyana, Nouveau Chantier. A – left forewing, B – right forewing.

Length of the preserved part of the wing, 21 mm. Probable length of the wing, 28 mm; width of the wing, 7.5 mm. Estimated length/width ratio of the wing, 3.7.

Hindwing. One hindwing is present but poorly preserved, 23 mm long. Its width is not determinable. Only the veins in the apical part of the wing are useful. The vein ScP is simple, without any branches. The vein RA presents two short apical branches. RP+MA is a long simple vein, parallel to RA, ending precisely at the wing apex. MP divides into three well-defined branches. CuA bears three to four branches. The other veins cannot be distinguished.

Thorax. It is poorly preserved, 4 mm long and 3.5 mm wide.

Fore legs. The fore legs are not well-preserved but the spines of the femora are visible. They are long and sharp (maximal length, 0.7 mm; minimal length, 0.5 mm). There are five stronger spines and six to ten smaller spines on femora.

Specimen R.10428. Forewing. It is similar to those of the two other specimens.

Hindwing. Folded over forewing and giving little information.

Thorax. It is very poorly preserved.

Fore legs. The fore femora and tibiae are not well-preserved, but their spines are distinctly visible. The femur presents a row of strong sharp spines, 1 mm long and a row of smaller spines, 0.5 mm long. The tibia presents many sharp spines, 2 mm long, apparently in two rows. There is no terminal hook but the apical spines are longer than the others and arranged symmetrically, as in the Recent species of *Chaeteessa* Burmeister, 1838 (Smart, 1956; Gratshev & Zherikhin, 1993).

DISCUSSION. It is probable that all the fossil insects described above belong to the same species because they have nearly the same wing venation and dimensions. The placement of *Arvernineura insignis* in the Mantodea: Chaeteessidae by Gratshev & Zherikhin (1993) is confirmed because its forewing is similar to those of the Recent *Chaeteessa* spp. It only differs in the following point: the forewing MP+CuA of *Arvernineura* bears five to six branches, but in that of *Chaeteessa* spp., only four branches are present.

The key of Gratshev & Zherikhin (1993) to Recent and fossil genera of Chaeteessidae is unsatisfactory because *Arvernineura* does not show the main difference used to separate it from *Chaeteessa* spp.: The forewing of *Arvernineura* is not three times longer than wide, but 3.7–3.8 times and thus very similar to the proportions of Recent *Chaeteessa* spp. In one Recent specimen of *Chaeteessa valida*, the number of branches of the main veins, especially CuA, is very variable, as are also the length and proportions of important veins such as ScP (Fig. 3A–B). Thus, the fact that *Arvernineura* presents five branches of CuA and the *Chaeteessa* spp. mostly only four appears to be of little value for separation into different genera. Also, the proposed differences between *Chaeteessa* and the fossil genus *Megaphotina* (Gratshev & Zherikhin, 1993) from the Oligocene of Asia appear to be of relatively little value because they concern the number of branches of MP and CuA. It is probable that the genera *Chaeteessa*, *Arvernineura* and *Megaphotina* will have to be synonymised in the future.

With the present state of our knowledge, separating *Arvernineura* from *Chaeteessa* is of little use. The three Recent species of *Chaeteessa* are based on the cercal structures (Giglio-Tos, 1927). It is very difficult, even impossible, to find a good diagnostic character for *A. insignis*.

Family uncertain (probably Chaeteessidae)

Protoneuridae Piton, 1940 (non Protoneuridae Tillyard, 1917, Odonata: Zygoptera; see Bridges, 1991).

Genus *Archaeophlebia* Piton, 1940

TYPE SPECIES: *Archaeophlebia enigmatica* Piton, 1940, monobasic.

Archaeophlebia enigmatica Piton, 1940

Archaeophlebia enigmatica Piton, 1940: 147–148, Fig. 23.

HOLOTYPE. Specimen MNHN-LP-R.06999 (specimen 640, coll. Piton).

PARATYPE. Specimen 641, coll. Piton, appears to have been lost.

TYPE LOCALITY. Menat, Puy-de-Dôme, France.

TYPE STRATA. Palaeocene, palaeolake, fossil Maar.

