

Insect biostratigraphy of the Euramerican continental Late Pennsylvanian and Early Permian

JOERG W. SCHNEIDER¹ & RALF WERNEBURG²

¹*TU Bergakademie Freiberg, B.v. Cotta-Strasse 2, D-09596 Freiberg, Germany (schneidj@geo.tu-freiberg.de)*

²*Naturhistorisches Museum Schloss Bertholdsburg, Burgstrasse 6, D-98553 Schleusingen, Germany (museum.schleusingen@gmx.de)*

Abstract: An insect zonation with a time resolution of 1.5–2 Ma for Late Pennsylvanian to Early Permian (Kasimovian to Artinskian) non-marine deposits is presented. The zonation is based on the directed morphogenetic evolution of colour pattern in the forewings of the blattid (cockroach) family Spiloblattinidae. This evolution is observed in lineages of succeeding species of three genera. All three genera are widely distributed in the palaeo-equatorial zone from Europe to North America, that is, in the Euramerican biota province. Increasing reports of spiloblattinid zone species in conodont-bearing, interfingered marine/continental strata of North American Appalachian, Mid-Continent and West Texas basins could be the key to direct biostratigraphical correlations of pure continental profiles, as are present in the most parts of the Hercynides, to the global marine scale.

Palaeozoological biostratigraphy of the continental late Palaeozoic

Traditionally, the biostratigraphy of continental Carboniferous and Permian deposits has been based on macro- and micro-floras. However, decreasing marine transgressions during the Pennsylvanian and the aridization during the Late Pennsylvanian and the Permian (cf. Roscher & Schneider 2006) generated a change from inter-regional, balanced wet macro- and meso-climates (with a maritime imprint of some degree) to increasingly drier continental climates with stronger seasonality and stronger accentuation of meso- and microclimatic effects. Consequently, edaphic differentiation of the floral associations occurred. The persistence of conservative Carboniferous hydro- to hygrophilous floral elements into Permian (local) wet biotopes and the local appearance of modern typical Permian meso- to xerophilous floral elements in the Carboniferous thus underlies the well-known problems of biostratigraphy with macro- and microfloras (e.g. Broutin *et al.* 1990; DiMichele *et al.* 1996; Kerp 1996).

During the last two decades a number of palaeozoological biostratigraphies were developed and tested. Tetrapod tracks, common in alluvial grey and red sediments, display a wide range in time and space (Haubold 1980, Gand & Haubold 1988, Haubold & Lucas 2003). Unfortunately, their time resolution is very low (Lucas 1998; Voigt 2005). Conchostracans (Spinicaudata) were successfully tested for

surface outcrops and drill cores as well (Schneider *et al.* 2005). They have a very high distribution potential because of their minute, drought-resistant and wind-transportable eggs, and they often form mass occurrences in lacustrine environments of grey and red facies. Hence, conchostracans belong to the most common animal fossils of the continental late Palaeozoic. Regrettably, the time range of single species is not well known at present (Martens 1983; Schneider *et al.* 2005).

Xenacanth shark teeth were applied to regional correlations between some neighbouring European basins. Their wider use is limited because the migration of fishes is restricted to joint river systems connecting the basins (e.g. Schneider 1996; Schneider *et al.* 2000). The fish zonation of Zajic (2000) is thus more a local ecostratigraphy than a biostratigraphy of some Bohemian basins.

Biostratigraphic zonations using osteologic species of aquatic or semi-aquatic amphibians were presented by Boy (1987) and Werneburg (1989*a, b*, 1996). The inter-regional amphibian zones of Werneburg (1996) are based on species-chronoclines with a time resolution of about 1.5–3.0 Ma (for details see Werneburg & Schneider 2006). For large-scale inter-regional subdivisions and correlations, Lucas (1998, 2002, 2006) has presented land-vertebrate faunachrons based on amphibian and reptile skeletons.

The first serious attempts to use insect wings for biostratigraphy were made by Scudder as early as 1879. He recognized the common

occurrence of genera and species of blattid insects (cockroaches) in North America and Europe and their potential for 'delicate discriminations of the age of rock deposits' (Scudder 1895). Later, Durden (1969, 1984) proposed blattid zonation for the Pennsylvanian and Permian, but his correlations remain very doubtful because of inadequate classifications. A revised classification of Pennsylvanian and Permian blattids was presented by Schneider (1983a ff.) based on comparative investigations of individual, sexual, intraspecific and interspecific variation of the wing venation of modern *Periplaneta americana* and *P. australasiae*, as well as fossil blattids (Schneider 1977, 1978). From these results came the first proposals of spiloblattinid zones (Schneider 1982, Schneider & Werneburg 1993) and later of archimylacrid/spiloblattinid/conchostracan zones (Schneider & Rössler, unpubl. internal report for gas exploration companies), which were tested and improved for the Early Pennsylvanian (Westphalian A, Late Bashkirian) through the late Early Permian (Cisuralian, Artinskian). The archimylacrid/conchostracan zonation for Westphalian time is published in Schneider *et al.* (2005). Here, new results and a completed spiloblattinid-zonation for the time interval from the Late Pennsylvanian Kasimovian up to the Middle Cisuralian Artinskian are presented. For species authors, synonymies and further taxonomic information see Schneider (1982, 1983a) and Schneider & Werneburg (1993).

