

Tetrapod footprint ichno-associations from French Permian basins. Comparisons with other Euramerican ichnofaunas

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Abstract: In order to take into account the studies of the European and American (USA) collections carried out by one of the authors, and of the recent nomenclatural revisions from new footprint discoveries, which have occurred during the last decade, the authors present a critical review of the French Permian palichnofauna. The distribution of the ichnospecies in the stratigraphy of the Lodève Basin, taken as a reference, is outlined. The ichno-associations are then compared with those of other French (Provence), European (Italy, Germany) and USA basins. Based on the ages of different ichnofossiliferous formations, three successive ichnofaunal units can be distinguished in the Permian of Europe. The first developed in the Cisuralian (Asselian to Kungurian). The second is found in the south of France in Kazanian to Lower Tatarian strata, equivalent to the Roadian–Wordian. The third and youngest, dated as Lopingian, is only found in Italy, in the Bolzano Basin. Because of sedimentary gaps, limited observations, sometimes erroneous determinations, and ichnospecies with great vertical distribution, it currently appears that footprints have a low utility for biochronological resolution. Nevertheless, they allow us to discriminate three time intervals in the Permian, as is also the case for skeletal remains.

There are 20 Permian basins in France (Fig. 1), but only a few of them have yielded tetrapod vertebrate tracks. The first were collected in 1903 by Delage (1912) near Neffiès, south of Lodève. After a long period during which no research was conducted, new observations were made in the Lodève Basin by Ellenberger & Ellenberger (1959) and by Heyler & Lessertisseur (1962). The latter two workers published a review of their finds, including descriptions of what were accepted as ‘14 new genera and 16 new species’ (Heyler & Lessertisseur 1963).

After 1963, research focused on other areas, and a second review of the Permian palichnofauna of southern France, based mainly on footprints from the Lodève Basin, was published briefly by Ellenberger (1983a–c, 1984). In his short notes, the author presented and named ‘almost 130’ new ichnotypes but without description. Thirty-nine ichnogenera, in addition to the seven described earlier by Heyler & Lessertisseur (1963), characterized for Ellenberger (1983a–c) ‘the marked individuality of the Lodève province as regards palaeontology, palaeogeography and palaeoecology’.

From 1980, in parallel with these works, Gand undertook a revision of French Permian footprints that involved prospecting in all the French basins and visiting several European

fossil collections or sites: the Prague Museum in the Czech Republic, the museums of Halle, Gotha, Nierstein and the University of Mainz in Germany, the museums of Oxford, Cambridge, Birmingham, Nottingham, Keyworth and Manchester in England and those of Dumfries, Edinburgh and Elgin in Scotland. Field studies were also conducted in Scotland, Saarland, Thuringia, and Val Gardena in the Italian Dolomites. Reviews were published upon completion of these studies (Gand 1987; Châteauneuf & Gand 1989) that recognized only 14 ichnogenera and 22 ichnospecies; among them are almost all the ichnogenotypes defined by Haubold (1970, 1971, 1973). From the new French palichnological results, stratigraphical correlations were suggested by using the continental stages ‘Autunian’ and ‘Saxonian’ (Gand 1987; Gand & Haubold 1988).

Since Gand’s work was presented, the data have been supplemented by new ichnogenus and ichnospecies descriptions from the Provence (Demathieu *et al.* 1992; Gand *et al.* 1995) and Lodève basins (Gand *et al.* 2000). If we include only footprints that represent the most faithful images of autopods, defined morphologically and morphometrically as ichnopopulations, the Permian French palichnofauna includes 21 ichnospecies accommodated in 15 ichnogenera.

