Available online at www.sciencedirect.com

C. R. Palevol 4 (2005) 7–16

Comptes Rendus Palevol

http://france.elsevier.com/direct/PALEVO/

Systematic Palaeontology

A fossil sawfly of the genus *Athalia* (Hymenoptera: Tenthredinidae) from the Eocene–Oligocene boundary of Altkirch, France

Torsten Wappler [a,*], Sebastian Hinsken [b], Jochen J. Brocks [c],
Andreas Wetzel [b], Christian A. Meyer [d]

[a] *Hessisches Landesmuseum, Department of Geology, Palaeontology & Mineralogy, Friedensplatz 1, 64283 Darmstadt, Germany*
[b] *Geological & Paleontological Institute, University Basel, Bernoullistraße 32, CH-4056 Basel, Switzerland*
[c] *Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge MA 02138, USA*
[d] *Museum of Natural History Basel, Augustinergasse 2, CH-4001 Basel, Switzerland*

Received 2 August 2004; revised and accepted 8 December 2004

Written on incitation of the Editorial Board

Abstract

A new species of coleseed sawfly (Tenthredinidae: Athaliini) is described and figured from the Eocene–Oligocene ‘Rebberg’ quarry within the Fossiliferous Zone, a member of the Middle Salt Formation. *Athalia vetuecclesiae* n. sp. is the first representative of the *Athalia* group from the geological record. The new species is most similar to members of the *A. vollenhoveni*-group represented by only six species from Africa, but can be distinguished by details of antennal structure and length of spurs of the hind tibia. The phylogenetic position of the fossil within the Tenthredinidae*, its palaeoenvironmental implication, and the geological setting of the quarry are briefly discussed. ***To cite this article: T. Wappler et al., C. R. Palevol 4 (2005)***.

Résumé

Une espèce de symphyte (Tenthredinidae: Athaliini) est décrite pour la première fois en enregistrement fossile, dans la « zone fossilifère » de la carrière Rebberg d’Altkirch (Sud de l’Alsace, France). La “zone fossilifère » fait partie de la zone salifère moyenne (approximativement Éocène supérieur–Oligocène inférieur. *Athalia vetuecclesia* n. sp. est le premier représentant fossile du groupe et présente beaucoup de similitudes avec *A. vollenhoveni*, dont seules six sous-espèces actuelles sont connues en Afrique. On l’en distingue cependant par certains détails de la structure des antennes ainsi que par la longueur des éperons des tibias postérieurs. La position phylogénétique de ce fossile au sein des Tenthredinidae* ainsi que les implications paléoécologiques sont discutées, et les caractéristiques géologiques de l’affleurement sont brièvement présentées. ***Pour citer cet article : T. Wappler et al., C. R. Palevol 4 (2005)***.

---

[*] Corresponding author.
E-mail address: wappler@hlmd.de (T. Wappler).

doi:10.1016/j.crpv.2004.12.001

Keywords: Insects; Basal Hymenoptera; Tenthredinidae; Eocene/Oligocene boundary; Potassic Basin; Altkirch

Mots clés : Insectes ; Hymenoptera basique ; Tenthredinidae ; limite Éocène–Oligocène ; Fossé rhénan ; Bassin potassique ; Altkirch

1. Introduction

In spite of its incompleteness, the hymenopteran record is rich enough to represent as many as 51 out of 54 extant families [40]. As many as 38 of these families are known at least since the Mesozoic, a time during that in many high-level phylogenetic events occurred, and 20 additional families are known to be extinct (mostly since the Mesozoic) [38,40]. The ecological diversity of the hymenopterans increased during the Early Cretaceous due to the appearance of indisputably phyllophagous Tenthredinidae [39].

Within the large symphytan family Tenthredinidae, *Athalia* is a member of the subfamily Allantinae, tribe Athaliini. The tribe is divided into four genera (three of them are monotypic). The genus *Athalia* represents a primitive form of hymenopteran insects. Therefore, in particular the relationships to other tenthredinid taxa are not always clearly cut. Apart from that, *Athalia* is considered as a sister-group of all other Tenthredinoidea *s.s.* [44,45,49].

Athalia contains in all 73 species with seven subspecies and occurs mostly in the Palaearctic region, but also extends into the Indo-Malayan and Ethiopian regions [1,2]. The host plants of the genus *Athalia* are restricted to herbaceous species in the families Compositae, Crassullaceae, Cruciferae, Labiatae, Plantaginaceae, and Scrophulariaceae [1,2].

One of the mostly commonly encountered species in Europe is *Athalia rosae* and it is from this species that most biological information is known (many species are unknown for their biology and so might be different from *A. rosae*). *Athalia rosae* predominantly feeds on several glucosinolate-containing plants and sequesters the glucosinolates of different hosts. Some examples of host plants include *Barbarea stricta*, *Sinapis alba*, and *Brassica nigra* (pers. commun. Dr M.S. Engel).

Fossils of the genus *Athalia* are rare and as such their palaeontological history is poorly understood. Earlier ‘coleseed sawfly’ fossils were variously assigned to different genera. Cockerell [7] described *Eriocampa wheeleri*, a fossil from the Eocene–Oligocene of Florissant, Colorado. Later, Cockerell [8] assigned four new species to the Tenthredinidae (*Tæniurites*, *Tenthredella*, and *Dineura*) and a second specimen of *Eriocampa wheeleri*. The latter were removed from the genus *Eriocampa* by Zhelochovtzev and Rasnitsyn [55] who considered the specimens probably belonging to, or near to, the genus *Athalia*. These fossils are best to considered *incertae sedis* because their generic assignment is doubtful (as done by Carpenter [6]).

Therefore, discovery of well-preserved and almost complete coleseed sawflies is particularly significant. The specimens described below are the first fossil representatives of the *Athalia*-group and, thus, the oldest known members of a major branch of Hymenoptera (Fig. 6).

In addition to the palaeontological importance of the found sawflies, these specimens have palaeoecological implications.