Occurrence, taphonomy and palaeoecology of spiloblattinids

Insect remains occur in all fine clastics, from claystones and siltstones to silty fine sandstones and volcanic ashes of different continental to nearshore marine depositional environments, ranging from swamps and lakes of the grey facies to alluvial plain, playa and sabkha deposits of the red-bed facies. By far the most common insects of the late Palaeozoic are blattids. Best preserved are the tegmina-like, strengthened forewings because of the generally high preservation potential of chitinous substances under subaerial and subaquatic conditions as well as their relatively high resistance to physical forces during water or wind transport.

Generally, insects have a high distribution potential because of active flight and passive distribution by air currents. Among blattid insects, the family Spiloblattinidae forms an exceptional group, characterized by their extensively coloured wings (Fig. 1; Schneider 1983a, 1984a). Based on venation and colour patterns of the



Fig. 1. Life reconstruction of *Syscioblatta dohrni* (Scudder 1879), male, based on the holotype and additional specimens (Schneider & Werneburg 1993, figs 4a, b). The reconstruction shows the colour pattern of fore- and hindwings as well as of the head shield (pronotum), which is typical of blattids ('cockroaches') of the family Spiloblattinidae (Handlirsch 1906a). Length of forewings 2.5 cm.

1.5–2.5-cm-long forewings, three genera of spiloblattinids are distinguished (Schneider & Werneburg 1993): *Sysciophlebia* Handlirsch, 1906, *Spiloblattina* Scudder, 1885, and *Syscioblatta* Handlirsch, 1906. All three genera are widely distributed in the palaeo-equatorial zone from Europe to North America, that is, in the Euramerican biotic province. In some places they occur together in one and the same horizon. Until now, a distinct biotope preference is not evident. Spiloblattinids are associated with hydro- to hygrophilous floras of the roof shales of coal seams, as in the Breitenbach Formation of the Saar–Nahe Basin and the Wettin Sub-formation of the Saale Basin, both in Germany, or in the roof shale of the Waynesburg coal, Dunkard Group, of West Virginia. Associated with meso- to xerophilous floral elements, such as callipterids and walchians, they are not rare in black-shale lake deposits, as in the Homigtal Lake of the Thuringian Forest Basin and the Svitavka-Zbonek Lake, Letovice Formation of the Boskovice Graben, Czech Republic, as well as in the lake deposits of the El Menizla and Oued Issene formations of the Moroccan Souss Basin (Hmich *et al.* 2005, 2006). *Syscioblatta* is unusually common in brackish–marine deposits of the Wild Cow Formation of New Mexico, and some spiloblattinids have been found, together with walchians and cordait leaves, in the nearshore lagoonal Red Tanks Member, Bursum Formation, of the Lucero Basin, New Mexico (Schneider *et al.* 2004 and new observations).

At present, spiloblattinids are absent in playa red beds, as in the still blattid-rich and very diverse insect faunas of the Salagou Formation of the Lodève Basin, southern France, and the playa lake deposits of the Wellington Formation of Kansas and Oklahoma. Obviously, spiloblattinids occur in a wide range of biotopes from humid to semi-arid conditions. They seem to disappear in Euramerica with the maximum of arid climate during the Kungurian (see Roscher & Schneider 2006). Typical of semi-arid to arid environments of this time in Euramerica are xeromorphic mylacrid blattids, as some opsiomylacrids and the genus *Moravamylacris* (Schneider 1980, Hmich *et al.* 2003). Because of the co-occurrence of *Moravamylacris* species with spiloblattinids, they are used to complete the spiloblattinid zones for the time of the general transition from interfingering grey/red to exclusively red beds in the Middle Cisuralian.

Basics of spiloblattinid zonation

The early evolution of spiloblattinids during the Westphalian is not really well known (Schneider 1984a). In the Late Westphalian some blattids appear with sparse venation and widened fields between the main veins. These features are very similar to the venation ground plan of spiloblattinids, but the characteristic light spots or patches on the dark wing surface are still missing. In this regard, '*Syscioblatta*' *corsini* Laurentiaux 1950 from the latest Westphalian or early Cantabrian (Loire Basin, France, Carrière de l'Éparre, Eighth seam) is transitional between '*Kinklidoblatta*' *morini* (Pruvost 1912) of Westphalian D age (northern France, top Faisceau de Dusoich to Faisceau d'Edouard) and the typical Early Stephanian spiloblattinids. The first unquestionable members of this family, detected by their typical wing colouration, appear in the Stephanian A (Barruelian, Kasimovian) (Fig. 2: *Sysciophlebia* n. sp. A and *Syscioblatta intermedia*). The colour pattern originates from the appearance of sharply bounded light patches on the wing. In the area of these patches the normally dark black, coalified wing surface lacks the coaly substance, and therefore the normal sediment colour and the sediment particles are visible. If the organic substance is oxidized or missing in any way, the patches appear somewhat rough compared to the wing surface outside the spots. It is assumed that the wing colour depends on the deposition of coloured organic substances (pigments), as in extant cockroaches.