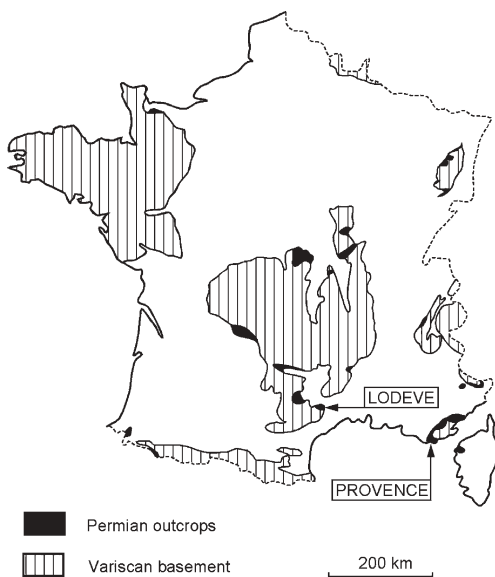


Fig. 1. Location of Permian basins in France.

This assessment is, of course, very distant from that of Haubold (2000), who reduced the southern French palichnologic content to four ichnogenera and eight ichnospecies. This is why we shall present the French footprints, discuss the nomenclatural changes of Haubold (1996, 1998a, 2000) and make comparisons between European and American ichnospecies. After that, we will discuss the stratigraphical aspects inferred from palichnological data.

The French palichnofauna

Footprints ascribable to temnospondyls

Branchiosauridea and/or *Micromelerpetondidea*

Batrachichnus salamandroides (Geinitz 1861) Haubold 1996 = *Anthichnium salamandroides* (Geinitz 1861) Haubold 1970; synonyms: *Nanipes minutus*, *Auxipes minor*, *Devipes caudatus*, *Crenipes abscurvus*, *Crenipes abrectus* Heyler & Lessertisseur 1963, and *Margennipes pansioti* Heyler 1984 (Figs 2a2, b3, c4&5, d4; 5a; 6a). These small prints of tetradactyl manus and pentadactyl pes were revised by Haubold (1970, 1971, 1973) and by Gand (1987, pp. 74). They are abundant with the same morphology in France, the Saar-Nahe (Germany) and the USA. They are attributed to small temnospondyls (Haubold 1970; Gand 1987).

While based on the morphology of *Batrachichnus* Woodworth 1900, and on its

nomenclatural priority over *Anthichnium* Nopcsa 1923, Haubold used the binomials *B. delicatulus* for the American material (Haubold *et al.* 1995a) and *B. salamandroides* for the European traces (Haubold 1996). Because he inferred no significant differences between the two ichnospecies, *B. salamandroides* could only be used to indicate *Anthichnium* footprints.

Salichnium pectinatus Gand 1987 (Fig. 2c3) (= *Serripes pectinatus* Heyler & Lessertisseur 1963) and *Salichnium decessus* Gand 1987 (Fig. 2c1&2) (= *Acutipes decessus* and *Folliipes abscurvus* Heyler & Lessertisseur 1963). These were allotted to microsauroians by Gand (1987). But for many of them, one can show that they represent slipped forms or undertracks of *Batrachichnus salamandroides* (Gand 1987; Haubold 1996) and *B. delicatulus* (Haubold *et al.* 1995a). So, they have no nomenclatural importance.

Eryopsidae

Linnopus (Permomegatherium) zeilleri (Delage 1912) Gand 1985; synonyms: *Permomegatherium zeilleri* Delage 1912, *Opisthopus ellenbergeri* Heyler & Lessertisseur 1963 (Figs 2b1&2, c6&7; 5p-r). This ichnospecies was described by Gand (1985, 1987), it is frequent in the Lower Permian lacustrine formation, and it is attributed to Eryopsidae. Many trackways were discovered in the uranium quarry worked by 'Cogema', where its morphological variability is quite clearly illustrated (Gand 1986, 1987). Dimensions and morphology of *L. zeilleri* resemble closely those of the American forms *Linnopus waynesburgensis* (Tilton 1931) Baird 1952 of the Lower Permian, and *L. littoralis* (Marsh 1894) Baird 1952 of the Upper Pennsylvanian.

Linnopus (= *Strictipes*) *regularis* (Heyler & Lessertisseur 1963) Haubold 1971; synonym: *Diversipes proclivis* Heyler & Lessertisseur 1963 (Fig. 2c8). We preserve this ichnotaxon that indicates centimetre traces with the digits definitively broader than those of *Batrachichnus salamandroides* (Gand 1987, p. 112). *Amphisauropus latus* (Fritsch 1901) Haubold 1970 (Fig. 2c10) is rare in France (Gand 1987, p.115).