PRESENTATION OF THE FOSSIL. A nearly complete hindwing of Mantodea with its anal area missing (Fig. 4).

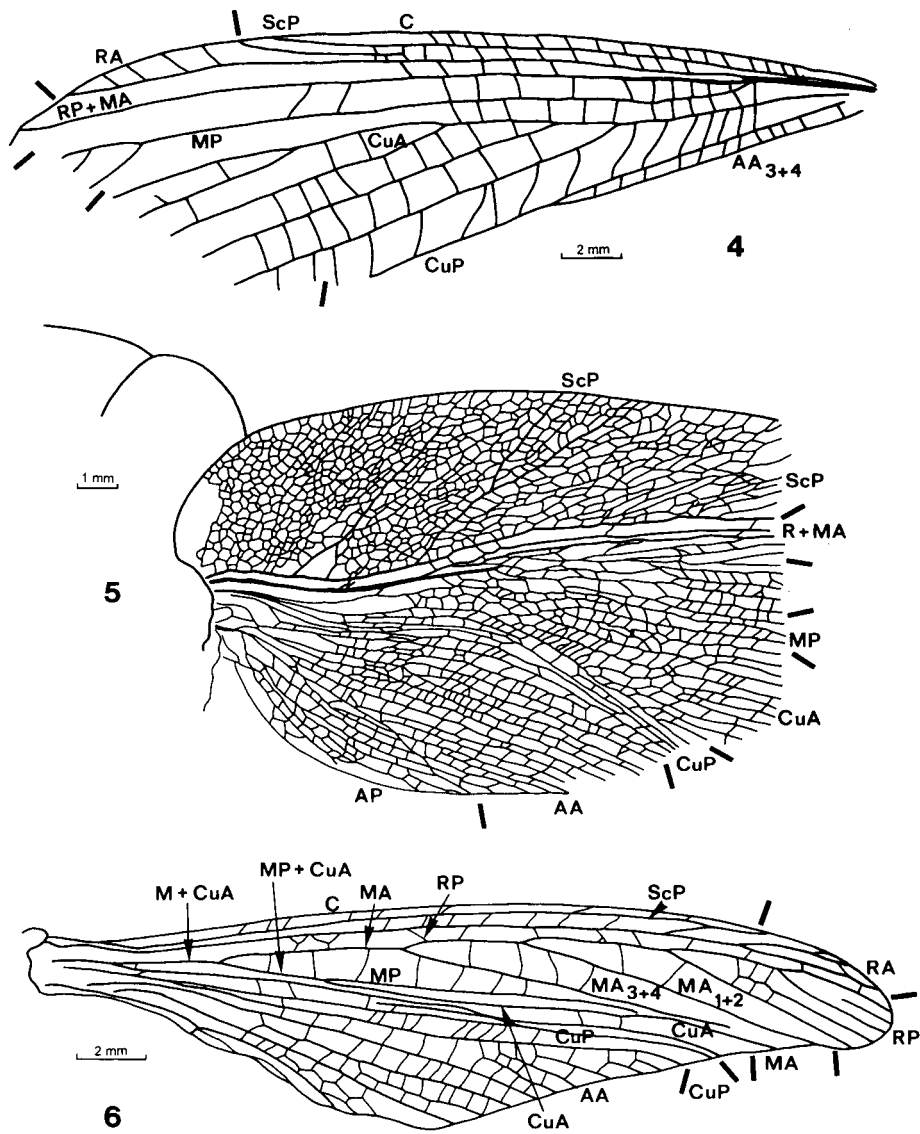
DESCRIPTION. ScP is a long (20 mm) simple vein ending on C, about 10 mm before the apex. The costal area is narrow (0.4 mm), as narrow as the subcostal area. There are many transverse veins between C and ScP. The costal area is widened slightly at the extreme base of the wing. There is a secondary longitudinal vein between RA and ScP, beginning 4.5 mm before ScP reaches the costal margin. RA is long, with four to five short apical branches ending 5 mm before the wing apex. RP+MA is a long simple vein ending 2 mm before wing apex. RA, RP+MA and MP are fused basally. They separate 4 mm from wing base, nearly at the same point. MP is straight, parallel with RP+MA, and divided into three short branches, 5 mm from wing apex. The crossvein mp-cua (MP sensu Sharov, 1962; M5 sensu Gratshev & Zherikhin, 1993; cv sensu Smart, 1956) is slightly oblique between MP and CuA, 0.7 mm long. CuA presents five branches. There are long sigmoidal crossveins between CuA and CuP. CuP is a long straight vein. The vein AA3+4 (A1 sensu Sharov, 1962) is also straight but it is distally fused with CuP, 13 mm from wing base. The anal area is missing.