The number, size and arrangement of light spots (maculae) and bands (fasculae) changed

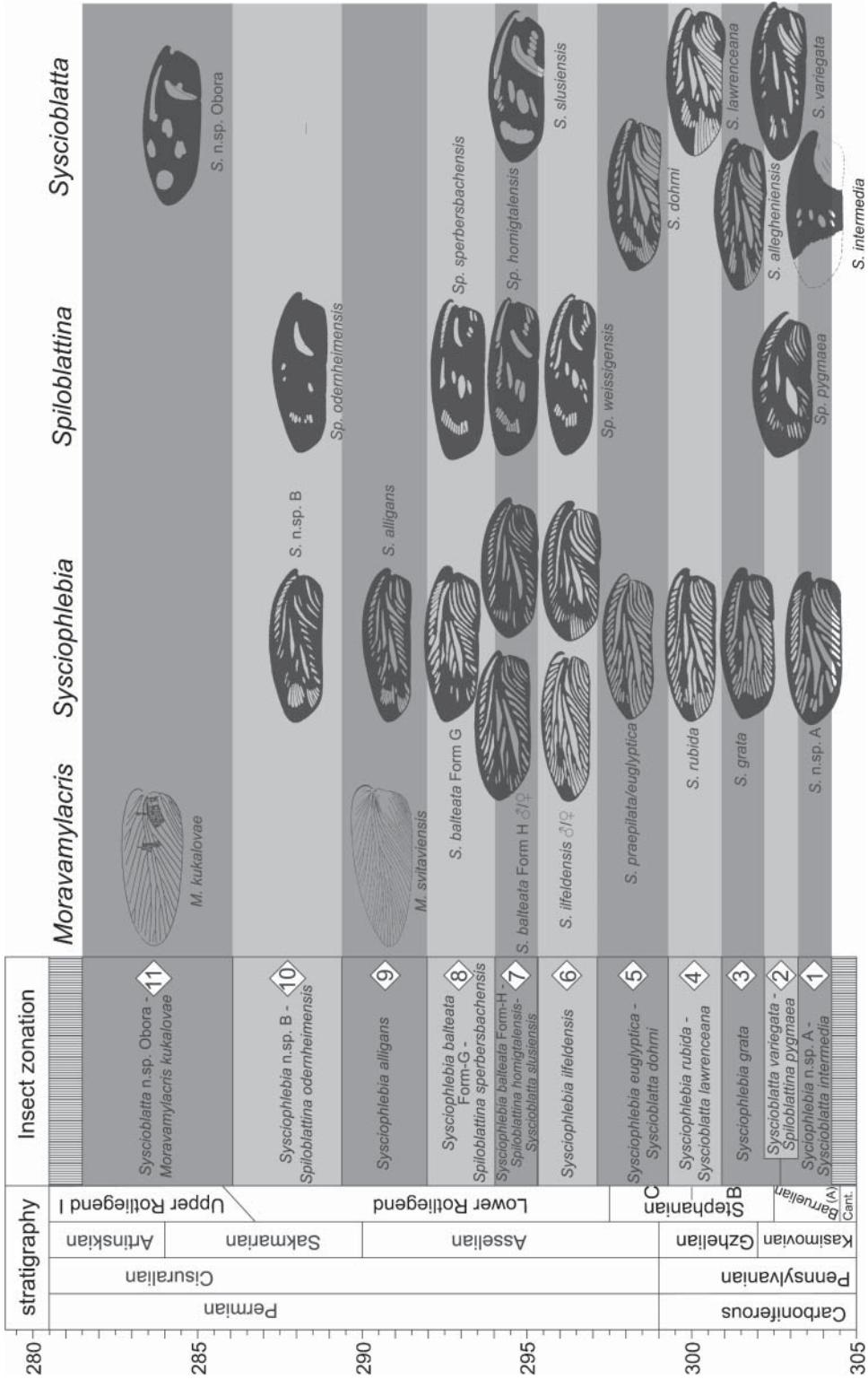
through time in continuous, directed sequences. First, they increased in number and extent, and later they decreased. The arrangement of the colour pattern during increase and decrease of light patches is quite different (Fig. 2: compare the increase in the sequence *Sysciophlebia* n. sp. A to *Sysciophlebia ilfeldensis* and the following decrease from *S. ilfeldensis* to *Sysciophlebia* n. sp. B).

Interestingly, in the genus *Sysciophlebia*, some differences in the wing colouration of both sexes are observed for *S. ilfeldensis* and *S. balteata* Form H. The stouter (supposed) female forewings (Fig. 2, nos 6 & 7, right) exhibit a stronger decrease of light patches than the contemporaneous forewings of (supposed) males (Fig. 2, nos 6 & 7, left). Such differences must be taken into account, in order to prevent incorrect stratigraphic conclusions. As far as is known, in the genera *Spiloblattina* and *Syscioblatta* only minor differences occur, which can be ignored (see Schneider & Werneburg 1993, figs 7 & 8).

Spiloblattinid specimens, sampled in a dense vertical sequence of lake horizons in the Goldlauter Formation (Figs 2 & 3, nos 7 & 8), indicate that the change of the colour patterns is a very continuous process. The distinct differences, which can be seen between the forms in Fig. 2, result simply from a discontinuous fossil record in continental deposits. Consequently, each of the sequences of 'species' of all the three genera in Figure 2 is in reality a continuous lineage of only one chronospecies. To handle the single forms as 'species' is merely a pragmatism due to their practical use in biostratigraphy. Regarded as formal species or biospecies, each of them has a First and Last Appearance Datum (FAD and LAD). Despite the theoretical questions of classification and systematics, these phylomorphogenetic lineages provide very precise biostratigraphic data for correlations.