Traces attributed to amniotes

Captorhinomorpha

Hyloidichnus major (Heyler & Lessertisseur 1963) Haubold 1971; synonyms: *Hyloidichnus* (= *Auxipes*) *major* (Heyler & Lessertisseur 1963) Haubold 1971, and *Garganolipes ballestrai* (Heyler & Montenat 1980) Gand 1987

(Figs 2d6&7,5h). The comparison between the French ichnospecies *H. major* and the holotype (n° 11518) *Hyloidichnus bifurcatus* Gilmore 1927 from the Hermit Shale Formation was studied at the National Museum in Washington, D.C., by G.G. It shows that there are few differences between these two ichnospecies. *H. major* is a very common footprint in the basins of south-eastern France (Gand 1987, 1993; Gand *et al.* 1995).

Varanopus curvidactylus Moodie 1929 (Figs 2d1, 5b&e), and *Microsauripus acutipes* Moodie 1929. Moodie (1929) described four ichnospecies from the northern slope of Castle Peak, upper Clear Fork Formation. Except for size, all have the same morphology with generally curvilinear fingers, a tetradactyl hand for *Erpetopus willistoni*, *Microsauripus clarki* and *M. acutipes*, whereas it is pentadactyl for *V. curvidactylus*: ichnospecies reduced to only one specimen. In their revision, Haubold (1971) and Haubold & Lucas (2001a) keep only *E. willistoni* and *V. curvidactylus*. After having studied the American material in the Yale Peabody Museum, it appears more suitable to also preserve *M. acutipes* in this list because the material is abundant enough and well preserved. All these ichnospecies represent pentadactyl foot-hand couples with the curvilinear fingers slightly clawed.

Varanopus rigidus Gand 1989 (Figs 2c9, 5f&g, 6b). This ichnospecies is rare in the Lodève Basin, but more frequent in Provence where one finds it with *Hyloidichnus major*, often on the same level (Gand 1987, p. 163; Demathieu *et al.* 1992). The fingers are generally straight with short claws.

Subsequent to the definition of *V. rigidus*, the study of the footprint collection in the United States National Museum (USNM) of Washington, D. C., enabled us to more closely compare the French ichnospecies with *Hylopus hermitanus* Gilmore 1927, which was found with *Hyloidichnus bifurcatus* Gilmore 1927, at the same place; at the base of the Hermit Shale Formation. The analysis of the various characters of the traces and the trackways show that the French couples *V. rigidus* / *H. major* and American *H. hermitanus* / *H. bifurcatus* are similar. Thus, one could consider in the future that all of the French and American material represent the same taxa.

Currently, points of view diverge on the best taxonomic names to use. *V. rigidus*, partly, was integrated in *Varanopus curvidactylus* by Haubold & Lucas (2001a), which we contest. In addition, Haubold (1971) replaced *Hylopus* with *Gilmoreichnus*, while explaining later (Haubold

et al. 1995a) that 'The ichnogenus *Gilmoreichnus* was introduced by Haubold (1971) because *Hylopus*, which was used by Gilmore (1927), should be restricted to certain Late Mississippian tracks'. This is a step that we do not accept. Otherwise, unlike Haubold (1971), Gand (1987) and Haubold *et al.* (1995a), we currently think that the *Gilmoreichnus* (*Hylopus*) *hermitanus* trackmakers are not small pelycosaurids but are captorhinomorphs, like the makers of *Hyloidichnus*.

Pelycosauria: Eupelycosauria

Dimetropus leisnerianus (Geinitz 1863) Haubold 1971 (Fig. 2c11,d2&3) is well represented in the Lodève Basin, in particular on two surfaces discovered and extended during the working of the Mas d'Alary quarry by 'Cogema'. One of them, known as C3, of 105 m², makes it possible to observe 16 trackways adding up 137 manus-pes pairs. The morphological variability of the ichnospecies is well illustrated by Gand (1986, 1987). The detailed study of *D. leisnerianus* was made by Gand (1987, p. 167).