2. Geographical and geological setting

2.1. Geological framework

The Upper Rhinegraben belongs to a major rift system within central Europe which started to develop during the Early Tertiary [35,56]. During the early rift stages in the Eocene, local depocentres formed, which became interconnected during the further development [46]. One of these basins is the so-called Potassic Basin in the southern Rhinegraben (Fig. 1).

In the Potassic Basin, up to 1600-m-thick marls and evaporites accumulated during the Late Eocene–Early Oligocene (Salt-Formation) [3]. The marginal parts of the basin and its southernmost part contain brackish, lacustrine, fluvial and terrestrial sediments. The basin border is characterized by fluvial conglomerates, which have been interpreted as alluvial fan deposits [10], which formed in response to the uplift of the graben flanks.

The Cainozoic sedimentary record in the Potassic Basin starts above a residual red, iron-rich soil (‘sidérolithique’) with Lutetian freshwater limestones

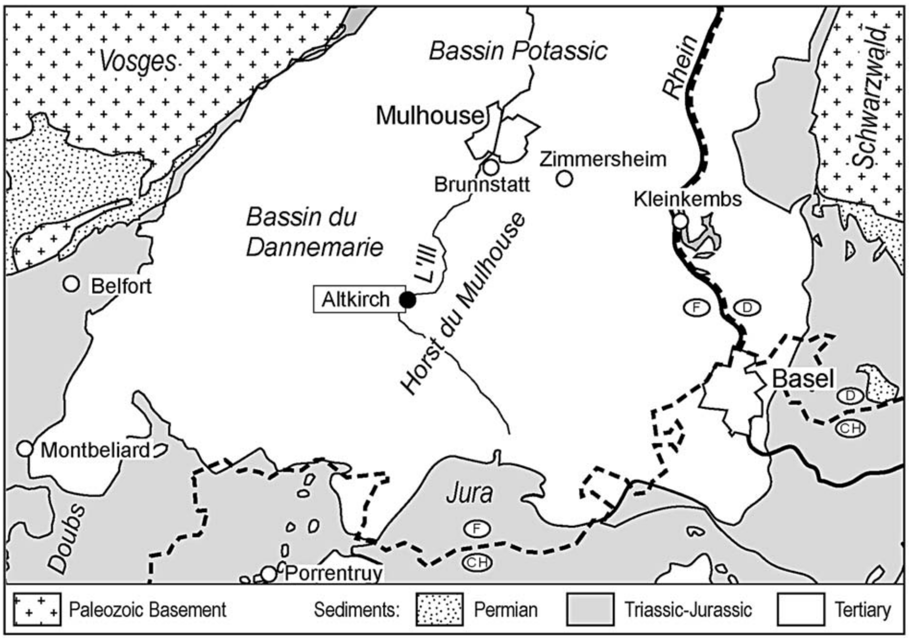

Fig. 1. Simplified geological map of the study area.
Fig. 1. Carte géologique simplifiée de la zone étudiée.

(‘Calcaire à Planorbes’). This is overlain by the Salt Formation, which is formed during the main rift phase during the Eocene–Oligocene [46]. The Salt Formation has been subdivided into the Lower Salt Formation (Lower Lacustrine Marls, Salt I, Upper Lacustrine Marls, Salt II), the Middle Salt Formation (Salt III, Fossiliferous Zone) and Upper Salt Formation Salt IV, Marls without Salt) (Fig. 2). Further up, the Members of the Grey Marl Formation, Foraminifera Marls, Fish Shales, Meletta Shales and Cyrenea Shales, which are covered by freshwater beds [3,10].

Due to the abundance of fossils and the generally articulated preservation of fish and insect skeletons, the Fossiliferous Zone of the Middle Salt Formation can be described as a Fossillagerstätte. Like many other comparable Palaeogene insect-bearing deposits in central Europe (e.g., Céreste/France [21–23,32,34,36,53]; Rott/Germany [17,23,25,28]), the environmental conditions under which the host sediments formed are still a matter of debate. Some authors postulate a lagoonal, marine-influenced setting [3,19,26,50] others favour a saline lake [5,10,13] similar to the Lower Eocene Green River Formation (Wyoming, USA) as interpreted by Eugster and Surdam [11] or Boyer [4].

2.2. Age constraints

In spite of abundant fossils, index fossils are rare and, hence, the stratigraphical position of the Salt Formation members has not been totally clarified yet. The most authors regard the Fossiliferous Zone as Earliest Oligocene [29]. Schuler [43] postulates the lower part of the member to be Latest Eocene in age. A biostratigraphical age based on mammals in the hanging Haustein member (Upper Salt Formation) of the ‘Rebberg’ quarry about 35 m above the horizon of discovery covers the time interval of the Mammal Reference Level MP21 and corresponds to the Lower Stampian and Upper Priabonian, thus coinciding with Stehlin‘s ‘Grande coupure’ [47]. So the stratigraphical position of the Fossiliferous Zone member seems to be close to the Eocene–Oligocene boundary (Fig. 2).

2.3. Sample location

Deposits of the Fossiliferous Zone were studied in the Rebberg quarry, near Altkirch (47°62’34”N/ 7’23’92”E; Fig. 1). This location is currently the only well exposed outcrop of the Fossiliferous Zone in the southernmost Upper Rhinegraben.