DISCUSSION. Piton (1940) considered this fossil as a forewing of Ephemeroptera: Protoneuridae Piton, 1940. True Protoneuridae Tillyard, 1917 are not Ephemeroptera but Odonata: Zygoptera (Bridges, 1991). Piton (1940: 146) indicated that *Archaeophlebia* must be considered as the type genus of a new family: "... et il y a lieu d'en faire les types de 2 familles nouvelles et pour l'instant limitées à l'époque éocène." Piton never indicated the type-genus of his Protoneuridae or even which genera are covered by this family name sensu Piton.

However, this fossil cannot be interpreted as an ephemeropteran forewing because the venational system is typical of the hindwings of Mantodea, especially Chaeteessidae (Smart, 1956). Nevertheless, it is safer to consider *Archaeophlebia enigmatica* Piton, 1940 as a Mantodea incertae familiae, probably Chaeteessidae.

Family Mantidae Latreille, 1804
Subfamily (?) Choeradodinae Kirby, 1904
Genus *Prochaeradodis* Piton, 1940

TYPE SPECIES: *Prochaeradodis enigmaticus* Piton, 1940, monobasic.



Figs 4–6. 4 – *Archaeophlebia enigmatica* Piton, 1940, specimen MNHN-LP-R.06999, holotype, hindwing, Menat, Puy-de-Dôme, France, Palaeocene; 5 – *Prochaeradodis aenigmaticus* Piton, 1940, specimen MNHN-LP-R.07003, holotype, forewing and pronotum, Menat, Puy-de-Dôme, France, Palaeocene; 6 – *Protempusa incerta* Piton, 1940, specimen MNHN-LP-R.07035, holotype, hindwing, Menat, Puy-de-Dôme, France, Palaeocene.

Prochaeradodis enigmaicus Piton, 1940

“...remarquable Mantide du genre actuel”: Piton, 1938: 301.

Prochaeradodis enigmaicus Piton, 1940: 132–135, Fig. 12.

HOLOTYPE. Specimen MNHN-LP-R.07003 (specimen 230, coll. Piton).

TYPE LOCALITY. Menat, Puy-de-Dôme, France.

TYPE STRATA. Palaeocene, palaeolake, fossil Maar.

PRESENTATION OF THE FOSSIL. Impression of the thorax, two basal halves of forewings perpendicular to the body axis and two poorly preserved hindwings. The first three to five abdominal segments are visible, attached to the thorax. The head and the legs are not preserved. It is probable that the ventral part of the body is visible because the forewings in part cover the impression of the expanded pronotum suggesting that it is unlikely that this insect was fossilised with its dorsal face visible.

REDESCRIPTION. Piton (1940) described the head, antenna and legs but they are not preserved in the holotype.

The preservation of the abdomen and hindwings is insufficient for a description.

The thorax presents pronotal lobes which are partly covered by the forewing bases. It is not possible to determine the exact shape of the pronotum. Thoracic width, 9 mm. The anterior part of the pronotum is truncate.

The two forewing bases are well-preserved (Fig. 5). The forewing is about 23 to 25 mm long and about 10 mm wide. The entire surface of the forewing is densely reticulate. The costal area between C and ScP is very wide (4.3 mm wide, 43 % of the width of the wing). ScP has several long oblique branches which are repeatedly forked. ScP is slightly undulated. The vein R+MA runs parallel and very close to ScP. There are short transverse crossveins between ScP and R+MA in the middle part of the wing. Proximally, MP is well separated from R+MA but distally there are many small transverse crossveins, anastomoses and small branches, thus the two veins cannot be differentiated in the middle of the wing. There are seven or eight MP branches but the exact number is difficult to determine. MP branches are not curved posteriorly, but are directed toward the wing apex.