Dimetropus nicolasi Gand & Haubold 1984 (Fig. 2b6,c12) is described in Gand & Haubold (1984) and Gand (1987, p. 178). Later discoveries showed that the *typus*-sample corresponds to undertracks of *Dimetropus leisnerianus*. *D. nicolasi* was used by Haubold *et al.* (1995a) to identify the American footprints.

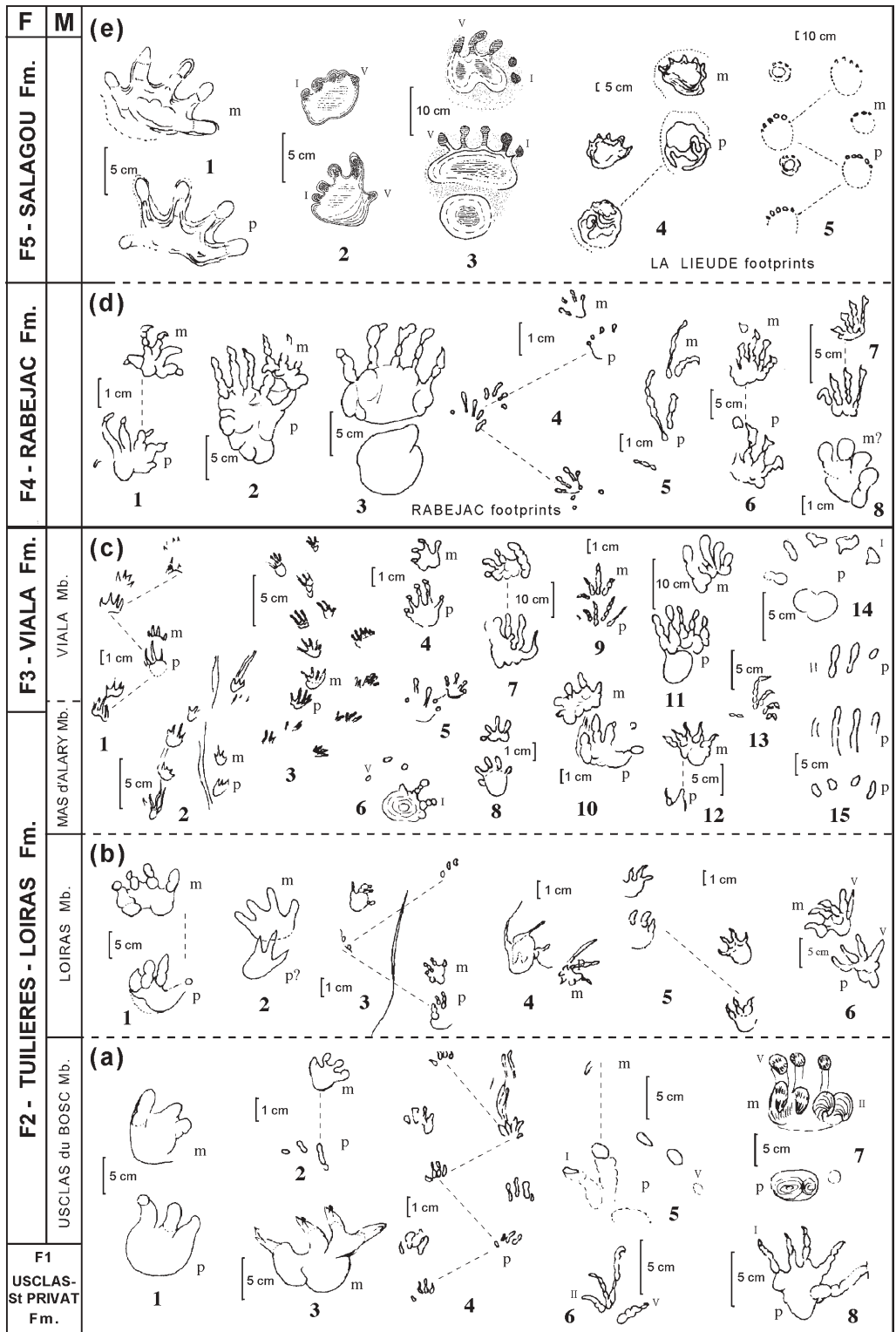
Dimetropus (Gonfaronipes) latus (Heyler & Montenat 1980) Gand 1987 is restricted to one sample, which is not well preserved and has no significance at this time.