Definition of the spiloblattinid insect zones

The zonation is based mainly on the *Sysciophlebia* lineage, the most complete lineage known thus far. If one of the *Sysciophlebia* zone species occurs together with species of the other two genera in the same lithostratigraphic horizon, this co-occurrence is used for the definition of the respective zone. If the co-occurrence is inferred only, the respective species will be mentioned as 'inferred accompanying' form. The respective base and top of any zone is defined by the FAD of the zone species. Because real species do not exist in lineages of continuously evolving features (see above), it is nearly insignificant if the rate of feature changes is different between the zone



species of different lineages (which will normally be the case). The numbers in the following descriptions refer to the numbers in the synthetic spiloblattnid zonation (Fig. 2), and in the correlation chart for most of the basins mentioned in the text as well as the stratigraphic levels of spiloblattnid occurrences (Fig. 3).

1 *Sysciophlebia* n. sp. A – *Syscioblatta intermedia* zone

Definition: From FAD of *Sysciophlebia* n. sp. A and/or *Syscioblatta intermedia* to FAD of *Sysciophlebia grata*.

Occurrences: Stephanian A (Barruelian, Kasimovian), Saar Basin, Germany, lower Ottweiler Subgroup, Göttelborn Formation.

Remarks: The typical colour design of spiloblattnids appears suddenly in the earliest Stephanian (Barruelian, Kasimovian) without transitional forms. However, some late Westphalian/earliest Cantabrian (Moscovian/Kasimovian) blattids, such as '*Syscioblatta*' *corsini*, *Kinklidoblatta morini* and *K. zavjalovenski*, could be precursors of true spiloblattnids (see above).

2 *Syscioblatta variegata* zone

Definition: From FAD of *Syscioblatta variegata* to FAD of *Syscioblatta allegheniensis*.

Occurrences: Virgilian, Appalachian Basin, Ohio, roof of the Ames Limestone; conodonts of the Ames Limestone (Ritter 1995), such as *Streptognathodus simulator* and *Streptognathodus elegantulus*, indicate an Early Gzhelian age.

Inferred accompanying species: *Spiloblattina pygmaea*, Stephanian A/B (Kasimovian), Saar–Nahe Basin, Germany, middle Ottweiler Subgroup, lowermost Heusweiler Formation;

early Stephanian B (Kasimovian), Morocco, Souss Basin, Ida Ou Zal Sub-Basin, upper El Menizla Formation; Ida Ou Ziki Sub-Basin, upper Oued Issene Formation.

Remarks: *S. variegata* is the successor of *S. intermedia* and the precursor of *S. allegheniensis*. However, up to now, we have no proof of the co-occurrence of *S. variegata* and *Sp. pygmaea*, and no co-occurring *Sysciophlebia* species are known so far. The range of *Sp. pygmaea* could overlap the range of *Sysciophlebia* n. sp. A and/or *S. grata*. Therefore, this zone is sandwiched with some overlap between the *Sysciophlebia* n. sp. A – *Syscioblatta intermedia* zone and the *Sysciophlebia grata* zone.

3 *Sysciophlebia grata* zone

Definition: From FAD of *Sysciophlebia grata* to FAD of *Sysciophlebia rubida* and/or FAD of *Syscioblatta lawrenceana*.

Occurrences: Stephanian B (Kasimovian/Gzhelian), Kladno Basin, Czech Republic, Slaný Formation, Hredle Member; early Stephanian B (Kasimovian/Gzhelian), Morocco, Souss Basin, Ida Ou Ziki Sub-Basin, upper Oued Issene Formation (together with *Spiloblattina pygmaea*: see above).

Inferred accompanying species: *Syscioblatta allegheniensis*, Virgilian, Appalachian Basin, Pennsylvania, Conemaugh Formation, Duquesne Shale.