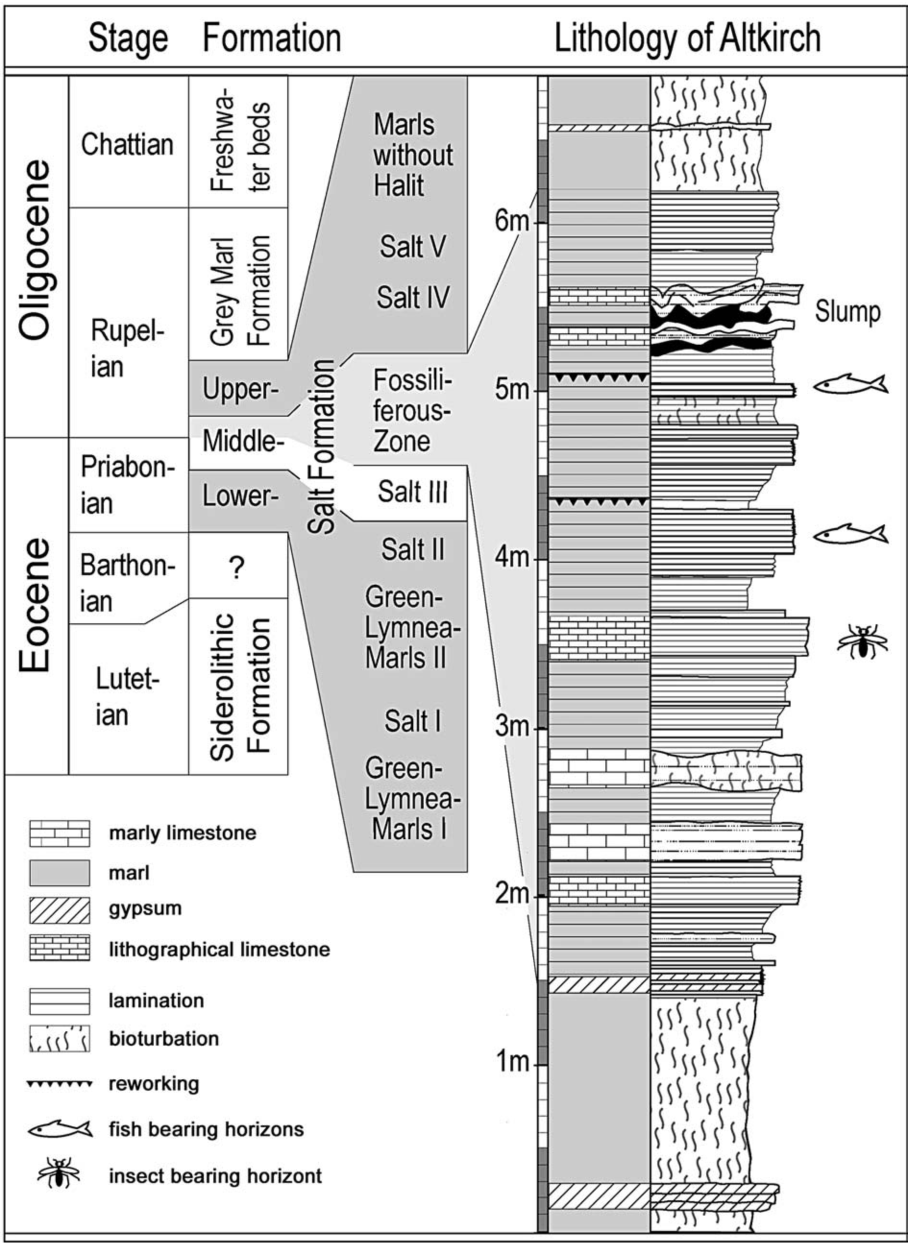

Fig. 2. Stratigraphical position of the *Athalia vetuecclesiae* n. sp. specimens. Left: chronostratigraphical correlation with Mediterranean Stages. Middle: Rhinegraben synrift Formations with close-up of the main stratigraphical subunits of the Salt Formation in the Potassic Basin. Right: close-up of the outcrop of the Fossiliferous Zone in the Rebberg quarry/ Altkirch including metre scale, lithology and observed section. Stratigraphy according to Blanc-Valleron and Schuler [3].

Fig. 2. Position stratigraphique des deux représentants de *Athalia vetuecclesiae* n. sp. À gauche : corrélation chronostratigraphique avec les étages méditerranéens. Au milieu: formations synrift du graben du Rhin avec détail des subdivisions de la Zone salifère dans le bassin potassique. À droite : détail de l'affleurement de la zone fossilifère dans la carrière du Rebberg (Altkirch), avec échelle métrique, lithologie et coupe étudiée. Stratigraphie selon Blanc-Valleron et Schuler [3].

The laminated marls, platy marls and lithographical limestones of the Fossiliferous Zone have been reported from many drill cores, quarries and outcrops in the southern Upper Rhinegraben. It reaches a maximum thickness of approximately 75 m in the Potassic Basin [3] and contains a typical brackish fossil assemblage [10,12,15,16,18]. The Fossiliferous Zone seems to be correlative within the whole basin except along margins where it interfingers with fluvial conglomerates [17].

To date, a total of some hundred insect specimens have been collected, most of them in no longer existing outcrops near Kleinkems (D), Brunstatt (F) and Zimmersheim (F) (Fig. 2). The first descriptions of fossil insects date back to the late 19th century [12,31] and the latest revision of the insect fauna was written by Théobald [48]. Therefore, an updated review, including the insects from the Rebberg quarry in Altkirch [16], is urgently required (pers. commun. Prof. Dr. Rust).

3. Material

The two specimens described in this study were discovered in the quarry ‘Rebberg’ (Figs. 1 and 2) within the Fossiliferous Zone, a member of the Middle Salt Formation. They were found in an approximately 40-cm-thick horizon of lithographical limestone, which can be correlated with the Horizon No. 6 of Gaudant [16]. The fossil insects from Altkirch are preserved chitinous (SEM) and are fixed in calcareous biolaminae. Preparation is not needed, but the specimens were covered with Laumin resin. The specimens studied are stored in the Naturhistorisches Museum Basel under the access number NHMB: Alt:Hy-01 and Alt:Hy-02.

4. Systematic palaeontology

Order: Hymenoptera Linneus, 1758
Suborder: ‘Symphyta’ Gerstaecker, 1867
Family: Tenthredinidae Latreille, 1804–1805
Subfamily: Allantinae Panzer, 1801
Tribe: Athaliini Benson, 1962
Genus: *Athalia* Leach, 1817
Type species: *Tenthredo rosae* Linnaeus, 1758 (= *T. spinarum* Fabricius, 1787).

Diagnosis (modified after Benson [2]): (1) Antennae 13–9-segmented, third segment prolonged, (2) flagellum subclavate, (2) C and Sc+R swollen as almost to obliterate cell C, (3) origin of M in fore wings from Rs+M after the latter has left Sc+R, (4) abscissa of Rs short (5) 2m-cu present, (6) anal cell complete with oblique cross vein, (7) cell 1M angular anteriorly, and (8) tarsal claw simple.