Pelycosauria: Edaphosauria

Ichniotherium cottae Pöhlig 1885 is abundant in the Tambach Formation (Germany) where it occurs with *Dimetropus leisnerianus*. Many and large slabs with these two ichnospecies are preserved at the Gotha Museum where one can study their variability (Voigt & Haubold 2000; Voigt 2001). In the Lodève basin, we could identify *Ichniotherium* cf. *I. cottae* in three isolated cases (Fig. 2c14&15). The trackways observed on the C3 level as well as those of the Riviéral are swimming traces. Based on the various *I. cottae* morphotypes, they were allotted to this ichnogenus (Gand 1986, 1987 p. 186, 1989 p. 18), although some of these traces could also be slipped *Limnopus zeileri*.

Caseomorpha, Therapsida or Therosauria?

The following five ichnospecies are numbered 1–5 in order to cross-reference them with the work of Ellenberger (1983a–c). 1: *Merifontichnus thalerius* Gand *et al.* 2000 (Fig. 2e1), 2: *Lunaepes*



ollierorum Gand *et al.* 2000 (Fig. 2e2), 3: *Planipes brachydactylus* Gand *et al.* 2000 (Fig. 2e3), 4: *Brontopus giganteus* Heyler & Lessertisseur 1963 (Fig. 2e4), and 5: *Brontopus circagiganteus* Gand *et al.* 2000 (Fig. 2e5).

Ichnospecies 1–3 and 5 were named by Ellenberger (1983a–c) as 1: *Macrochelichnus thaleri*, 2: *Paranomodontipus ollieri*, 3: *Eocynodontipus antecursor* and *Pseudopithecopus recurvidigitus* (written also *Pseudopithecopus recurvidigitus*), and 5: *Moschopopus enormis*, but these taxa were held to be invalid because they were given without any diagnosis and description as required by the International Code of Zoological Nomenclature (ICZN). This is the reason why, from the advice of the reviewer M.A. Conti, Gand *et al.* (2000) again described these footprints by modifying slightly the epithets of Ellenberger (1983a,b,c) in order to be in accordance with the recommendations of the ICZN. The ichnospecies *Lunaepes fragilis* Gand *et al.* 1995 (Fig. 6g) described in Provence is similar to *Lunaepes ollierorum*, which abounds in the Lodève Basin. Except *B. circagiganteus* and *B. giganteus* Heyler & Lessertisseur 1963, close to *Chelichnus titan* Jardine 1851–1853, attributable to a caseomorph, all the others are therapsid or therosaurian tracks (Gand *et al.* 2000).

Ichniotherium (Cyclopus) aequalis (Heyler & Lessertisseur 1963) Haubold 1971 is a trackway that is always unclear and debatable. *Planipes caudatus* Gand *et al.* 1995 (Fig. 6f) differs from *P. brachydactylus* in the presence of the tail trace. *Chelichnus incurvus* Gand *et al.* 1995 (Fig. 6c) is abundant in the St-Raphaël ichnofossiliferous site but was never found elsewhere.