There is no visible “eye spot” between ScP, R+MA and MP in the middle part of the wing, unlike Recent *Choeradodis* spp. which have an obvious spot visible on the dorsal and another less visible on the ventral side of the forewing. However, only the ventral side of the fossil wing is visible, so the absence of the eye spot may be a facet of its preservation.

CuA is slightly curved posteriorly and with seven or eight branches directed toward the wing apex and parallel with the branches of MP. The area of CuA is very wide, nearly as wide as the anal area. CuP is an indistinct vein posteriorly curved, parallel with the branches of AA but never distally fused with them. The branches of AA are enriched, eleven or twelve in number, with numerous smaller branches between them.

AP divides into five to six longer branches and many shorter branches connected by crossveins.

DISCUSSION. The assignment of the wing to the Mantodea is supported by the cubital and anal areas, which are different from those of the “Orthoptera”. In fact, very similar forewings occur in the Recent genus *Choeradodis* Serville, 1831 (Mantidae: Choeradodinae). This genus is present in the Neotropical evergreen forests from Guatemala to Brazil and in the Oriental region (India, Ceylon). Piton (1940) suggested that *Prochaeradodis*

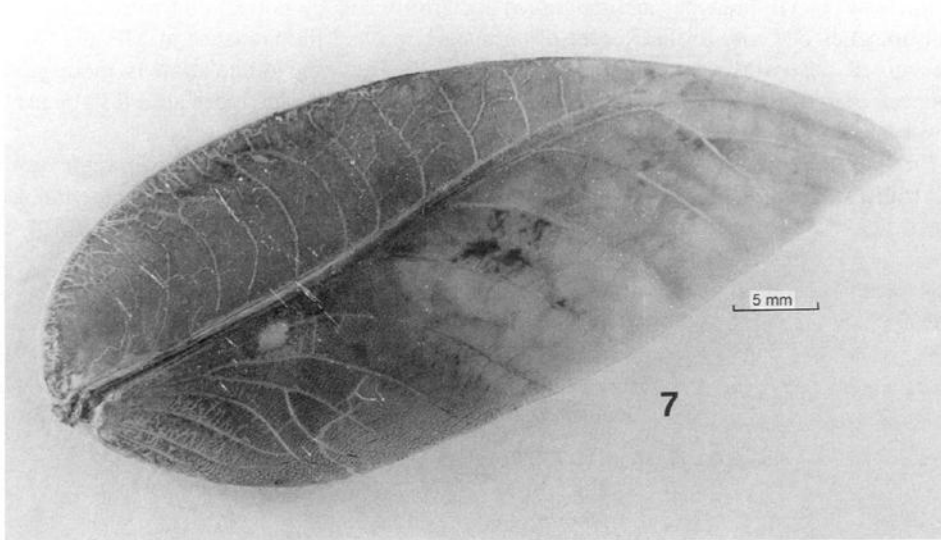


Fig. 7. *Choeradodis stalii*, forewing, Recent, French Guyana.

enigmaticus should be placed in the subfamily Choeradodinae. The main diagnostic features which support this placement are the broad side lobes of the pronotum and the reticulated forewing with a very wide costal area.

These last two characters are also present in some other subfamilies of Mantidae. For example, the Neotropical genera *Chopardiella* Giglio-Tos, 1914, *Pseudoxyops* Saussure & Zehntner, 1894 and *Oxyopsis* Caudell, 1904, of the subfamily Vatinae, bear very wide costal areas but no large pronotal side lobes. The genera *Deroplatys* Westwood, 1839 and *Brancsikia* Saussure & Zehntner, 1895 (subfamily Deroplatyinae) have broad side lobes of pronotum and broadened costal area in the forewings. They do not have the same conspicuous forewing reticulation as in *Prochaeradodis* and Recent Choeradodinae. The Mantinae, *Rhomboderella* Giglio-Tos, 1912 (Central Africa) and *Rhombodera* Burmeister, 1838 (Indo-Malaysia) also have similar wing venations, but the costal area is somewhat narrower at base than that of *Prochaeradodis*, and the pronotum is anteriorly narrowed.