Athalia vetuecclesiae n. sp.

Etymology: From Latin for ‘old’ and ‘church’, in reference to the type-locality Altkirch.

Holotype: Alt:Hb-02, probably ♀, leg. J. J. Brocks at the Altkirch locality, ‘Rebberg’ quarry /Holcim AG, ‘Zone fossilifère’, $x = 7°14’50”/y = 47°37’75”$, France.

Referred material: Alt:Hb-01, leg. S. Hinsken at the Altkirch locality, [see above], France.

Type locality and horizon: Altkirch locality, [‘Rebberg’ quarry /Holcim AG, ‘Zone fossilifère’, 7°14’50’’E/ 47°37’75’’N, France. Middle Salt Formation, ‘Zone fossilifère’, which can be correlated with the Horizon No. 6 of Gaudant [16].

Diagnosis: This species is most similar to the *Athalia vollenhoveni*-group. *A. vetuecclesiae* n. sp., however, can be distinguished by (1) extended labrum, (2) medially excised clypeus, and (3) 6th flagellomere prolonged.

Dimensions (in mm): Total body length ~6.92, head length 1.02, head width ~1.92, interocular space 1.92, diameter of antennae socket 0.15, length of flagellomere III–VIII: 0.38, 0.15, 0.17, 0.27, 0.17, 0.16, length of inner hind tibial spur 0.2, length of tarsal segment I-V: 0.97, 0.33, 0.25, 0.1, 0.24, wing length 6.76.

Description (Figs. 3–5): Head more or less rectangular. Compound eyes strongly converging below and emarginated. Ocelli not enlarged. Antennal sockets near base of clypeus, separated by less than antennal socket diameter. Malar space shorter than basal mandibular width. Mandible with strong apical tooth. Labrum elongated, covering apical edge of mandibles. Clypeus medially shorter than distance between antennal sockets, apical margin doubly arcuate (Fig. 4B), supraclypeal area, face, and vertex smooth. Antennae probably composed of nine segments, scarcely longer than width of head. Sixth segment prolonged and from the seventh segment onwards longer than broad (Fig. 4E). Last two segments fused to a small club. Wings strongly infuscated; stigma and venation black. Basal vein straight and strongly basal to cu-a. First abscissa of Rs short, cells R and 1R barely touching. Cell 1M angular anteriorly. Marginal cell apex slightly bent away from ante-

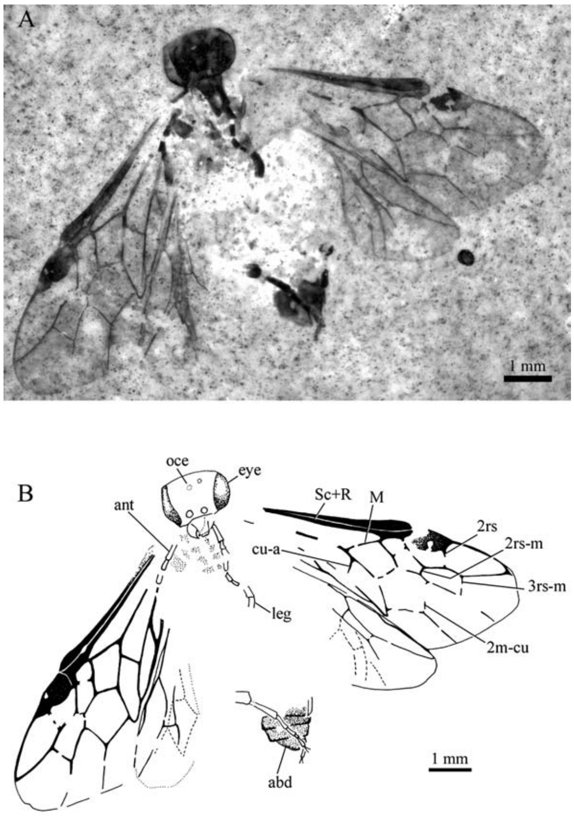

Fig. 3. *Athalia vetuecclesiae* n. sp. (**A**) Photomicrograph of holotype specimen (Hb-02); (**B**) Camera lucida drawing of holotype specimen (Hb-02).

Fig. 3. *Athalia vetuecclesiae* n. sp. (**A**) photo de l'holotype (Hb-02) ; (**B**) dessin de l'holotype (Hb-02).

rior wing margin. 2rs originating beyond midpoint of pterostigma. 3rs-m entering marginal cell in its apical half. 2m-cu slightly arched and distad 2rs-m by three times vein width. Posterior anal vein fused to anterior anal vein in the middle of anal cell, not reaching hind wing margin. Mesonotum black. Inner hind tibial spur shorter than apical width of tibia (Fig. 4H). Tibiae and tarsal segments of hind legs broadly ringed with black. Claws simple.

5. Discussion of taxonomy

Although not complete, the fossils are well preserved and show all characteristic features such as head structure, antennae and wing venation, necessary to admit a determination on generic level. An important character to distinguish the Tenthredinidae from most other families of the Tenthredinoidea *s.s.* is the 9-segmented antenna. This type of antenna is found in the diverse genera of the subfamilies Selandriinae, Tenthredininae, Nematinae, Allantinae. In particular members of the Athaliini show a progressive reduction in antennal segments from 18–21 of *Hennedyia* and *Hennedyella* to 10(9)–13 of *Hypsathalia* and *Athalia* [2]. However, the antennae are distinctly more apomorphically developed in Athalia than in the other members of the Athaliini (i.e., antennae have more segments in the former).