Eosuchia and Araeoscelidia

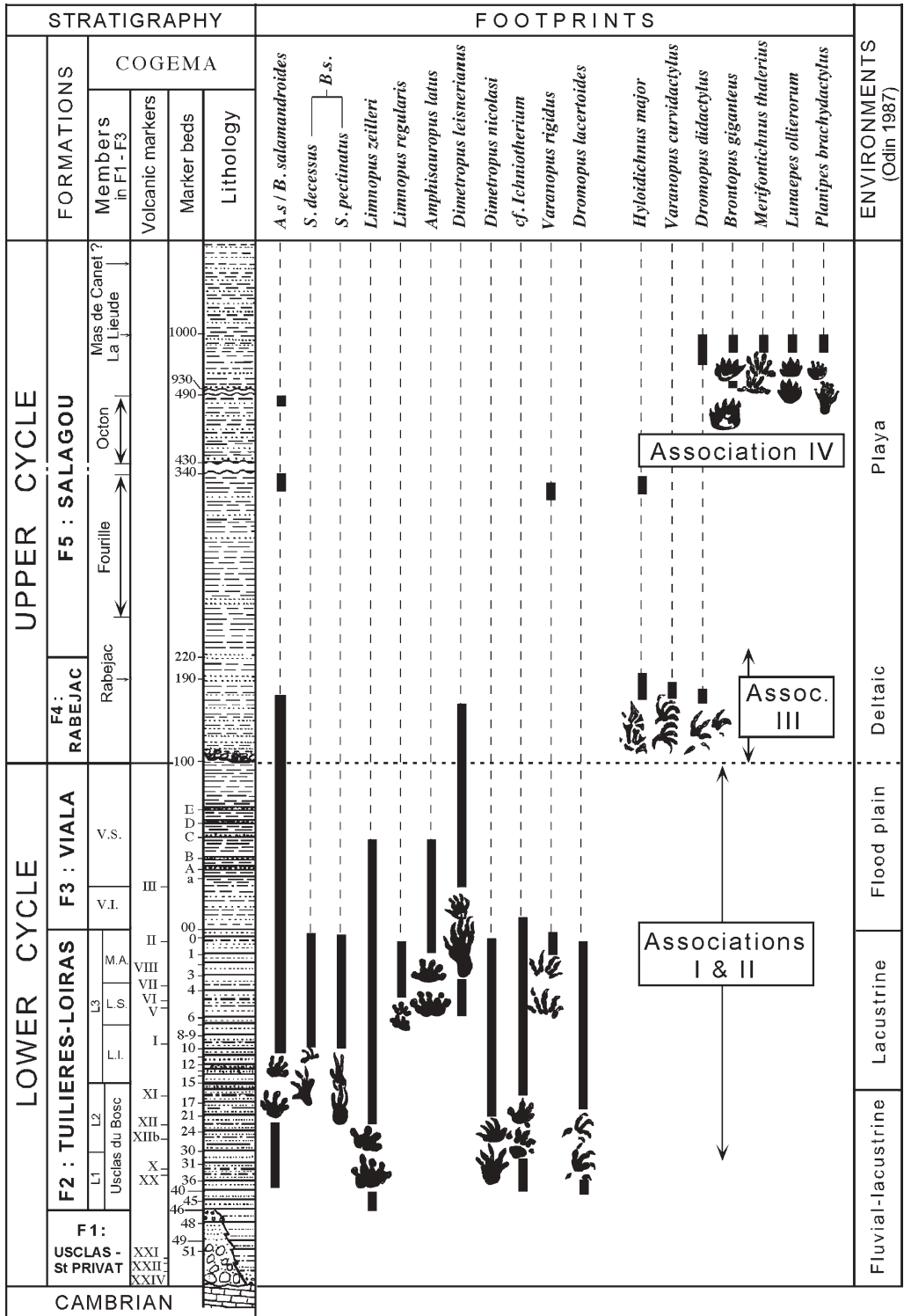
Dromopus lacertoides (Geinitz 1861) Haubold 1971 (Fig. 2a6,b4,c13). Associated with *B. salamandroides* and *Limnopis zeilleri*, this ichnospecies is frequent in the playa facies. When it is reduced to manus-pes sets with only two fingers each, it is impossible to discriminate them

from *Dromopus didactylus* (see above). *D. lacertoides* is very close to *D. agilis* Marsh 1894 from the Upper Carboniferous of the United States, which is also twinned with *Limnopis* (see above).