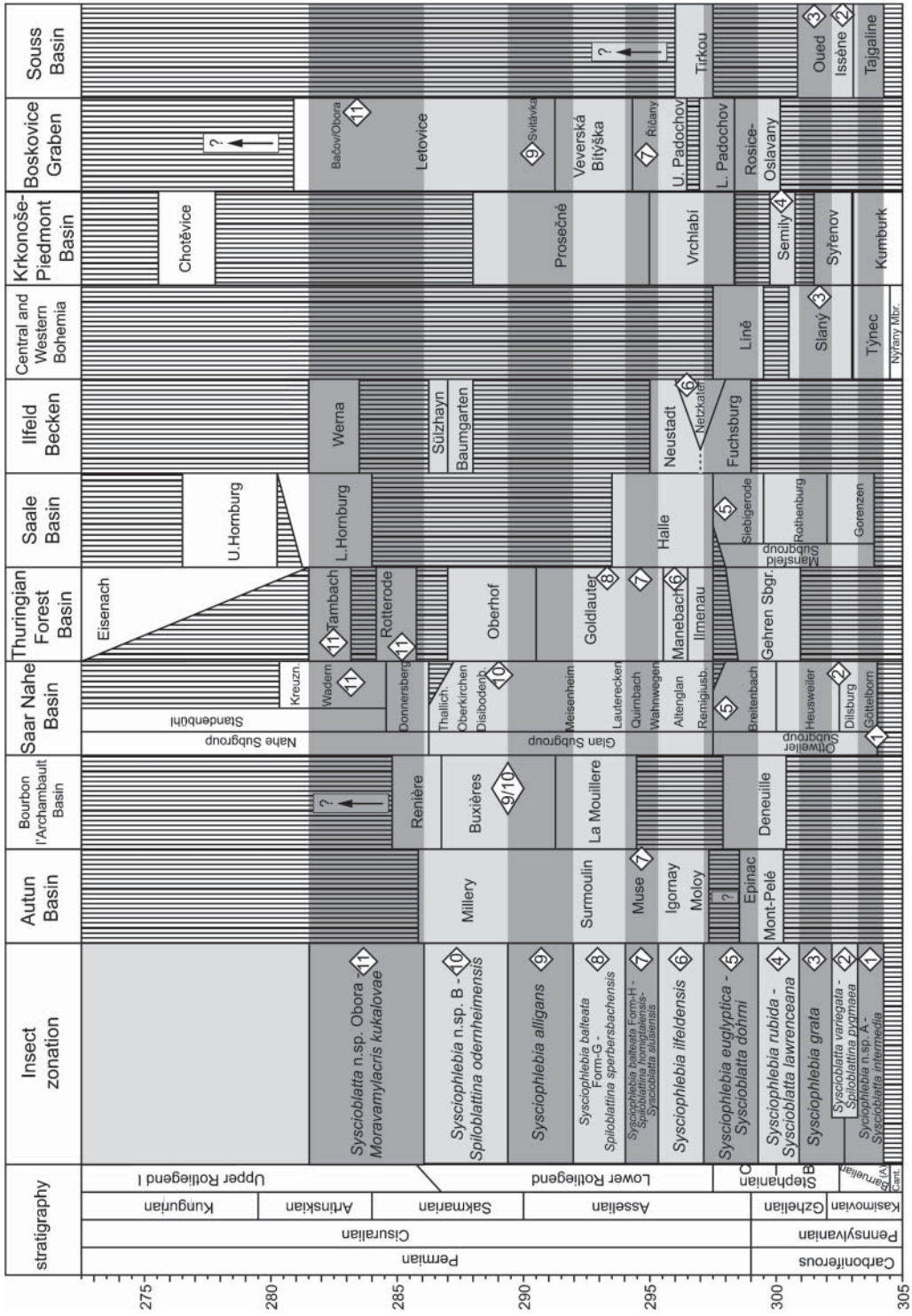
Discussion: Based on colour pattern, *S. allegheniensis* is intermediate between the preceding *S. variegata* and the following *S. lawrenceana*. The latter co-occurs with the succeeding species of *S. grata*, namely *S. rubida*. Therefore, it could be assumed that *S. allegheniensis* covers a time interval similar to that of *S. grata*.

4 *Sysciophlebia rubida* – *Syscioblatta lawrenceana* zone

Definition: From FAD of *Sysciophlebia rubida* and/or *Syscioblatta lawrenceana* to FAD of *Sysciophlebia euglyptica* and/or *Syscioblatta dohrni*.

Occurrences: Both species occur together at the type locality of *S. rubida*, in the Late Stephanian B (Gzhelian) Plouznice Horizon of the Semily Formation in the Krkonoše-Piedmont Basin, Czech Republic; *S. lawrenceana*, Virgilian, Mid-Continent Basin, Kansas, Lower Douglas Group, Lawrence Shale, *Streptognathodus firmus*-conodont zone after Ritter (1995), Early to Middle Gzhelian; *S. lawrenceana* together with

Fig. 2. Zone species of the spiloblattnid insect zonation of Late Carboniferous (Pennsylvanian) and Early Permian (Cisuralian). Figured are the three species lineages of the spiloblattnid genera *Sysciophlebia*, *Spiloblattina* and *Syscioblatta* as known from the fossil record. Biostratigraphically significant is the evolution of colour pattern of the approximately 1.5–2.5-cm-long forewings. In the *Sysciophlebia* lineage, a well-expressed sexual dimorphism is observed in the colour pattern as shown for *S. ifeldensis* and *S. balteata* Form H (male forewing left, female forewing right). Numbers in diamonds refer to the zone descriptions in the text. Numerical ages are based on Ogg (2004), Menning *et al.* (2003) and Lützner *et al.* (2003).



a form intermediate between *S. grata* and *S. rubida*, Stephanian B/C transition (Gzhelian), Blanz-Montceau Basin, French Massif Central, Montceau Formation.

5 *Sysciophlebia euglyptica* – *Syscioblatta dohrni* zone

Definition: From FAD of *Sysciophlebia euglyptica* and/or *Syscioblatta dohrni* to FAD of *Sysciophlebia ilfeldensis*.

