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Insects from the Lower Toarcian of Middle Europe and England

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Abstract. Lower Toarcian insect localities of Middle Europe and England are reviewed. The insects come from carbonate concretions (*falciferum* zone) which are intercalated in Northern Germany within the marine clay of the "Green Series" and elsewhere in the Posidonia Shale. Beside one spider and one scorpion, insects of 21 orders were recognized. The species composition of the different insect taphocoenoses is very similar, differences exist only in the composition of the Fulgoromorpha (Homoptera: Auchenorrhyncha), which may indicate a kind of provincialism. Palaeobiogeographical, palaeoecological and taphonomical problems are discussed. Apart from a number of taphonomical filters, the distance to the shore line is the most delimiting factor for the composition of marine taphocoenoses. A faunal exchange between Laurasia and Gondwana was possible in the Lower Jurassic.

Key words: Lower Toarcian, Jurassic, insects, Germany, Europe, palaeobiogeography, palaeoecology, taphonomy.

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I. INTRODUCTION

The Upper Liassic insect faunas of Middle and Western Europe belong to the most important older Mesozoic faunas in the world. From localities in Northern and Southern Germany, Switzerland, Luxembourg, Belgium and England many thousand insects are kept in museum and private collections.

All insects originate together with marine fossils like ammonites, theuthoideans, bivalves, fishes and marine saurians from early diagenetic limestone concretions which are intercalated within marine clay of the "Green Series" or the famous Posidonia Shale. The salinity in the depositional area of the "Green Series" clay was reduced and the water was rather brackish, because large rivers drained Fennoscandia to the south.

In accordance with the Lower Toarcian palaeogeography the insects originate from the surrounding mainlands (Fennoscandia, Bohemian Mass, London-Brabant Mass) or offshore islands (Fig. 1).

In most cases only isolated wings are preserved, complete specimens are more often to be found in near shore localities. Aquatic larvae are completely absent; ground dwelling arthropods are extremely rare. The insects got lost during own active dispersion flights over the sea or during strong seaward wind, a smaller number was washed by rivers to the sea.

Taphonomic and fossil diagenetic processes delimiting the input from the biocoenoses are the main factors during the set up of the marine insect taphocoenoses. The best preservation, even of non sclerotized body parts is to be noticed in Grimmen (Western Pomerania) and Dobbertin (Mecklenburg), where even beetles are preserved in three dimensions. Preservation is also good in fine grained limestone layers of the Lower Saxonian *borealis* concretions; beetles, however, are more or less flattened like in all other localities. The insects in the Posidonia Shale localities of Southern Germany are in worse condition, only insects with more heavily sclerotized wings are sufficiently preserved.

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II. UPPER LIASSIC INSECTS LOCALITIES

The occurrence of insects in the Upper Liassic of Middle and Western Europe is restricted to a short period at the beginning of the Lower Toarcian (Table I). During an Oceanic Anoxic Event (OAE) black shales (Posidonia Shale) were deposited in the European epicontinental sea (JENKYNS 1988). Fine grained micritic calcerous nodules or layers, in which fossils are extraordinary well preserved, generated under anoxic calm water conditions without bioturbation of the sediment.

Carbonate concretions with insects occur exclusively in the lower part of the *falciferum* ammonite zone (*elegantulum*, *exaratum* subzones). In a few cases beetle elytra were recognized in the *siemensi* nodules (uppermost part of *tenuicostatum* zone) of Grimmen and Schandelah (Lower Saxony).

A correlation of nodule layers is limited to Northern and Southern Germany (e.g. *elegantulum* nodules of Grimmen and Ahrensburg; "Unterer Stein" of SW Germany and *siemensi* nodules of Upper Franconia). Probably the "Unterer Stein" is time aequivalent to the *elegantulum* nodules of Northern Germany.

Table I

Ammonite zones of the Lower Toarcian with insect occurrences in the *elegantulum* and *exaratum* subzones

Lower Jurassic	**Lower Toarcian** **185 Mio. years**	*bifrons*-zone			
		falciferum-zone	*falciferum*-subzone *elegans*-subzone *exaratum*-subzone *elegantulum*-subzone	**insects**	
		tenuicostatum-zone			**sea level rise**

The insect faunas from all deposits are very similar; a number of species was recorded in each major locality. Table II shows the composition of the insect orders in the investigated localities. All fragments which were determinable at least to the order level were taken into the account from authors collection. The new data are set in comparison with the data gathered from HANDLIRSCH (1906-08, 1939) for Dobbertin and BODE (1953) for Braunschweig. It is to note that most of the species described by HANDLIRSCH and BODE were based on the holotype only and so the species number corresponds to the number of specimen. The revision of certain groups with many de-

Table II

Distribution of insect orders in major German localities in percent, data from author's collection in comparison to HANDLIRSCH (Dobbertin), BODE (Braunschweig) and BRACHERT (Kerkhofen). Hemiptera comprise Heteroptera + Coleorrhyncha, Amphiesmenoptera comprise Trichoptera + Lepidoptera + Necrotauliidae

	Dobbertin		Braunschweig		Grimmen	Kerkhofen		Mistelgau	Holzmaden
	Handlirsch	Ansorge	Bode	Ansorge	Ansorge	Brachert	Ansorge	Ansorge	Ansorge
Ephemeroptera	–	–	–	–	0.05	–	–	–	–
Odonata	7.2	4.3	7.2	6.5	3.2	16.5	2 expl.	2.3	11 expl.
Saltatoria	19.1	11.6	10.5	6.2	14.4	6.8	3 expl.	5.1	1 expl.
Phasmatodea	–	–	1.4	0.3	0.1	1.0	–	–	–
Grylloblattida	1.6	0.2	3.5	0.1	0.6	x	–	–	–
Blattodea	7.2	4.3	3.0	0.4	2.0	2.0		1.6	2 expl.
Plecoptera	–	0.2	–	–	0.1	–		–	–
Dermaptera	–	0.2	–	–	0.2	–		0.5	–
Auchenorrhyncha	20.1	14.0	18.5	24.8	7.9	25.2	1 expl.	24.3	12 expl.
Sternorrhyncha	0.5	4.0	–	3.4	1.6	–	–	–	–
Hemiptera	2.0	7.7	6.7	2.7	15.5	–	2 expl.	6.2	–
Psocoptera	0.2	0.2	–	1.3	0.2	–	–	–	–
Lophioneurida	–	1.6	–	0.4	3.8	–	–	–	–
Coleoptera	9.5	11.5	22.2	1.5	14.7	21.3	2 expl.	28.4	3 expl.
Hymenoptera	–	0.4	–	–	–	–	–	0.5	–
Planipennia	4.2	4.3	7.4	9.6	3.3	12.6	1 expl.	5.1	4 expl.
Megaloptera	0.2	–	–	–	–	–	–	–	–
Raphidiodea	–	0.2	0.2	0.3	–	–	–	–	–
Amphiesmenoptera	8.3	8.0	1.2	6.7	6.6	1.0	2 expl.	6.2	4 expl.
Mecoptera	6.5	1.6	4.9	1.3	1.8	11.6	1 expl.	2.2	–
Diptera	10.8	23.0	13.4	33.9	23.4	2.0	6 expl.	17.6	3 expl.
Chelicerata	–	–	1 scorpio	–	1 spider	–	–	–	–
total specimen	**433**	**958**	**432**	**663**	**2042**	**103**	**20**	**176**	**39**

scribed species (Saltatoria: Elcanidae, Blattodea: Blattulidae, Amphiesmenoptera: Necrotauliidae, Diptera: Limoniidae) reduced the number of valid species considerably (ZESSIN 1987, ANSORGE 2002a, b, VRŠANSKÝ & ANSORGE in prep., KRZEMIŃSKI & ANSORGE in prep.). A revision of the most abundant group of *Fulgoridium* HANDLIRSCH, 1906 (Homoptera: Fulgoromorpha) will surely reduce the number of more than 100 described species considerably.