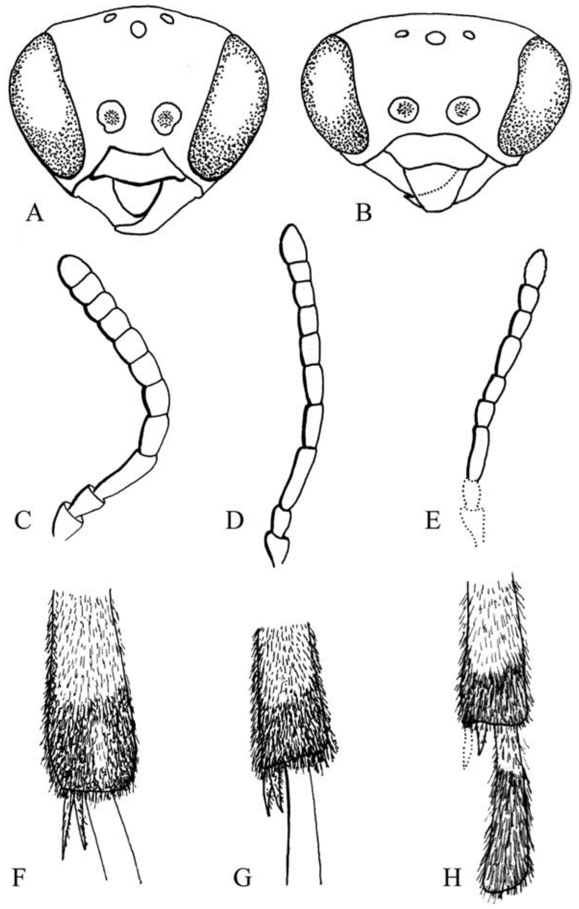

Fig. 4. Face without antennae, antennae, and apex of hind tibia of different *Athalia* specimens. (**A**, **F**) *A. rosae* (♀). (**C**) *A. glabricollis* (♀). (**D**) *A. lugens* (♀). (**B**, **E**, **H**) *A. vetuecclesiae* n. sp. (reconstruction).

Fig. 4. Tête sans antennes, antennes, apex de tibia postérieurs de plusieurs exemplaires d'*Athalia*. (**A**, **F**) *A. rosae* (♀). (**C**) *A. glabricolis* (♀). (**D**) *A. lugens* (♀). (**B**, **E**, **H**) *A. vetuecclesiae* n. sp. (reconstitution).

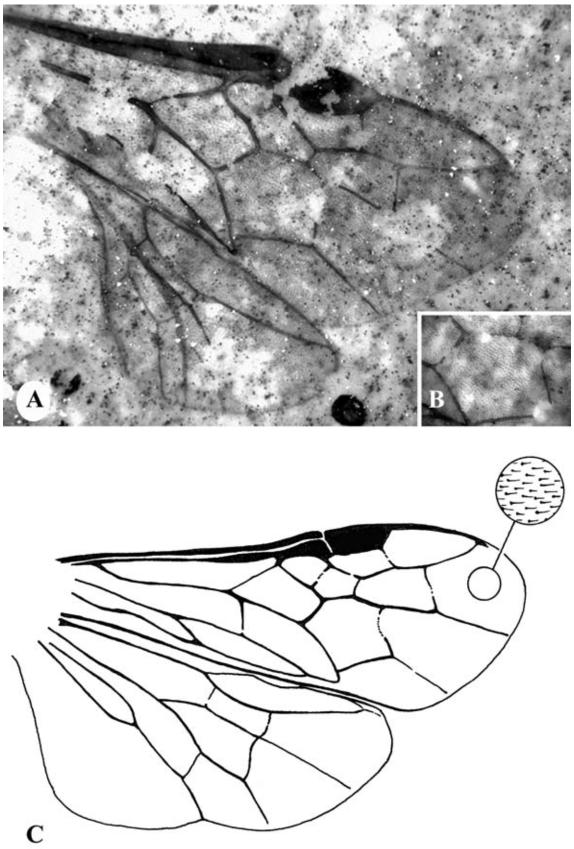

Fig. 5. *Athalia vetuecclesiae* n. sp. **(A)** Photomicrograph of left fore and hind wing (Hb-02). **(B)** Enlarged photomicrograph of the strongly infuscated wing membrane (Hb-02). **(C)** Reconstruction of wing venation of *A. vetuecclesiae* n. sp.

Fig. 5. *Athalia vetuecclesiae* n. sp. **(A)** Photo des ailes antérieure et postérieure gauche (Hb-02). **(B)** agrandissement de l'aile fortement 'infuscated' (Hb-02). **(C)** reconstitution des nervures alaires de *A. vetuecclesia* n. sp.

The wing venation of the fossil specimens excludes the Selandriinae, Tenthredininae and Nematinae as possible candidates, but it is highly similar to representatives of the Allantinae. Within Allantinae, preserved details of the fossil wings suggest membership to the genus *Athalia* within the tribe Athaliini (Fig. 3). Characteristic for Athaliini, and also observed in the fossil specimens, is the presence of the first abscissa of Rs (Fig. 3) [27,45,49]. Moreover, in addition to the previous character, C and Sc+R are swollen as almost to obliterate cell C, and the third flagellomere is prolonged, a combination of characteristics solely known from *Athalia* (pers. commun. Dr S. Schulmeister).

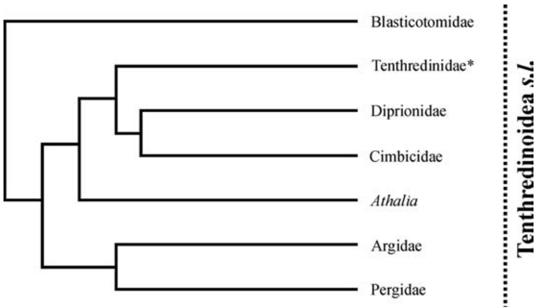

Fig. 6. Phylogeny of the Tenthredinoidea *s.l.* (modified after Schulmeister [43]). Tenthredinidae are still indicated as a paraphyletic grade, with respect to the remaining Tenthredinoidea *s.s.*. Tenthredinidae* = Tenthredinidae minus *Athalia*.

Fig. 6. Phylogénie des Tenthredinoidea *s.l.* (modifié d'après Schulmeister [43]). Les Tenthredinoidea sont encore considérés comme une famille paraphylétique, en regard du Tenthredinoidea *s.s.* restant. Tenthredinoidea* = Tenthredinoidea moins *Athalia*.