Occurrences: Both the zone species are known from the Stephanian C, Gzhelian/Asselian transition, Saale Basin, Germany, Siebigerode Formation, Wettin Subformation, and the Saar Basin, Germany, Ottweiler Subgroup, Breitenbach Formation; *S. dohrni* is common in the marine-lagoonal Wild Cow Formation, Pine Shadow Member, Virgilian, Estancia Basin, New Mexico; marine limestones of this member contain the conodonts *Adetognathus lautus* and *Idiognathodus delicatus* (Krukowski 1992); spiloblattnid fragments from the Bursum Formation, Red Tanks Member, of the Lucero Basin, New Mexico, most probably belong to *S. dohrni* and *S. euglyptica*; the first conodont investigations of this member give a Virgilian age (Orchard *et al.* 2004).

Discussion: *Sysciophlebia praepilata* from the Grande Couche, Commentry Basin (Schneider 1983b), French Massif Central, the famous insect locality with *Meganeura*, is very close to *S. euglyptica*. Both species can hardly be distinguished by small differences in the colour pattern (see Basics of spiloblattnid zonation). No new material from Commentry is known for further study, so a separate *praepilata* zone will not be used. The occurrence of *S. praepilata* covers the latest Stephanian B to possibly earliest Stephanian C.

Accompanying species: A common mylacrid species in this zone is *Dictyomylacris densistriata*, the successor species of *D. insignis* from the late Stephanian B of Commentry (Schneider 1983b);

a very typical accompanying species of *Spiloblattina praepilata* at Commentry is *Opsiomylacris thevenini*, which occurs in Morocco together with *Spiloblattina pygmaea* in the Oued Issene and El Menizla formations of the Souss Basin (Hmich *et al.* 2003, 2005).

6 *Sysciophlebia ilfeldensis* zone

Definition: From FAD of *Sysciophlebia ilfeldensis* to FAD of *Sysciophlebia balteata* and/or *Spiloblattina homigtalensis*.

Occurrences: Lower Rotliegend, Asselian, Ilfeld Basin, Germany, Netzkater Formation; Lower Rotliegend, Asselian, Lower Austria, Permian of Zöbing (southern continuation of the Czech Boskovic Graben); fragments of *S. ilfeldensis* are known from the Manebach Formation, Lower Rotliegend, Asselian, of the Thuringian Forest Basin, Germany.

Accompanying species: In the Netzkater Formation the zone species occur together with *Opsiomylacris phyloblattoidea*.

Inferred accompanying species: *Spiloblattina weissigensis*, Lower Rotliegend, Asselian, Weissig Basin near Dresden, Germany; *Sp. weissigensis*, Wolfcampian, Asselian, Midcontinent Basin, Colorado, Fairplay, Maroon Formation, Pony Spring Member.

Discussion: Based on the colour pattern, *Sp. weissigensis* is the immediate precursor form of *Sp. homigtalensis*, which co-occurs with *S. balteata*, the succeeding form of *S. ilfeldensis*. Because of these relationships, it is concluded that *Sp. weissigensis* covers a time interval similar to that of *S. ilfeldensis*. *S. ilfeldensis* marks the turning point in the development of colour pattern in the *Sysciophlebia* lineage. The size of the light areas increases from *Sysciophlebia* n. sp. A up to *S. ilfeldensis*; the next form, *S. balteata*, indicates the subsequent decrease of these light areas.

7 *Sysciophlebia balteata* Form H – *Spiloblattina homigtalensis* – *Syscioblatta slusiensis* zone

Definition: From FAD of *Sysciophlebia balteata* Form H and/or *Spiloblattina homigtalensis* and/or *Syscioblatta slusiensis* to FAD of *Sysciophlebia balteata* Form G and/or *Spiloblattina sperbersbachensis*.

Occurrences: All three zone species occur together in the Homigtal Lake Horizon of the Lower Goldlauter Formation, Lower Rotliegend, Asselian, Thuringian Forest Basin, Germany; *S. balteata*, Autunian, Asselian,

Fig. 3. Correlation chart of the most important European basins and the Moroccan Souss Basin, where spiloblattnid insect zone species were collected. Correlations are based on the insect biostratigraphy presented here and the amphibian biostratigraphy of Werneburg & Schneider (2006). Numbers in diamonds show the lithostratigraphical levels of respective basin profiles in which zone species occur and refer to the zone descriptions in the text. Numerical ages are after Ogg (2004), Menning *et al.* (2003) and Lütznier *et al.* (2003).

Autun Basin, French Massif Central, Muse Formation; *S. balteata*, Wolfcampian, Asselian, Appalachian Basin, West Virginia, Dunkard Group, Cassville Shale, roof of the Waynesburg Coal; *Sp. homigtalensis*, Lower Rotliegend, Asselian, Boskovice Graben, Czech Republic, Padochov Formation, Říčany Horizon.

Accompanying species: *Opsiomylacris procerus* occurs with the zone species in the Homigtal Lake Horizon of the Thuringian Forest Basin; in the Říčany Horizon, Boskovice Graben, *Sp. homigtalensis* is accompanied by *Moravamylacris ricanyensis*.

Discussion: The holotype specimen of *S. balteata* (Scudder 1879) is not well preserved (see Schneider & Werneburg 1993, pl. 1, (Fig. 2a, b,) text-Fig. 2), therefore the certain assignment of the specimens from the lower Goldlauter Formation to this species is not absolutely clear. Nevertheless, this species designation is used to prevent too many new species names. For the same reason, immediately succeeding forms of *S. balteata* in the *Sysciophlebia* lineage are designated as 'Forms'.