On the other hand many new, either rare or very small species were described in the last years. Most of the material presented here is kept in authors collection and will later be housed in Museum für Naturkunde der Humboldt Universität Berlin (LGA=Grimmen, LDA=Dobbertin, S=Schandelah). The material from Holzmaden (H) will later be housed in Staatliches Museum für Naturkunde Stuttgart.

In the references to the fossil sites all papers are cited which deal with original material from the locality.

Grimmen

(Fig. 1, 1)

In the open cast of Klein Lehmhagen, near Grimmen (Western Pomerania) Upper Liassic clay of the "Green Series", dislocated by Pleistocene glaciers, is mined. Insects occur usually in flat 1-10 cm large kidney shaped calcareous nodules of the *exaratum* subzone and in lesser degree in the larger *elegantulum* nodules (ANSORGE 1996). Very seldom insects were also found in living chambers of *Eleganticeras elegantulum* macrochonchs and in fish coprolites which are the most frequent fossils at all.

In the *elegantulum* nodules mainly isolated beetle elytra occur, what is together with thin quartz sand layers an indicator for fluvial input. In the *exaratum* nodules a fluvial input is hardly to note, what is in accordance with a global sea level rise at the beginning of the Lower Toarcian (Table I). On the other hand, complete beetles (Fig. 4B), bugs (Heteroptera, Fig. 3D), coleorrhynchans (Fig. 3B-C) and archijassid cicadas (Fig. 3F) occur in these nodules. These heavier insects are rather poor fliers and sink more rapidly after landing on the water surface. The relatively high percentage of beetles and bugs indicates a near shore deltaic complex as was suggested by ERNST (1967, 1991).

The highest percentages of elcanids (Saltatoria; Fig. 2C) in all stages of decay are also to state in Grimmen. Most probably these insects swarmed in near shore regions to settle next islands.

Aeroplankton is extraordinarily well preserved in Grimmen, the most abundant representatives of the aeroplankton (~3 mm) are lophioneurids (*Undacypha europaea* ANSORGE, 1996; Fig. 3A), which are more rare or totally absent in other localities. Species of Sternorrhyncha (aphids, psyllids and archiconiopterygids like *Archiconiopteryx liasina*, Fig. 3E) are very rare.

R e f e r e n c e s: ANSORGE 1986, 1994, 1996a, 1999c, 2000, 2002; ANSORGE & KRZEMIŃSKI 2002, KRZEMIŃSKI & ZESSIN 1990; RASNITSYN, ANSORGE & ZESSIN in press, VRŠANSKÝ & ANSORGE in prep.; ZESSIN 1983a, 1987, 1988, 1991.

Dobbertin

(Fig. 1, 2)

Pleistocene dislocated Liassic "Green Series" clay crops out in the former clay pit of Schwinz near Dobbertin (Mecklenburg) (MALZAHN 1937; ERNST 1992). Fossil insects were first described by Franz Eugen GEINITZ (1880-94), later studied by Anton HANDLIRSCH (1906-08, 1920-21, 1939). Two similar types of insect bearing nodules occur, which are different from the *elegantulum* nodules from Grimmen and Ahrensburg. These concretions resemble the *exaratum* nodules of Grimmen, but are much larger (10-20 cm). Ammonites which are associated with the insects indicate the *exaratum* subzone. The Pleistocene deformation of the sediment and the restricted outcrop situation of today hinder to measure a complete section.

Due to careful search small insects (~3 mm) are much more abundant in authors collection than in the historical material of GEINITZ and HANDLIRSCH. On the other hand, larger insects (Odonata, Elcanidae, Grylloblattida, Mecoptera) are over represented in the older material, what means that the smaller insects were only overlooked.

In contrast to Grimmen and Ahrensburg fluvial input can not be fixed on quartz sand or silt, but on the presence of conchostracans with articulated shells. Furthermore, whole bedding planes are covered by algae substituted by Ca-phosphate, already noticed by GEINITZ (1880: 531). In these layers insects are more abundant. Algae and conchostracans were probably washed by slowly run-