Similar large side lobes on pronotum and broadened costal area of the forewing may be found in other Recent families: the Hymenopodidae: Epaphroditinae (genera *Parablepharis* Saussure, 1870 and *Phyllocrania* Burmeister, 1838) or the Empusidae (genus *Idolomantis* Uvarov, 1940). However, the wing morphology of these last genera is quite different from *Prochaeradodis*. These hypertrophies of thorax and costal areas may be interpreted as symplesiomorphies or convergences in the evolution of the Mantodea.

In conclusion, although *Prochaeradodis* appears to be related to the Recent Choeradodinae, the main characters (and the only ones used by Piton) for that placement appear uncertain because they could be convergences or symplesiomorphies. However, in the absence of characters that would contradict this attribution, we follow with some reserve the classification of *Prochaeradodis* in the Choeradodinae.

Prochaeradodis differs from the Recent *Choeradodis* spp. (Fig. 7) in the following characters: (1) MP branches are not curved posteriorly and are not parallel with the proximal branches of CuA. In the Recent *Choeradodis* spp., all the branches of MP and CuA are curved posteriorly and running in parallel. (2) The wing reticulation is more pronounced than in Recent *Choeradodis* spp. (3) The prothoracic side lobes appear to be narrower than in Recent *Choeradodis*.

Prochaeradodis appears to be more closely related to the Neotropical *Choeradodis* spp. (*C. stalii*, *C. rhombicollis* or *C. laticollis* for example) than to the Indian species. Indian species have a narrower costal area than the Neotropical species and *Prochaeradodis*.

Order Ensifera
Superfamily Tettigonioidea Karny, 1907
Family Tettigoniidae Karny, 1907 (sensu Sharov, 1968)
Subfamily uncertain
Genus *Protampus* Piton, 1940

TYPE SPECIES: *Protampus incerta* Piton, 1940, monobasic.

Protampus incerta Piton, 1940

Protampus incerta Piton, 1940: 135–136, Fig. 13.

HOLOTYPE. Specimen MNHN-LP-R.07035 (specimen, 718, coll. Piton).

PARATYPE. Specimen 719 (coll. Piton), probably lost.

TYPE LOCALITY. Menat, Puy-de-Dôme, France.

TYPE STRATA. Palaeocene, palaeolake, fossil Maar.

PRESENTATION OF THE FOSSIL. A nearly complete hindwing (Fig. 6). The anal area in part covers the rest of the wing.

DESCRIPTION. ScP ends at 6.1 mm before the wing apex, it is a long, simple and straight vein with only few, short crossveins between C and ScP. The costal area is narrow (0.2 mm wide), a little narrower than the subcostal area (0.3 mm wide). RA is parallel to ScP ending only 1 mm before the wing apex. RA forks close to apex, 2.5 mm long. RP separates from RA 11.5 mm from the wing base and 14 mm before the wing apex. Its free part is an oblique vein between RA and MA, 0.8 mm long. RP fuses with MA 2.7 mm before the divergence of MA1+2. RP sends off three short branches to the wing apex. There are eleven crossveins between the media and RA. M+CuA or MA are not fused with the stem of R nor RA (minimal distance between M and R or RA, 0.4 mm). MP+CuA separates from MA at 5.5 mm from base. MP+CuA is a straight vein which soon separates into a simple CuA and a simple MP. MP is distally fused again with MA3+4. Basally, CuP is clearly separated from M+CuA. CuP and the longitudinal veins of the cubito-anal area (AA1, AA2, etc.) are long and straight veins with secondary longitudinal veins between them, as in a hindwing of a Recent Ensifera: Tettigonioidea but the exact organisation of the anal area is very difficult to interpret because of the wing folding.

Length of the wing, 26 mm; width of the part of the wing between costa and CuA2, 3 mm. Approximate width of the cubito-anal area, 5 to 6 mm.