8 *Sysciophlebia balteata* Form G – *Spiloblattina sperbersbachensis* zone

Definition: From FAD of *Sysciophlebia balteata* Form G and/or *Spiloblattina sperbersbachensis* to FAD of *Sysciophlebia alligans*.

Occurrences: Both zone species occur together in the Acanthodes Lake Horizons, lower Goldlauter Formation, Lower Rotliegend, Asselian, Thuringian Forest Basin, Germany.

Accompanying species: *Opsiomylacris procerus* occurs together with the zone species in the Acanthodes Lake Horizons.

9 *Sysciophlebia alligans* zone

Definition: From FAD of *Sysciophlebia alligans* to FAD of *Sysciophlebia* n. sp. B and/or *Spiloblattina odernheimensis*.

Occurrences: Lower Rotliegend, Asselian/Sakmarian, Boskovice Graben, Czech Republic, Letovice Formation, Svitavka–Zboněk Horizon; fragments of forms transitional between *S. alligans* and *Sysciophlebia* n. sp. B were found in redeposited fossiliferous pyroclastics above the Lien Vert volcanic ash horizon of the Buxieres Formation, Upper Autunian, Bourbon l'Archambault Basin, French Massif Central.

Accompanying species: *Moravamylacris svitaviensis* occurs with the zone species in the Svitavka–Zboněk Horizon.

10 *Sysciophlebia* n. sp. B – *Spiloblattina odernheimensis* zone

Definition: From FAD of *Sysciophlebia* n. sp. B and/or *Spiloblattina odernheimensis* to FAD of *Syscioblatta* n. sp. Obora.

Occurrences: Both the zone species occur together in the Humberg Lake Horizon, upper Meisenheim Formation, and Körborn Lake Horizon, lower Disibodenberg Formation, upper Lower Rotliegend, Sakmarian, Saar–Nahe Basin, Germany.

Discussion: Because of some small differences in the colour pattern, Schneider & Werneburg (1993) distinguished *Sp. odernheimensis* Form H from the Humberg Lake Horizon and *Sp. odernheimensis* Form K (Fig. 2, no. 10, right) from the Körborn Lake Horizon. In the forewings of the latter, the light spot between the medialis and radius veins is missing, which is still present in Form H. At this time, it was not clear whether this is simple variability or of stratigraphical significance. A newly discovered wing from the uppermost Humberg Lake level show the same more reduced pattern as Form K, therefore both forms are biostratigraphically significant (Poschmann & Schindler 2004).

11 *Syscioblatta* n. sp. Obora – *Moravamylacris kukalovae* zone

Definition: From the FAD of *Syscioblatta* n. sp. Obora and/or *Moravamylacris kukalovae* to LAD of *Syscioblatta* n. sp. Obora and/or *Moravamylacris kukalovae*.

Occurrences: *Syscioblatta* n. sp. Obora occurs together with *M. kukalovae* in the Upper Rotliegend I, Sakmarian/Artinskian, Boskovice Graben, Czech Republic, Letovice Formation, Obora Horizon; *M. kukalovae* alone in the Upper Rotliegend I, Sakmarian/Artinskian, Boskovice Graben, Czech Republic, Letovice Formation, Bačov Horizon; *M. kukalovae* is widespread in red beds of the Upper Rotliegend I, Late Sakmarian to Artinskian, as the Rotterode and Tambach Formations, Thuringian Forest Basin, Germany, and the Sobernheim Horizon, Wadern Formation, Nahe Subgroup, Saar–Nahe Basin, Germany.

Discussion: *Syscioblatta* n. sp. Obora was primary regarded as a Permian species of the Triassic genus *Subioblatta* Lin 1978, and a new family Subioblattidae was introduced by Schneider (1983a). Now it seems more likely that the late Early Triassic to Jurassic *Subioblatta* is related to Permian spiloblattinids of the genus *Syscioblatta*.

If the similarity in the venation ground plan and the arrangement of colour pattern (compare Schneider 1984a, pl. 6, figs 1 & 2; Papier *et al.* 1994, fig. 23a–d) is not the result of homeomorphism, the spiloblattnid zonation could possibly be extended through the Mid- and Late Permian into the Mesozoic. In this regard, the late Cisuralian to Lopingian entomofauna of the Lodève Basin (Gand *et al.* 1997) will provide promising new data.

State of the art and perspectives on insect biostratigraphy – conclusions

As shown above, the insect zonation as well as the amphibian zonation of Werneburg (1996) and Werneburg & Schneider (2006) are primarily based on the sequence of species in absolutely reliable vertical successions of collecting horizons of the Thuringian Forest Basin and, for insects, of the Saar–Nahe Basin, especially (Figs 2–3). They become increasingly completed with the addition of forms from other basins. This is based on the assumption that, if parts of an evolutionary or morphogenetic lineage are well known from one vertical sequence, than this lineage can be completed with forms that fit into the morphogenetic trend from elsewhere. Sometimes, insects and amphibians were found in the same lake horizon or in different succeeding lake horizons of the same basin profile. Such cases are used for cross-checks of the biostratigraphical age delivered by each method. If available, isotopic ages and xenacanth shark teeth were included in these cross-checks. For examples see Werneburg (2003) and Werneburg & Schneider (2006).