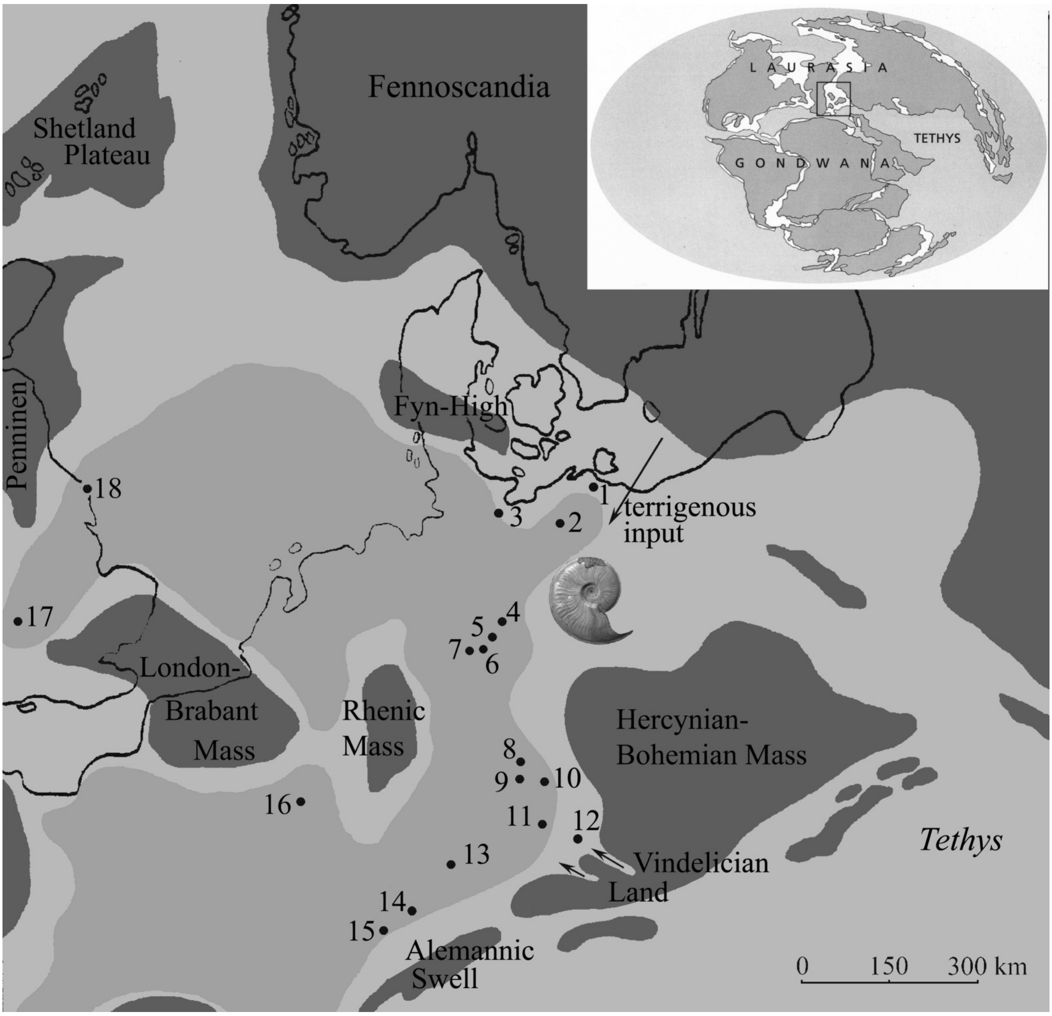

Fig. 1. Lower Toarcian palaeogeography with fossil insect sites. 1 Grimmen (Western Pomerania), 2 Dobbertin (Mecklenburg), 3 Ahrensburg (Schleswig-Holstein), 4 Braunschweig area (Lower Saxony), 5-7 surroundings of Harz Mountains, Lower Saxony (5 Haverlahwiese, 6 Hainberg, 7 Wenzen), 8 Trimeusel/Pferdsfeld (Upper Franconia, Bavaria), 9 vicinity of Bamberg (Upper Franconia, Bavaria), 10 Mistelgau (Upper Franconia, Bavaria), 11 Kerkhofen (Oberpfalz, Bavaria) 12 Regensburg (Oberpfalz, Bavaria), 13 Holzmaden near Stuttgart (Suevia, Baden-Württemberg), 14 Aselfingen, Wutach valley (Baden-Württemberg), 15 Hemmiken (canton Baselland, Switzerland), 16 Bascharage (Luxembourg and neighbouring Belgium), 17 Alderton and Dumbleton (Gloucestershire, England), 18 Whitby (Yorkshire, England).

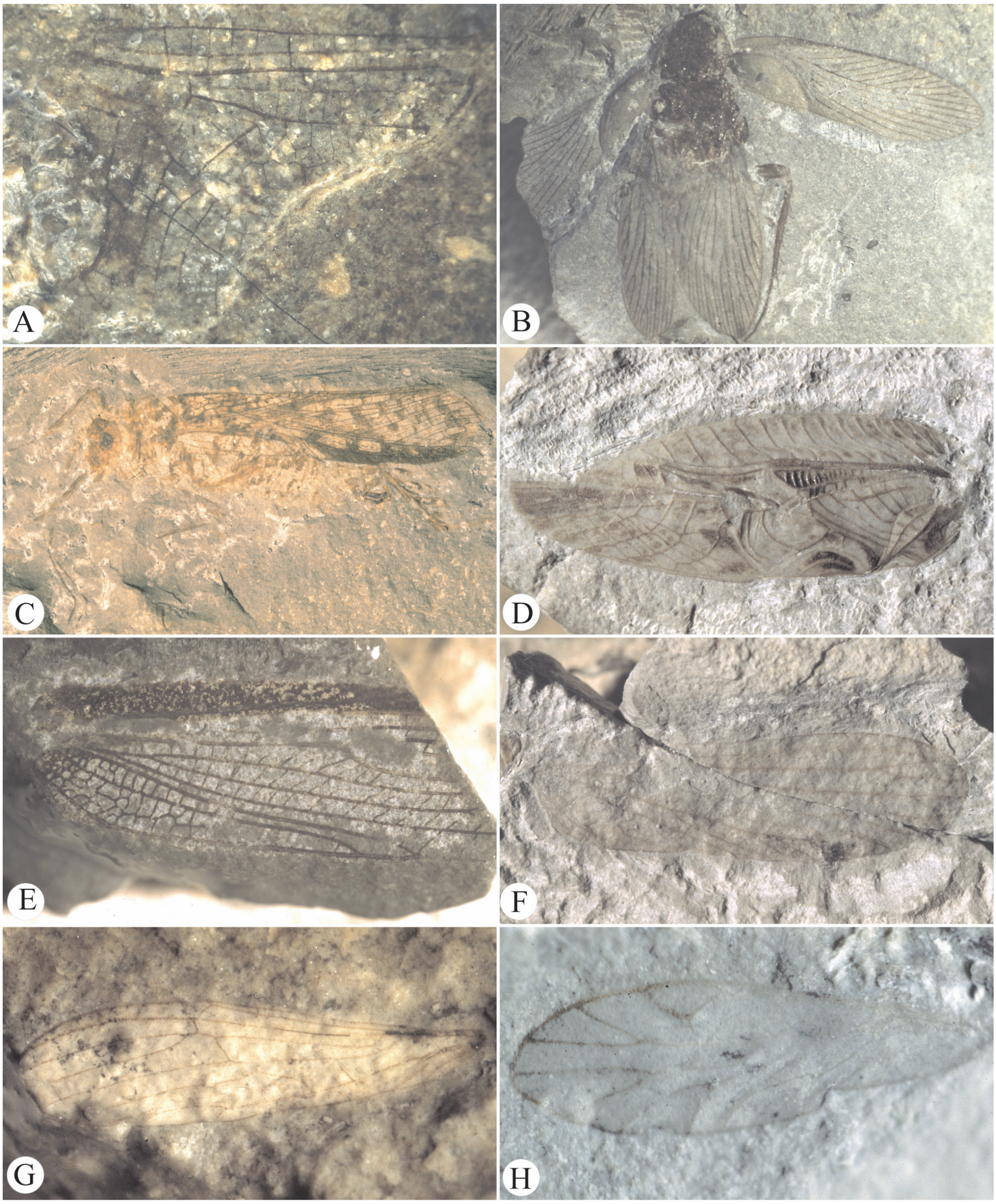

Fig. 2. Insects from the Lower Toarcian of Germany. A: *Liassogomphus brodiei* (BUCKMAN, 1843), (Odonata, Liassogomphidae), H 15, Holzmaden, basal width 11 mm. B: *Elisama langfeldti* (GEINITZ, 1880), (Blattodea: Blattulidae), LGA 1820, Grimmen, forewing length 8 mm. C: *Elcana geinitzi* HANDLIRSCH 1906 male (Saltatoria: Elcanidae), LGA 445, Grimmen, 15 mm forewing length. D: *Protogryllus dobbertinensis* (GEINITZ 1880) male (Saltatoria: Protogryllidae), LGA 1267, Grimmen, 12.1 mm. E: *Durnovaria parallela* WHALLEY 1985, (Phasmatodea: Aerophasmatidae), LGA 1086, Grimmen, 14 mm. F: *Nele jurassica* ANSORGE 1996 (Grylloblattida: Neleidae), LGA 1310, Grimmen, 17.5 mm. G: *Dicronemoura furcata* ANSORGE 1996 (Plecoptera: Perlariopseidae), LGA 1278, Grimmen, 7.2 mm. H: *Liassopsocus lanceolatus* ANSORGE 1996, (Psocoptera: Psocidiidae), LGA 997, Grimmen, 4 mm.

ning streams in to the sea. The algae were probably an important eutrophication factor which contributed considerably to the black shale formation in the Lower Toarcian.

The insect taphocoenosis of Dobbertin is most similar to that of Grimmen. Although both localities are only 100 km apart, they show, however, remarkable differences. While fulgoridiids (*Fulgoridium* sp.) dominate among cicadas in Dobbertin, archijassids (*Archijassus*, *Ardela*) are most abundant in Grimmen (Table III). The aeroplankton percentage of both localities is similar; however, sternorrhynchans (aphids like *Juraphis* SHAPOSHNIKOV, 1979 and *Grimmenaphis* ANSORGE, 1996, psyllids like *Liadopsylla* HANDLIRSCH, 1920) are considerably more abundant in Dobbertin than in Grimmen.