DISCUSSION. Piton (1940) classified this wing as a forewing of a Mantodea: Empusidae, but his figure is incorrect. The great width of the anal area shows that it is a hindwing. The presence of the stem of M, the fusion between RP and MA, the basal fusion of MP with

CuA and the RP branches arranged in a continuous series with MA branches imply that it is an orthopteroid hindwing and not a hindwing of Mantodea. The oblique vein between radial and median veins is to be interpreted as the base of RP (Rs sensu Ragge, 1955), which is then fused with MA, as in Ensifera. The separation of RA and RP far from base and the non basal fusion of median vein with radial vein implies that this fossil is a hindwing of Tettigoniodea: Tettigoniidae. The subfamily assignment of the wing within the Tettigoniidae is difficult because of the lack of body and forewing characters. The presence of two well-defined apical branches of RA is probably a plesiomorphic condition within the Tettigoniidae.

PALAEOCLIMATIC AND BIOGEOGRAPHIC IMPLICATIONS

As *Archaeophlebia enigmatica* has been identified as a Mantodea, the Ephemeroptera from the Menat outcrop are now only known from a single still undescribed larva (Olivier, pers. comm.). Mayflies and other aquatic forms appear to be very rare in this palaeolake.

(1) Odonata are known only by one or two uncertain specimens ("*Lestes*" *zaleskyi* Piton, 1940, considered by Nel & Paicheler [1994] as a very uncertain Zygoptera: Lestidae, and an undetermined abdomen of an *Aeshna* sp., Anisoptera: Aeshnidae). A fine zygopterous specimen has been discovered recently.

(2) Trichoptera are known from one wing fragment interpreted as a Phryganeidae by Piton (*Phryganea nigripennis* Piton, 1940), but considered by us to be of a very uncertain position, and from several larval casts of uncertain family position (*Prodontoceram ligniticum* Piton, 1940 attributed by Piton to the Leptoceridae).

(3) Aquatic Coleoptera are known by two species of Gyrinidae, each of them based on one specimen (Nel, 1989): *Gyretes giganteus* (Piton, 1940) and *Orectochilus* sp.

(4) Other aquatic groups have not yet been discovered and it is probable that they are absent: Plecoptera, aquatic Heteroptera, Diptera, etc.

This brief overview indicates that the Menat paleolake had probably a reduced aquatic insect fauna.

The presence of fossil Chaeteessidae at Menat indicates that the palaeoclimate was very hot and wet and that there was an evergreen forest around the palaeolake. Recent Chaeteessidae are found in the evergreen forests of Brazil and Guyana. The presence of one crocodile, one species of Iguanidae, many fossil Blattodea and large Coleoptera Buprestidae and Cerambycidae confirms the hypothesis of a forest growing in a hot and wet palaeoclimate around a maar palaeolake.

Although the position of *Prochaeradodis* appears somewhat uncertain, the Recent mantid genera which present broad prothoracic side lobes and broadened costal areas with reticulate forewing live in warm to hot wet climate usually in evergreen forests. The presence of a fossil genus with similar structures in the paleolake of Menat reflects the paleoclimatic conditions indicated by the presence of a Chaeteessidae.

The presence of fossil Chaeteessidae in the Palaeocene of France, the Oligocene of Siberia but also the Cretaceous of Kazakhstan and Siberia (Gratshev & Zherikhin, 1993) clearly shows that this group had a wider distribution than its present occurrence restricted to South America.

Similar conclusions (although less certain) can be reached from the presence of a Choreradodinae in the Palaeocene of France. This subfamily is found in two disjunct areas: the

Neotropical and the Oriental regions. Its discovery in the Palaeocene of Menat shows that it was more widely distributed in the past than it is today.

The historical biogeography of Mantodea is to be made but it is obvious that the fossil data must be integrated in such study, even though the fossil record is still fragmentary. The study of new fossil material should be developed, especially in exceptional outcrops like the palaeolake of Menat.

ACKNOWLEDGEMENTS. We thank our friend P. Olivier (University of Paul Sabatier, Toulouse) for the loan and deposition of his material of fossil Mantodea from Menat. We also thank J. Kukulová-Peck (Carleton University, Ottawa) and P. Štys (Charles University, Prague) for their comments on the manuscript.

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Received January 13, 1995; accepted July 12, 1995