The fossil *Athalia* specimens show even more a mosaic of characters common to different *Athalia*-groups. Interestingly, this species appears most similar in respect to the clypeus structure and to the infuscated wings (Fig. 5b) to the extremely rare *A. vollenhoveni*-group represented by only six species from Africa [2]. Both, the new species and the representatives of the *vollenhoveni*-group, have a clypeus with an apical doubly arcuate margin. Aside from the characters given above, the new species can be distinguished from the members of the *A. vollenhoveni*-group by the antennal structure and the length of spurs of the hind tibia. Exceptional long spurs occur in *A. armata* of the *A. furvipennis*-group [2]. In *A. vetuecclesiae*, the antennal segments are from the seventh segment onwards only inconspicuously longer than broad. In contrast, in the *A. vollenhoveni*-group, all flagellar segments are longer than broad. Moreover, the spurs of the hind tibia are longer than the width of tibia in the *A. vollenhoveni*-group, but shorter in *A. vetuecclesiae*. Regarding the form of the elongated labrum in the *A. vollenhoveni*-group, the new species is most comparable to representatives of the *A. bicolor*-group (in particular *A. bicolor* mainly distributed in southeastern Europe and the eastern Mediterranean) and the *A. furvipennis*-group (in particular *A. mellis* only known from Africa) [2].

The fossil species presented herein is most similar to the *A. vollenhoveni*-group and is presumably the basal most taxa of *Athalia* and thereby of the Tenthredinidae* *sensu* Schulmeister [44,45] as a whole (Fig. 6). For these reasons it may be advisable to place *Athalia* *vetuecclesiae* n. sp. near members of the *A. vollenhoveni*-group once a cladistic analysis of the Tenthredinidae* has been finalized.

It does seem reasonable, however, that the Tenthredinidae* as a whole must be quite ancient. Each of the major representatives of the Tenthredinoidea *s.l.* probably arose and became differentiated rapidly at the end of the Cretaceous, with subsequent diversification within each lineages progressing from that time on [40,55].

6. Palaeoenvironmental implications

Fossil insects are often good palaeoclimatic indicators. As insects are poikilotherm, their metabolism is closely adjusted to the thermal conditions of their habitat. Therefore, single species, and often also higher taxa, are restricted to a specific climatic realm. Moreover, insect species and genera have a particularly long geological life-span, commonly many million years [24,41,51,52]. Fossil insects have proven to be a useful and reliable indicator for reconstructing ancient climate and environment ('nearest-living-relative method'). They are sensitive indicators of climate, and they could be, in a sense, a thermometer of the past. Although physiological aspects are not preserved in fossils, it is possible to examine morphological characters that show strong correlations with climate.

From these clues, the occurrence of *Athalia* sp. in deposits of the basal Oligocene could be regarded as an implication for climatic change in the Palaeogene of Central Europe coherent to the global Eocene-Oligocene boundary 34 Myr ago [9,37,54].

Nevertheless, the vegetation distribution indicates a gradual trend from the Eocene paratropical/subtropical evergreen forest vegetation through vegetation, with an increasing proportion of temperate deciduous elements resulting in the Oligocene in establishments of broad-leaved mixed deciduous and evergreen forests across Eurasia between about palaeolatitudes 55° and 40° north [9]. Further evidence from leaf floras, palynology and sedimentology seems to indicate that the belt with common sclerophylls in southern Europe was, at least in places, a vegetation adapted to a humid warm temperate climate but with a slighter drier interval, probably in winter [9,28,37]. These trends are also identical in the ecological diversity pattern of mammals. In particular, the mammalian ecological diversity is suggestive for drier and more open habitats in southern France [14,20]. Evidence from the palaeoecology of mammals for drier more open habitats in the Oligocene has been put forward for Europe.

In western Europe, the transition is more gradual with the loss of paratropical elements and incoming of deciduous elements from the late Middle Eocene [9]. Typical leaf floras of the Late Eocene have been interpreted as evergreen to semi-evergreen mesophilic, e.g., Célas, France (leaf assemblage illustrated by Mai [28]).

Similarly, an 'aridisation' is also reflected in the highly diverse insect palaeofaunas from Céreste [21,23,32,42] or Florissant [30]. The abundance of distinctly specialized insect taxa that as far as known primarily inhabit open meadows to fairly dry rangelands does well correspond with the climatic change at the Eocene/Oligocene transition and supports this theory [9,34,36,53]. If the climatic requirements of *A. vetuecclesiae* n. sp. were comparable to its very close and distinctly specialized living relatives, then the appearance of this insect confirms that the shift to a 'cooler' climate had already occurred when the laminated carbonates of the Fossiliferous Zone were deposited. This interpretation is also supported by other plant and animal fossils recovered at the Altkirch locality. The dominance of conifer remains [43] and the occurrence of salmonid fishes (smelts) [16], are typical for temperate zones.

Clearly, the nearest-living-relative method for estimating palaeoclimate, whether used with plants or insects, present contradictions [30,33].

Nevertheless, the climate shift from the Eocene to the Oligocene opened a probably vast new habitat for *Athalia* in the Palaearctic region and might mark the onset of a major radiation of the genus. So *Athalia* probably dispersed to, or persisted in higher latitudes, where most of their descendents remain today.

Acknowledgements

We are indebted to Dr S. Schulmeister (New York), Dr M.S. Engel (Lawrence) for providing valuable advices to the Tenthredinidae, and two anonymous reviewers for comments on the manuscript. In particular, we would like to thank Dr R. Güsten (Darmstadt) for the loan of several pinned *Athalia* specimens from the collection of the HLMD (Hessisches Landesmuseum Darmstadt). We are also grateful to Prof. Dr. J. Rust (Bonn) for providing valuable advice. This work would not have been possible without the generous support of M. Moser, Director of Holcim SA Altkirch, who provided access to the quarry and supported S. Hinsken during work on his Masters thesis. We also greatly appreciate the technical support of the miners.