R e f e r e n c e s: ANSORGE 1991, 1993a,b,c, 1994, 1995, 1996a 1999a,b, 2000, 2001a,b, 2002; ANSORGE & KRZEMIŃSKI 1995, 2002; ANSORGE & RASNITSYN 2000; ANSORGE & SCHLÜTER 1990; ENDERLEIN 1909; GEINITZ 1880, 1883, 1884, 1887, 1894; HANDLIRSCH 1906-08, 1909, 1920-21, 1939; HERRIG & NESTLER 1989; KRZEMIŃSKI & ANSORGE 2000; LUKASHEVICH et al. 1998; NEL et al. 1993; PONOMARENKO & SCHULZ 1988; POPOV 1989, 1992; POPOV & SHCHERBAKOV 1991; POPOV & WOOTTON 1977; RASNITSYN, ANSORGE & ZESSIN in press; VRŠANSKÝ & ANSORGE in prep.; WENDT 1940; WILLMANN 1978, 1984b, 1989; ZESSIN 1981, 1982, 1983a, 1985, 1987, 1988, 1991; ZESSIN & ANSORGE 1987; ZESSIN & KOENIGSTEDT 1993; ZEUNER 1939, 1942.

Ahrensburg

(Fig. 1, 3)

Lower Toarcian e*legantulum* nodules of similar petrography and fossil content to those of Grimmen were frequent in the Pleistocene (Weichselian) so called Ahrensburg erratic boulder assemblage, near Hamburg (LEHMANN 1968; LIERL 1990). A few insects, mostly beetle elytra, one limoniid dipteran, a liassogomphid dragonfly, a blattulid roach and *Protogryllus* HANDLIRSCH, 1906 were recognized. The most remarkable insect fossil is a 4 cm long beetle elytron, which is the largest beetle in the Upper Liassic.

Table III

Distribution of hemipterous plant sucking insects in major Lower Toarcian insect localities of Germany

	Grimmen	**Dobbertin**	**Schandelah**	**Kerkhofen**	**Mistelgau**	**Holzmaden**
total insects	**2042**	**958**	**663**	**103**	**176**	**39**
Homoptera	**9.5 %**	**18.0 %**	**28.2 %**	**25.2 %**	**27.8 %**	**30.1 %**
Sternorrhyncha	16.9 %	22.1 %	12.3 %	–	–	–
Auchenorrhyncha	83.1 %	77.9 %	87.7 %	100 %	100 %	100 %
Fulgoridium s.l.	4.6 %	60.5 %	79.2 %	50 %	83.8 %	58.3 %
Fulgoridulum	10.8 %	0.6 %	–	–	–	–
Elasmocelidium	–	–	1.1 %	26.9 %	–	16.7 %
other Fulgoroidea	3.1 %	2.3 %	2.6 %	19.2 %	9.3 %	25 %
Procercopidae	4.1 %	4.1 %	3.2 %	3.9 %	2.3 %	–
Archijassidae	60.5 %	10.4 %	1.6 %	–	4.6 %	–
Tettigarctidae	–	–	BODE (1953)	NEL (1996)	–	–
Heteroptera	**5.5 %**	**3.7 %**	**2.4 %**	**x**	**4.5 %**	**–**
Coleorrhyncha	**10.0 %**	**4.0 %**	**0.3 %**	**–**	**1.7 %**	**–**

Braunschweig

(Fig. 1, 4)

Fossil insects from the vicinity of Braunschweig (Lower Saxony), mainly from the village Schandelah, were first reported by BODE (1905, 1953): the northern most insects in this region come from the city of Wolfsburg (KIERST & WIESNER 1974).

Detailed sections on the Posidonia Shale of Schandelah were published by WUNNENBERG (1927) and WELLNHOFER & VAHLDIEK (1986). According to these authors insects are to be found in the lower *elegans* nodules (*elegantulum* subzone) and the upper *borealis* nodules (*exaratum* subzone). Both types of nodules can reach 30 cm thickness with 60 cm diameter and are lithologically similar to the *siemensi* nodules of Franconia. Concentrations of insect remains, up to 30 on 60 cm^2, frequently occur on bedding or event planes in thin very fine grained blue limestone layers of the *borealis* nodules. Similar concentrations are only very seldom to notice in other localities. These concentrations most probably generated as a result of strong storms during which large amounts of aeroplankton were blown over the sea. At this point it is to note again, that the fossils determined by BODE (1953) as midges larvae are in fact wingless dipterans bodies and that aquatic insect larvae are totally absent from marine insect taphocoenoses.

A comparison between the BODE material and non selective collected new material shows, as in Dobbertin, that larger insects are over represented. Beetles, archijassids, heteropterans and coleorrhynchans, which indicate a near shore deposit as in Grimmen, are considerably rare in the *borealis* nodules of Schandelah. On the other hand dragonflies, being good fliers, are more abundant offshore. Furthermore, the content of dipterans and neuropterans is higher than in Grimmen and Dobbertin, aphids are absent up to now and lophioneurids are very rare.

The greater distance of the Braunschweig depositional area to the shore does not allow to state from which mainland the insects originate. In accordance to the palaeogeography the insects could either come from the Bohemian Mass in the South or the Rhenic Mass in the West. The long distance to Fennoscandia in the North and the record of *Elasmocelidium* MARTYNOV, 1926 (Homoptera: Fulgoromorpha) [Fig. 3 I], a genus which is only present in southern localities, rather excludes northern origin.

R e f e r e n c e s: ANSORGE 1993c, 1996a,b, 2001, 2002; ANSORGE & KRZEMIŃSKI 1995, 2002; BODE 1905, 1951, 1953; HANDLIRSCH 1939, KRÜGER 1983; GOROCHOV 1993, KRZEMIŃSKI & KOVALEV 1988; LUKASHEVICH et al. 1998, NEL et al. 1993; PONOMARENKO 1992, 1995, POPOV 1989, POPOV & WOOTTON 1979; RASNITSYN, ANSORGE & ZESSIN in press, STOROZHENKO 1988, VRŠANSKÝ & ANSORGE in prep.; WILLMANN 1978, 1984a, 1989, 1994; ZESSIN 1983a,b, 1985, 1987.

Surroundings of Harz Mountains

(Fig. 1, 5-7)

In the western and northern surroundings of the Harz Mountains (Lower Saxony) there exist a number of smaller outcrops of the Posidonia Shale which delivered a few insects. The former iron ore open mine of Haverlahwiese, Hainberg near Bockenem and a railway cutting near Wenzen are worth of mentioning. Lithology is the same as in the region of Braunschweig.

Trimeusel/Pferdsfeld

(Fig. 1, 8)

In Upper Franconia (Bavaria) the Posidonia Shale has its greatest thickness near Staffelstein (SCHIRMER 1974). At the base of the *falciferum* zone *siemensi* nodules are intercalated within the bituminous paper shale. Half a meter above is a concretion like carbonate layer with abundant snails of *Coelodiscus minutus* (ZIETEN 1832).