From the synthesis of isotopic ages and biostratigraphical data, it is learned that isotopic ages *per se* give only very rough ideas of the real age. This has been demonstrated by the repeated publications of Menning (e.g. 1995) and Menning *et al.* (1997, 2000, 2005) on attempts to calibrate time scales. Menning *et al.* (2005, p. 189) show that isotopic ages of Carboniferous and Permian rocks give in the best case a 2σ – error of ± 2.4 to ± 7.4 Ma. These are graphical error bars of 4.8–14.8 Ma long! The Cisuralian has a duration of roughly 22 Ma, the Guadalupian only 12 Ma, the Asselian 9 Ma and the Artinskian about 5 Ma. These uncertainties result partly from repeated volcano-tectonic reactivations in the European Variscides and multiple Mesozoic thermal events, which have upset the geochronological systems throughout large areas.

On a very tight sequence of isotopic ages in the profile of the Thuringian Forest Basin,

Lützner *et al.* (2003, 2006) have demonstrated that only the careful proof of consistency of isotopic ages and the cross-check against independent data, for example, from biostratigraphy, can deliver reliable numerical ages. The time resolution of the spiloblattnid zonation is on average 1.5–2 Ma and of the amphibian zonation (Werneburg & Schneider 2006) on average 1.5–3 Ma, which is very well suited for such cross-checks and the calibration of numerical time scales.

In Figures 2 and 3, the insect zones and the basin profiles are correlated with the series and stages of the global marine scale. Until now, those non-marine/marine correlations are based nearly exclusive on isotopic ages from volcanites of the continental basins, not on biostratigraphy. On the other hand, most of the numerical ages used for the stage boundaries are estimated ages only, not really measured in the marine sections (see Ogg 2004; Menning 1995; Menning *et al.* 2000). Possibly, the insect biostratigraphy can deliver a solution to this problem. An increasing number of marine/non-marine interfingerings in brackish marine-lagoonal and estuarine settings with specimens of the spiloblattnid-zone species and conodonts have been discovered, such as the Ames limestone, Virgilian of Ohio, the Lawrence Shale, Virgilian of Kansas as well as the Wild Cow Formation and Bursum Formation of New Mexico. The conodonts and spiloblattnids of both the New Mexico occurrences could be the long-sought tools for reliable correlations of the marine Carboniferous/Permian boundary into the purely continental sections of the Euramerian Hercynides (Schneider *et al.* 2003, 2004). Very promising prospects for marine/non-marine correlations of the Permian stages are also the mixed marine/continental deposits of the North American Mid-Continent Basin and of the Volga-Kama region of Tatarstan in eastern Europe. Future research should focus on those sections.

Both zonations, the amphibian-based one and the spiloblattnid zonation, cover the Late Pennsylvanian Kasimovian and Gzhelian up to the late Early Permian (Cisuralian) Artinskian. After the Early Artinskian wet phase (Roscher & Schneider 2006), the biotopes of spiloblattnids and the aquatic to semi-aquatic amphibians, used for the zonation, disappear by increasing aridization in the central Euramerican region. Therefore, xerophilous insects, such as some mylacrid blattids, could be useful to extend the insect zonation into the Guadalupian. First in the Moroccan Lower Stephanian (Kasimovian/Gzhelian transition), and later in the European Lower Rotliegend (Asselian), mylacrids of the genus *Opsiomylacris* became increasingly common besides phylloblattnids and the

spiloblattinid guide forms (Hmich *et al.* 2003, 2006). A further genus, *Moravamylacris*, displays strong, sclerotized, beetle-like elytra (Fig. 2, nos 9 & 11, left). These, together with their common occurrence in red beds, demonstrate that *Moravamylacris* was a xeromorphic blattid. Species of both genera are mentioned as accompanying species or zone species in the description of the spiloblattinid zones above.

Additionally, advanced phylloblattids of the genus *Phylloblatta* appear in the Artinskian, as in the Elmo insect bed of the Wellington shales of Kansas and Oklahoma, the Obora insect beds of the Boskovic Graben (Schneider 1984b) and the Tambach vertebrate site (Werneburg & Schneider 2006) in the Thuringian Forest Basin. Together with other insects of a diverse entomofauna, they are common throughout the Late Cisuralian and Guadalupian succession of the Lodève Basin (Gand *et al.* 1997, Bethoux *et al.* 2002). Species of the phylloblattid *Aisoblatta*, which are common in the Kungurian and Tatarian of eastern Europe, China and the German marine Zechstein, could be useful for subdivision and correlation of Late Guadalupian and Lopingian time.

Generally, in late Palaeozoic continental settings each method – tetrapod track biostratigraphy, reptilian zonation, macro- and micro-palaeobotany, insect or amphibian zonation etc. – has its own advantages and disadvantages. We know lake sediments with thousands of amphibian skeletons but not one single insect wing, red beds with hundreds of tetrapod tracks but no bones. So, any biostratigraphical information is of importance for local to inter-regional correlations, especially in the red beds of the Mid- and Late Permian. Stepwise improved annotated correlation charts based on multidisciplinary information, as presented by Roscher & Schneider (2005), will give a realistic picture of progress, precision and further demands for stratigraphical research.

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