References

[1] M. Abe, A biosystematic study of the genus *Athalia* Leach of Japan (Hymenoptera: Tenthredinidae), Esakia 26 (1988) 91–131.

[2] R.B. Benson, A revision of the Athaliini (Hymenoptera: Tenhredinidae), Bull. Brit. Mus. (Nat. Hist.), Entomol. 2 (7) (1962) 333–382.

[3] M.-M. Blanc-Valleron, M. Schuler, The salt basins of Alsace (southern Rhinegraben), in: G. Busson, B.C. Schreiber (Eds.), Sedimentary Deposition in Rift and Foreland Basins in France and Spain (Palaeogene and Lower Neogene), Columbia University Press, New York, 1997, pp. 95–135.

[4] B.W. Boyer, Green River Laminites: Does the playa lake model really invalidate the stratified lake model?, Geology 10 (1982) 321–324.

[5] G. Braun, Zur Morphologie der Umgebung von Basel, Verh. d. naturf. Ges. Basel 25 (1914) 128–142.

[6] F.M. Carpenter, Superclass Hexapoda, in: R.C. Moore, R.L. Kaesler (Eds.), Treatise on invertebrate paleontology. Part R. Arthropoda 4 (3–4), Geol. Soc. Am, Univ. Kansas Press, Boulder, Colorado, 1992, 655 p.

[7] T.D.A. Cockerell, Fossil saw-flies from Florissant, Colorado, Bull. Am. Mus. Nat. Hist. 22 (1906) 499–501.

[8] T.D.A. Cockerell, Hymenoptera and a Caddis Larva from the Miocene of Colorado, Ann. Mag. Nat. Hist. 20 (9) (1927) 429–435.

[9] M.E. Collinson, Vegetational and floristic changes around the Eocene/Oligocene boundary in western and central Europe, in: D.R. Prothero, W.A. Berggren (Eds.), Eocene–Oligocene Climatic and Biotic Evolution, Princeton University Press, Princeton, NJ, USA, 1992, pp. 437–450.

[10] P. Duringer, Les conglomérats des bordures du rift cénozoique rhénan. Dynamique sédimentaire et contrôle climatique, PhD thesis, University Louis-Pasteur, Strasbourg, 1988, 278 p. (unpublished).

[11] H.P. Eugster, R.C. Surdam, Depositional environment of the Green River Formation of Wyoming: a preliminary report, Geol. Soc. Am. Bull. 84 (1973) 1115–1120.

[12] B. Förster, Die Insekten des „plattigen Steinmergels“ von Brunnstatt, Abh. geol. Specialkt, Elsass-Lothringen 3 (1891) 333–594.

[13] J.-C. Fontes, A. Filly, J. Gaudant, P. Duringer, Origine continentale des évaporites paléogènes de haute Alsace : arguments paléoécologiques, sédimentologiques et isotopiques, Bull. Soc. géol. France 162 (4) (1991) 725–737.

[14] J.L. Franzen, Revision der Gattung Palaeotherium Cuvier 1804 (Palaeotheriidae, Perissodactyla, Mammalia), Inaugural Diss., Freiburg im Breisgau, Univ. Freiburg, 1968, 181 p.

[15] J. Gaudant, Sur la présence de *Gobiidae* (poissons téléostéens) dans l'Oligocene inferieur de Rouffach (Haut-Rhin), Sci. Géol. 32 (2) (1971) 131–137.

[16] J. Gaudant, Un nouveau *Cyprinodontidae* (Poisson téléostéen) de l'Oligocène inférieur de Kleinkembs (pays de Bade, Allemagne): *Prolebias rhenanus* nov. sp. *Erratum* et *corrigendum*, Sci. Géol. 37 (2) (1984) 173–174.

[17] J. Gaudant, Mise au point sur l'ichthyofaune oligocène de Rott, Stösschen et Orsberg (Allemagne), C. R. Acad. Sci. Paris, Ser. II 306 (1988) 831–834.

[18] J. Gaudant, T. Burkhardt, Sur la découverte de poissons fossiles dans les marnes grises rayées de la Zone fossilifère (Oligocène basal) d'Altkirch (Haut-Rhin), Sci. Géol. 37 (2) (1984) 137–152.

[19] P. Hoffmann, A.Y. Huc, B. Carpentier, P. Schäffer, P. Albrecht, B. Keely, et al., Organic matter of the Mulhouse Basin, France: a synthesis, Org. Geochem. 20 (8) (1993) 1105–1123.

[20] J.J. Hooker, British mammalian palaeocommunities across the Eocene–Oligocene transition and their environmental implications, in: D.R. Prothero, W.A. Berggren (Eds.), Eocene–Oligocene Climatic and Biotic Evolution, Princeton University Press, Princeton, NJ, USA, 1992, pp. 449–515.

[21] H. Lutz, Beitrag zur Kenntnis der Unteroligozänen Insektenfauna von Céreste (Süd-Frankreich), Documenta Naturae 21 (1984) 1–25.

[22] H. Lutz, Eine fossile Stielaugenfliege aus dem Unter-Oligozän von Céreste, Frankreich (Diptera: Culicidae), Paläont. Z. 59 (1985) 1–2 75–78.

[23] H. Lutz, Eine fossile Stechmücke aus dem Unter-Oligozän von Céreste, Frankreich (Diptera: Culicidae), Paläont. Z. 59 (3/4) (1985) 269–275.

[24] H. Lutz, Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt, Cour. Forsch., Inst. Senckenberg 124 (1990) 1–165.

[25] H. Lutz, Die fossile Insektenfauna von Rott, in: W. von Koenigswald (Ed.), Fossillagerstätte Rott bei Hennef am Siegengebirge. Das Leben an einem subtropischen See vor 25 Millionen Jahren, Siegburg, Rheinlandia Verlag, 1996, pp. 41–56.

[26] H. Lutz, Taphozönosen terrestrischer Insekten in aquatischen Sedimenten- ein Beitrag zur Rekonstruktion des Paläoenvironments, N. Jahrb. Geol. Paläont. Abh. 203 (1997) 173–210.