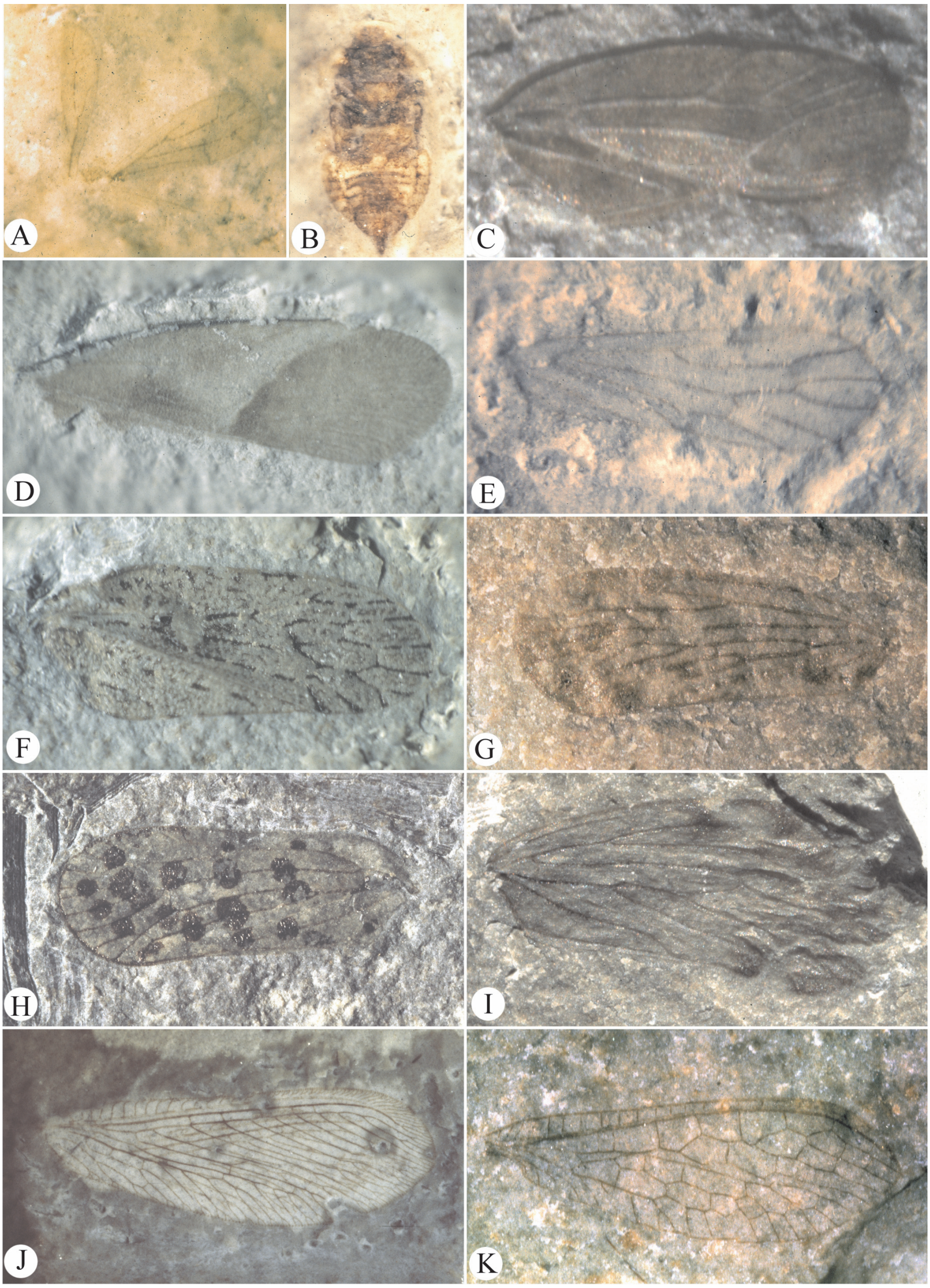

Fig. 3. Insects from the Lower Toarcian of Germany. A: *Undacypha europaea* ANSORGE 1996 (Lophioneurida: Lophioneuridae), LGA 1364, Grimmen, forewing 2.2 mm. B: Wingless female Progonocimidcidae gen. et sp. indet. (Coleorrhyncha), Grimmen, 3 mm. C: *Progonocimex* sp. (Coleorrhyncha: Progonocimicidae), Grimmen, forewing, 4 mm. D: Heteroptera gen. et sp. indet., LGA 936, Grimmen, 6 mm. E: *Archiconiopteryx liasina* (HANDLIRSCH, 1906) [Sternorrhyncha: Archiconiopterygidae], LGA 620, Grimmen, 2.4 mm. F: *Ardela grimmenensis* ANSORGE 1996 (Auchenorrhyncha: Archijasside), LGA 1216, Grimmen, 5.4 mm. G: *Fulgoridium* cf. *balticum* (GEINITZ, 1880), [Auchenorrhyncha: Fulgoridiidae], S 32, Schandelah, 7 mm. H: *Fulgoridulum egens* HANDLIRSCH 1939 (Auchenorrhyncha: Fulgoridiidae), FGWG 125, Grimmen, 6.4 mm. I: *Elasmocelidium boreale* (BODE, 1905), [Auchenorrhyncha: Fulgoridiidae], S 28, Schandelah, 7 mm. J: *Polyosmylus excelsus* ANSORGE 1996 (Planipennia), LGA 1033, Grimmen, 8.2 mm. K: Raphidiodea gen. et sp. nov., S 38, Schandelah, 7.2 mm.

The only known insect from Trimeusel was reported by THEODORI (1840); this *Libellula* was never formally described and seems to be lost today.

A few insects were recently found at Trimeusel, a steep cliff of the river Main near Staffelstein and in Pferdsfeld, a village 5 km to the south in the *coelodiscus* nodules above the *siemensi* nodules. Besides some beetle elytra, wingless dipteran bodies, an imago of *Necrotaulis parvulus* (GEINITZ, 1884) and a forewing of *Fulgoridium* sp. were found.

Bamberg

(Fig. 1, 9)

From the Posidonia Shale in the vicinity of Bamberg (Upper Franconia) two insects (*Geisfeldiella benkerti, Schesslitziella haupti*) were described by KUHN (1951, 1952), the latter was revised by ANSORGE (1996b). Unfortunately the outcrop situation is very poor, so that no new findings could be made there.

Mistelgau

(Fig. 1, 10)

Upper Liassic (Upper Toarcian) clay is mined for brickworks in an open mine at Mistelgau (near Bayreuth, Upper Franconia). The Posidonia Shale below is only infrequently open and exposes large (diameter of half and more meter) *siemensi* nodules at its base. A section of the Posidonia Shale was measured by KRUMBECK (1932). Basing on some lithological differences it can be doubted whether the *siemensi* nodules of Mistelgau and Trimeusel are time equivalent. Insects are rather frequent in this nodules which split after frost weathering very well. Most abundant are isolated beetle elytra with one third of all insects. This predominance of isolated beetle elytra corresponds well with the supposed palaeogeographical position of Mistelgau near the crystalline basement of the Bohemian Mass.

Up to now only a female of *Xyelula benderi* RASNITSYN, ANSORGE & ZESSIN (in press) (Hymenoptera: Sepulcidae) was described.

Kerkhofen

(Fig. 1, 11)

The Posidonia Shale was temporary exposed near the village Kerkhofen during excavation of the Rhine Main Donau canal (Oberpfalz, Bavaria). Insects from this locality were first published by BRACHERT (1987); further insects were figured by BERGER (1989) and SCHMIDT-KAHLER et al. (1992). The insects of BRACHERT come exclusively from the lower *siemensi* nodules. BERGER and SCHMIDT-KAHLER et al. (op.cit.), however, reported insects also from the above layer of carbonate nodules. An adequate description exists only of *Liassotettigarcta mueckei* NEL, 1996 (Auchenorrhyncha: Tettigarctidae) which is most probably a younger synonym of *Liassocicada antecedens* BODE, 1953. The BRACHERT collection housed at Staatliches Museum für Naturkunde Stuttgart contains predominantly large, easy recognizable insects; small insects were obviously overlooked. The high percentage of beetles in Kerkhofen corresponds well with the position of this locality close to the Bohemian Mass.

Regensburg

(Fig. 1, 12)

Near shore Posidonia Shale with sand and paralic coal is exposed in the Regensburg bight at the margin of the Bohemian Mass. Since the record of isolated beetle elytra by AMMON (1875) no insects were reported from the Irlbach slates.

Holzmaden

(Fig. 1, 13)

Rather sensational was the record of insects in the famous Posidonia Shale of Holzmaden (near Stuttgart, Baden-Württemberg), which for more than 200 years is famous for its marine vertebrates, like ichthyosaurs (ANSORGE 1999a). Insects were believed to be absent from the Suevian Posidonia Shale due to preservation reasons (SEILACHER 1990).

During own field work about 40 insects were collected from a carbonate layer, the so called "Unterer Stein", which is at the base of *exaratum* subzone (RIEGRAF 1985, RIEGRAF, WERNER & LÖRCHER 1984, RÖHL 1998, URLICHS et al. 1994). This very hard nodule laminated carbonate layer is of about 20 cm thickness and splits conchoidally. The "Unterer Stein" splits only in accordance with its lamination where fossils are discontinuity surfaces. In this stone only more sclerotized insect remains are well preserved, soft wings are only to recognize by their shape or the faint relief of veins. Considerably many dragonflies (Fig. 2A) and neuropterans indicate an offshore deposition far from the coast.

Aselfingen

(Fig. 1, 14)

The Posidonia Shale is exposed in the Wutach valley near Aselfingen (southern Baden-Württemberg). The "Unterer Stein" is of similar lithology as in Holzmaden. One *Fulgoridium* sp. fore wing was collected at this locality (Homoptera: Auchenorrhyncha).

Hemmiken

(Fig. 1, 15)

A first fossil insect, an articulated female of the dragonly *Liassogomphus brodiei* (BUCKMAN, 1843), was described by ETTER & KUHN (2000) from the "Unterer Stein" of a temporary Posidonia Shale outcrop at Hemmiken (canton Baselland, northern Switzerland).

Bascharage

(Fig. 1, 16)

A considerable number of insects were collected in the Posidonia Shale of Bascharage (Luxembourg) (HENROTAY et al. 1998) and localities in the bordering Belgium (DELSATE et al. 1992). The insects come from carbonate nodules which are intercalated in bituminous paper shale of *exaratum* subzone.

Selected species of Coleoptera, Odonata and Planipennia were described by NEL and co-authors.

R e f e r e n c e s: HENROTAY et al. 1998; HENROTAY, NEL & JARZEMBOWSKI 1997; MAUBEUGE 1973; NEL 1989; NEL & HENROTAY 1992, 1994; NEL et al. 1993, DELSATE et al. 1999.

Gloucestershire

(Fig. 1, 17)

Insects from the historical Lower Toarcian localities of Alderton and Dumbleton in Gloucestershire (England) are known since the 19th century from nodules intercalated in the Posidonia Shale. A comprehensive overview of insects from the English Upper Lias is still not published. Only selected groups were studied by various authors.

R e f e r e n c e s: BRODIE 1845; BUCKMAN 1843; SCUDDER 1886; HANDLIRSCH 1906-08; TILLYARD 1925, 1933; VRŠANSKÝ & ANSORGE in prep.; WESTWOOD 1849, 1854; WHALLEY 1988; ZEUNER 1939.

Whitby

(Fig. 1, 18)

Until present, insects were unknown from the Upper Lias of Yorkshire. Through the courtesy of H.-J. LIERL (Hamburg) I had the opportunity of studying a pyritized *Locustopsis* sp. (Saltatoria: Locustopsidae) on the surface of a pyrite concretion collected at the cliff of Rosedale Wyke (Whitby).

III. PALAEOBIOGEOGRAPHY

As it was mentioned above the insect faunas of all Lower Toarcian localities are very similar. Numerous common species are known from all major localities. Good fliers were able to cross the sea and to disperse very regularly; the aeroplankton was passively distributed by aerial currents.

Conspicuous differences exist in the species and percentage composition of the plant sucking hemipterans (Table III).

Different share of particular taxa has either taphonomical reasons, or may reflect a kind of faunal provincialism, first of all recognizable within Fulgoromorpha (Homoptera: Auchenorrhyncha). A representative of these cicadas, *Fulgoridium* sp. (Fig. 3G), is present everywhere and very abundant in many localities, except for Grimmen. *Fulgoridulum egens* HANDLIRSCH, 1939 (Fig. 3H) is up to now only known from its type locality Dobbertin and Grimmen, where it is more common than *Fulgoridium* sp. In contrast, another fulgoridiid species, *Elasmocelidium boreale* (BODE, 1905) (Fig. 3 I), which is only known from the Braunschweig area, Kerkhofen and Holzmaden, is absent from Dobbertin and Grimmen. This may indicate a northern "faunal province" with *Fulgoridulum egens* and a southern one with *Elasmocelidium boreale*. Tettigarctidae, known from Kerkhofen and Braunschweig, were probably also restricted to the southern land masses, because they were still not recorded from the north. On the other hand, these animals are generally rare in the Lower Toarcian insect taphocoenoses.

Differences within other groups like Diptera and Blattodea are rather to be explained by palaeoecological causes.

A number of Recent cosmopolitan insect families existing in Europe at least since the Lower Jurassic indicate the possibility of faunal exchange between Laurasia and Gondwana in that period (e.g. Coleoptera: Staphylinidae, Cupedidae, Mecoptera: Bittacidae; Planipennia: Osmylidae, Chrysopidae; Megaloptera: Sialidae; Diptera: Tanyderidae, Psychodidae, Trichoceridae, Anisopodidae, Limoniidae, Chironomidae, Rhagionidae).

Some Lower Jurassic localities are known from Siberia (Kubekovo, Novospasskoye), Kyrghyzstan, China and India (MARTYNOV 1937; KALUGINA & KOVALEV 1985; LIN 1986; RASNITSYN 1985; MOSTOVSKI & JARZEMBOWSKI 2000), however, there are obviously no localities from exactly the same Lower Toarcian age as the European ones. Most Asian localities are of terrestrial origin and the age determination is not based on marine guiding fossils. Although some corresponding genera are known, we found no correspondence on species level. On the other hand the Jurassic was probably a stable time for insect evolution as a number of genera common in the Lower-Upper Liassic of Europe and in the Middle/Upper Jurassic of Karatau (Kazakhstan) suggest.

IV. PALAEOECOLOGICAL IMPLICATIONS

Flyable terrestrial insects are quite exclusively preserved in the Lower Toarcian marine insect taphocoenoses, with semiaquatic bugs present. Aquatic larval stages are completely absent.

Rich flora on the mainland (WILDE 2001) is not only indicated by terrestrial palynomorphs and drift wood, but also by high percentage of phytophagous insects. Plant sucking hemipterans (cica-