[27] A.D. MacGillivray, A study on the wings of the Tenthredinoidea, a superfamily of Hymenoptera, Proc. US Nat. Mus. 29 (1438) (1906) 569–654.

[28] D.H. Mai, Tertiäre Vegetationsgeschichte Europas, G. Fischer, Jena, Germany, 1995, 691 p.

[29] E. Martini, Die Gattung *Eosphäroma* (Isopoda) im europäischen Alttertiär, Senckenb Lethaea 53 (1–2) (1972) 65–79.

[30] H.W. Meyer, The fossils of Florissant, Smithsonian Books, Washington, 2003, 258 p.

[31] M. Mieg, G. Bleicher, P. Fliche, Note complémentaire sur le gisement de Roppenzwiller et le gisement à insectes et à plantes de Kleinkembs, Bull. Soc. géol. France 20 (1892) 375–385.

[32] A. Nel, Analyses d'entomofaunes cenozoiques : intérêts de la paléoentomologie pour les sciences de la terre et de la vie, thèse, Paris, 1991, 890 p. (unpublished).

[33] A. Nel, The probabilistic inference of unknown data in phylogenetic analysis, in: P. Grancolas (Ed.), The origin of Biodiversity in insects: phylogenetic tests on evolutionary scenarios, Mém. Mus. natl Hist. Nat. 173 (1997) 305–327.

[34] A. Nel, J. Nel, C. Balme, Un nouveau Lépidoptère *Satyrinae* fossile de l'Oligocène du Sud-Est de la France (*Insecta, Lepidoptera, Nymphalidae*), Linn. Belg. 14 (1) (1993) 20–36.

[35] R. Pflug, Bau und Entwicklung des Oberrheingrabens, Wissenschaftl. Buchges, Darmstadt, 1982, 145 p.

[36] H.U. Pfretzschner, Ein weiteres Exemplar von Lethe? corbieri Nel 1993 (Lepidoptera, Satyridae) aus dem Unter-Oligozän von Céreste (Süd-Frankreich), Paläont. Z. 72 (1–2) (1998) 56–64.

[37] D.R. Prothero, The Eocene–Oligocene Transition, Columbia University Press, New York, 1994, 291 p.

[38] A.P. Rasnitsyn, An outline of evolution of the hymenopterous insects (order Vespidae), Orient. Insects 22 (1988) 115–145.

[39] A.P. Rasnitsyn, X. Martínez-Delclòs, Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain, Acta Geol. Hist. 35 (2000) 65–95.

[40] A.P. Rasnitsyn, D.L.J. Quicke, in: History of insects, Kluwer Academic. Publisher, Dordrecht, The Netherlands, 2002 517 p.

[41] J. Rust, Biologie der Insekten aus dem ältesten Tertiär Nordeuropas, Habil. Biol. Fak. Univ. Göttingen, Göttingen, 1999 482 p.

[42] N. Schmidt-Kittler, G. Storch, Ein vollständiges Theridomyiden-Skelett (Mammalia: Rodentia) mit Rennmaus-Anpassungen aus dem Oligozän von Céreste, S-Frankreich, Senckenb. Lethaea 66 (1–2) (1985) 89–109.

[43] M. Schuler, Environments et paléoclimats paléogènes : palynologie et biostratigraphie de l'Éocène et l'Oligocène inférieur dans les fossés rhénan, rhodanien et de Hesse, Doc. BRGM 190 (1990) 1–535.

[44] S. Schulmeister, Review of morphological evidence on the phylogeny of basal Hymenoptera (Insecta), with a discussion of the ordering of characters, Biol. J. Linn. Soc. 79 (2003) 209–243.

[45] S. Schulmeister, Genitalia and terminal abdominal segments of male basal Hymenoptera (Insecta): morphology and evolution, Org. Divers. Evol. 3 (4) (2003) 253–279.

[46] M.E. Schumacher, Upper Rhinegraben: Role of preexisting structures during rift evolution, Tectonics 21 (1) (2002) 1006; doi: 10.1029/2000TC001265.

[47] H.G. Sthelin, Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Bassin de Paris, Bull. Soc. géol. France 9 (1909) 488–520.

[48] N. Théobald, Les insectes fossiles des terrains oligocènes de France, Mém. Soc. Sci. Nancy, N.S. 1 (1937) 1–437.

[49] L. Vilhelmsen, Phylogeny and classification of the extant basal lineages of the Hymenoptera, Zool. J. Linn. Soc. 131 (2001) 393–442.

[50] W. Wagner, Woher und wann trat das Tertiärmeer zum ersten Mal in die Rheintalsenke ein, Notizbl. Ver. Erdk. Hess. Geol. L.-Anst. Darmstadt 5 (7) (1924) 56–89.

[51] T. Wappler, Die Insekten aus dem Mittel-Eozän des Eckfelder Maares, Vulkaneifel, Mainzer naturwiss. Arch., Beiheft 27 (2003) 1–234.

[52] T. Wappler, Systematik, Phylogenie, Taphonomie und Paläoökologie der Insekten aus dem Mittle-Eozän des Eckfelder Maares, Vulkaneifel, Clausthaler Geowiss. 2 (2003) 1–241.

[53] T. Wappler, The first lace bug (Insecta: Heteroptera: Tingidae) from the Lower Oligocene deposits near Céreste, France, N. Jahrb. Geol. Paläont. Mh. 5 (2004) 277–287.

[54] J.A. Wolfe, Climatic, floristic, and vegetational changes near the Eocene/Oligocene boundary in North America, in: D.R. Prothero, W.A. Berggren (Eds.), Eocene–Oligocene climatic and biotic evolution, Princeton University Press, Princeton, 1992, pp. 421–436.

[55] A.N. Zhelochovtzev, A.P. Rasnitsyn, On some Tertiary sawflies (Hymenoptera, Symphyta) from Colorado, Psyche 79 (1972) 315–327.

[56] P.A. Ziegler, Geological Atlas of Western and Central Europe, Shell Internationale Petroleum Maatschappij, The Hague, The Netherlands, 1990, 239 p.