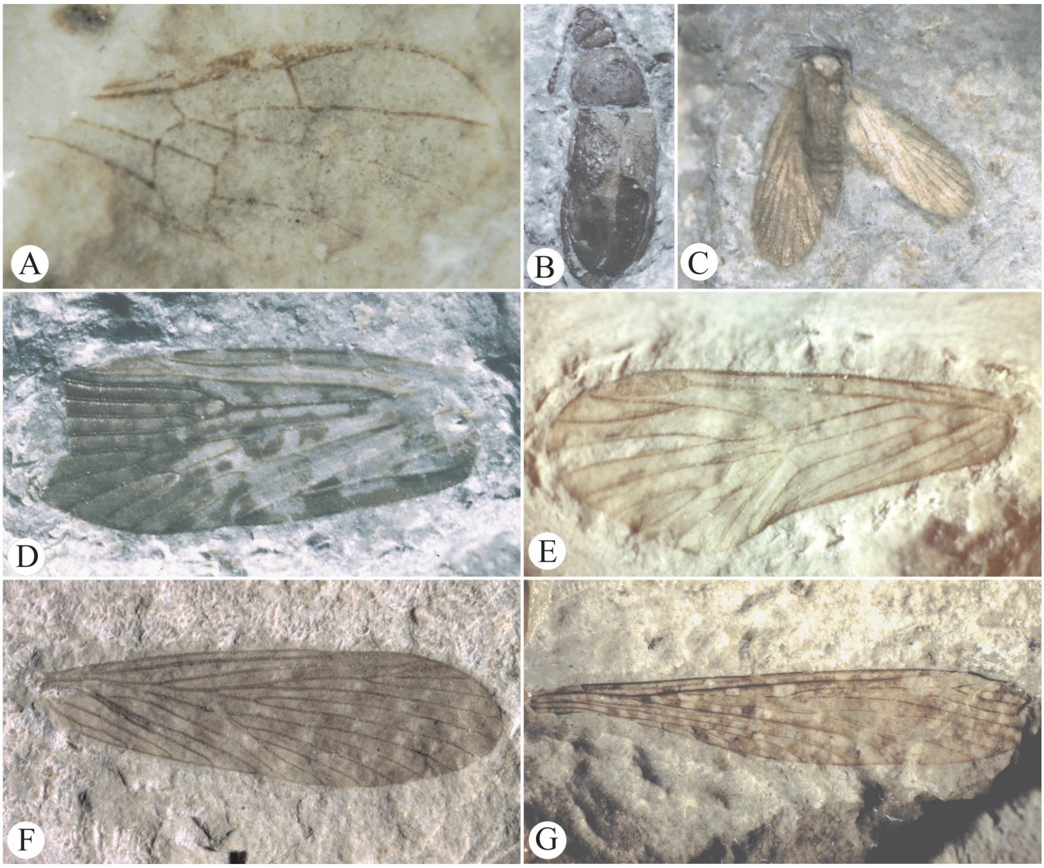

Fig. 4. Insects from the Lower Toarcian of Germany. A: *Thilopterus lampei* RASNITSYN, ANSORGE & ZESSIN, in press, (Hymenoptera: Ephialtitidae), Pt 60/1-20, Schandelah, 2,9 mm. B: Coleoptera gen. et sp. indet., LGA 1230, Grimmen, 7 mm. C: *Necrotaulius parvulus* (GEINITZ, 1884) female, LGA 1097, Grimmen, forewing length 3.4 mm. D: *Liadotaulius maior* (HANDLIRSCH, 1906) female (Trichoptera), LGA 2188, 7 mm. E: *Pseudopolycentropus triangularis* HANDLIRSCH 1920 (Mecoptera: Pseudopolycentropidae), LGA 925, Grimmen, 5.5 mm. F: *Orthophlebia germanica* HANDLIRSCH 1906 (Mecoptera: Orthophlebiidae), LGA 811, Grimmen, forewing 9.3 mm. G: Cimbrophlenbiidae gen. et sp. nov. (Mecoptera), LGA 1608, Grimmen, 27 mm.

das, bugs and coleorrhynchans), psocopterans (Fig. 2H) and lophioneurids share more than one third of all insects in most localities (Table II, III).

Orthopterans (*Elcana* HANDLIRSCH, 1906; *Locustopsis* HANDLIRSCH, 1906) and phasmatodeans (*Schesslitziella* KUHN, 1952, *Durnovaria parallela* WHALLEY 1985, Fig. 2E) most probably fed on leafs and produced similar frass patterns as those known from the Triassic of Germany (GRAUVOGEL-STAMM & KELBER 1996). Cockroaches together with terrestrial larvae of Bibionomorpha (Diptera) and certain groups of Coleoptera lived on rotting vegetation. Out of 6 species known, at least two very distinct Lower Toarcian roach species covered different ecological niches, probably in different sized leaf litter. The most common roach, *Elisama langfeldti* (GEINITZ, 1880) (Fig. 2B), was probably a good flier, while the large and rare *Caloblattina mathildae* (GEINITZ, 1883) seldom left the ground (VRŠANSKÝ & ANSORGE in prep.).

Larvae of mycetophiloid dipteran ancestors (Pleciofungivoridae, Pleciomimidae, Eoditomyidae, Eomycetophilidae) most probably lived on mushrooms, like their modern relatives.

Ground dwellers were represented by spiders (Fig. 5G) and scorpions, but also by grylloids (*Protogryllus dobbertinensis* (GEINITZ, 1880) (Fig. 2D), grylloblattoids (e.g. *Nele jurassica* ANSORGE, 1996; Fig. 2F) and dermapterans. These insects never left their place of living for far and are generally very rare in the taphocoenoses. Spiders, scorpions and earwigs entered the sea probably as rafters on logs.

Abundance of elcanids (Saltatoria; Fig. 2C) is very high in near shore localities and indicates most probably their swarming behavior. Their leaf like appendages on tibiae were interpreted as an adaption to swim after landing on the water surface during long flights over the sea (ZESSIN 1987).

Larvae of Recent plant wasps often exhibit a strict affinity to certain plant species. Accordingly it can be supposed that the rare but widely distributed sawfly, *Xyelula benderi* RASNITSYN et al. (in press), fed in all regions on one and the same host plant. Parasitic ephialtitids (Fig. 4A) known by four small sized species, probably laid their eggs in wood boring beetle larvae by use of long ovipositor.

Among the insects with aquatic larvae only dragonflies and certain dipteran groups are relatively frequent. Dragonflies, probably with exception of damselfly like Protomyrmeleontidae, were able to cross large distances over the sea. Ephemeroptera, Plecoptera (Fig. 2G), Megaloptera are very rare in the marine taphocoenoses, because their adults did not leave their place of emergence for far (ANSORGE 1993, 2001b). Within Diptera (Fig. 5B-F) and Trichoptera (Fig. 4D) the connection of the larvae with the places of their development is not so strict.

The restriction of certain dipteran groups to particular localities may result from specific adaptions to distinct biota. For example, *Praemacrochile decipiens* (BODE, 1953) (Diptera: Tanyderidae) is rather common in the Braunschweig area, very rare in Dobbertin and absent from Grimmen, while the small *Nannotanyderus krzeminskii* ANSORGE, 1994 is a rather common insect. Another dipteran, *Aenne liasina* ANSORGE, 1999 (Chironomidae, Fig. 5B), is known from several specimens only from Grimmen. Noteworthy is also general scarcity of Eoptychopteridae in Grimmen, which are rather common in Braunschweig and Dobbertin. Predatory rhagionids (Fig. 5E) probably fed on other small insects. The supposed nemestrinoids (Fig. 5D) were probably visitors of benettitalen or earliest angiospermian “flowers”.

Larvae of necrotauliids (stem group of Amphiesmenoptera) were probably terrestrial, as indicated by the well developed female ovipositor (Fig. 4C). Lepidopterans related to Micropterygidae were apparently pollen feeders.

The abundance of necrotauliids and moth like lepidopterans (Fig. 5A) can rather be explained by active swarming than by passive drifting in the wind, as it was shown by RUST (2000) for the Lower Eocene Danish Mo Clay.

Predatory insects (Odonata, Mecoptera: Fig. 4F-G, Planipennia: Fig. 3J, Raphidiodea: Fig. 3K) at the end of the food chain, were themselves probably prey of pterosaurs, which are known of some species from the Posidonia Shale (WELLNHOFER 1993).

V. TAPHONOMY

The composition of marine insect taphocoenoses depends not only on the input of terrestrial insects, but on the influence of taphonomical filters, like direction of aerial currents, ocean drift, oxygen content and grain size of the sediment, predatory fishes, salinity, rainfall, etc.

As a rule, the main factor is the distance to the shore line. Apart from the aeroplankton which is distributed by strong seaward wind, most insects use thermal currents during warm weather to fly actively over the sea. Good flyers are able to cross far distances over the sea and reach the next mainland. Compact insects like many beetles, bugs, coleorrhynchans and some cicadas (Membracoidea) are only able to short flights after which they land on water surfaces and start to sink to the bottom rather soon after their death. Among cicadas, however, also persisting fliers seem to exist, like some Fulgoromorpha (as *Fulgoridium* in the Lower Toarcian). Very diverse Fulgoromorpha belong to most common insects in the Lower Eocene marine Mo Clay of Denmark too. On the other hand cicadellids are rather rare in the Danish offshore sequences. In contrast, the Lower Eocene Mo

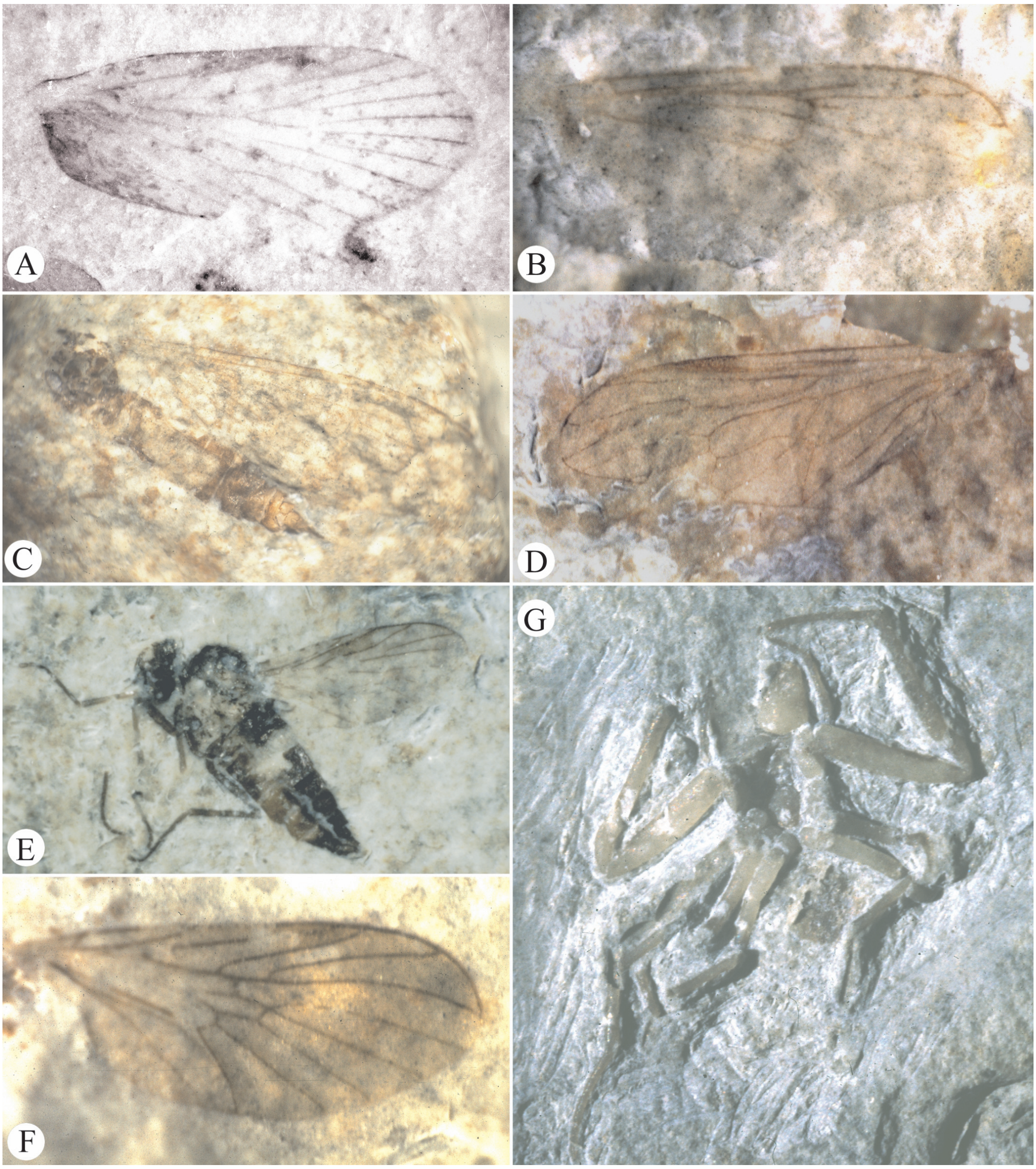

Fig. 5. Insects from the Lower Toarcian of Germany. A: Lepidoptera: Micropterygidae gen. et sp. indet., LGA 1500, Grimmen, 4.8 mm. B: *Aenne liasina* ANSORGE 1999 (Diptera: Chironomidae), LGA 1474, Grimmen, 2.8 mm. C: *Mesotipula* sp. female (Diptera: Limoniidae), Grimmen. D: Nemestrinoidea gen. et sp. nov. (Diptera): Brachycera), S 2(2) Schandelah, 7 mm. E: Rhagionidae gen. et sp. nov. (Diptera: Brachycera), LDA 1300, Dobbertin. F: *Protorhyphus simplex* (GEINITZ, 1887), (Diptera: Protorhyphidae), LGA 1002, Grimmen. Araneae gen. et sp. nov. (Chelicerata).

Clay on the island Greifswalder Oie (Baltic Sea, Germany), which is a near shore deposit, contains a considerable number of small cicadellids (ANSORGE 2000).

The same is to be observed in the Lower Toarcian. In the near shore Grimmen locality archijassids (precursors of cicadellids) are the most common homopterans, which are still present in Dobbertin and quite absent from the Braunschweig area. The abundance of archijassids in the Lower Toarcian near shore localities can be correlated with high numbers of true bugs and coleorrhynchans (Table III). This situation is not a rule and cannot be transferred without comments on offshore deposits of younger systems, as it was shown by the abundance of certain true bugs in the Danish Mo clay (RUST 1998).

Like the composition of marine insect taphocoenoes, also the content of pollen and spores first of all depends on the distance to the shore line. The most diverse pollen and spores associations in the Lower Toarcian are to be observed in northeastern Germany (SCHULZ 1967) and in Southern Sweden (GUY-OHLSON 1986). WALL (1965) found an increasing share of *Inaperturopollenites* from 30 to 90 % in the *exaratum* subzone of Whitby (Yorkshire, England) which corresponds to a global sea level rise in the Lower Toarcian. According to WILLE (1982), *Inaperturopollenites* dominates (99 %) the pollen and spores association of the Suevian Posidonia Shale which indicates an offshore deposition far from the coast.

In vicinity of river mouths the dominate isolated beetle elytra and other heavily sclerotized insect remains washed by rivers to the sea. Predominance of isolated beetle elytra is at least a good indicator for near shore sedimentation, as it can be shown for Grimmen during the *elegantum* subzone and Mistelgau during *exaratum* subzone. With increasing distance to the shore the share of compact insects reduces and the number of good fliers increases.

In the Lower Toarcian tiny insects with wing length around and below 4 mm (aphids, psylloids; lohioneurids, limoniids and other tiny dipterans, hymenopterans) were part of the passively drifted aeroplankton. The abundance of planipennian wing fragments in offshore localities as Braunschweig and Holzmaden is probably explained by passive drifting too.

It cannot be stated with certainty that the distribution of very small aeroplankton (~3 mm) depends on distance to the shore, since various groups dominate in different localities (Grimmen: lophioneurids, Dobbertin: aphids + lophioneurids), Braunschweig (liadopsyllids).

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