Dromopus didactylus (Moodie 1930) Gand & Haubold 1984, Gand 1987 (Figs 2d5, 5i–m). Moodie (1929) wrote about three ichnospecies with the same geological origin as *Varanopus curvidactylus*. They are *Varanopus palmatus*, *V. impressus* and *V. elrodi*, which were described on the basis of limited and fragmentary material. All have a lacertoid structure with the prevalence of two toes II–III or/and III–IV and the more subtle mark of I and V. The manus, smaller, has the same form. All these ichnospecies correspond to the manus-pes pairs, on small slabs probably coming from the same level. As they all have the same morphology, they can be assigned the same ichnospecies, *Varanopus palmatus* Moodie 1929, if it is admitted that the first ichnospecies described in a paper has priority. But, the holotype (n° 1241) is incomplete due to breakage, and *V. impressus* or *V. elrodi* are not appropriate because the toes are not fully printed. This is the reason why, following Sarjeant (1971), Gand & Haubold (1984) and Gand (1987) chosen the ichnospecies *Varanopus didactylus* Moodie 1930 to indicate these didactyl footprints, placing it in the ichnogenus *Dromopus* Marsh 1894, which has priority (Gand 1987, p. 204). The taxon *Dromopus didactylus* was accepted by Haubold in his revision of 1996 but he now prefers *Dromopus palmatus* (Haubold & Lucas 2001a). To validate this choice, a neotype would have to be created, which has not been done. Based on these different data, we prefer to use the name *Dromopus didactylus*.

Notice that this ichnospecies name was not well selected by Moodie because the didactyl aspect also appears in *Dromopus lacertoides*, which is rather localized in the basal part of the Lower Permian. Only the distance between the base of the IV toe and that of V makes it possible

Fig. 2. Main Permian footprints from the Lodève Basin. Stratigraphy: F = formations (Odin 1986); M = Autunian members from 'Cogema' (Laversanne 1976). Palichnofauna: (a) Usclas St-Privat Fm. and Tuilières-Loiras Fm. (Usclas du Bosc Mb.), 1–3, cf. *Limnopis*; 2, *Anthichnium salamandroides* = *Batrachichnus salamandroides*; 5, *Ichniotherium* sp.; 6, *Dromopus lacertoides*; 7, cf. *Ichniotherium*; 8, cf. *Dimetropus*. (b) Tuilières-Loiras Fm. (Loiras Mb.), 1 and 2, *Limnopis zeilleri*; 3, *Batrachichnus salamandroides*; 4, *Dromopus lacertoides*; 5, '*Gilmoreichnus brachydactylus*' = *B. salamandroides*; 6, *Dimetropus nicolasi*. (c) Tuilières-Loiras Fm. (Mas d'Alary Mb.) and Viala Fm., 1 and 2, *Salichnium decessus*; 3, *Salichnium pectinatus*; 4 and 5, *Anthichnium salamandroides* = *Batrachichnus salamandroides*; 6 and 7, *Limnopis (Permomegathierium) zeilleri*; 8, *Limnopis regularis*; 9, *Varanopus rigidus*; 10, *Amphisauropus latus*; 11, *Dimetropus leisnerianus*; 12, *Dimetropus nicolasi*; 13, *Dromopus lacertoides*; 14, *Ichniotherium* cf. *cottae*; 15, *Ichniotherium* cf. *cottae*. (d) Rabejac Fm., 1, *Varanopus curvidactylus*; 2 and 3, *Dimetropus leisnerianus*; 4, *Anthichnium salamandroides* = *Batrachichnus salamandroides*; 5, *Dromopus didactylus*; 6 and 7, *Hyloidichnus major*; 8, *Limnopis* sp. (e) Salagou Fm., 1, *Merifontichnus thalerius*; 2, *Lunaepes ollierorum*; 3, *Planipes brachydactylus*; 4, *Brontopus giganteus*; 5, *Brontopus circagiganteus*.



to differentiate the two ichnospecies. This requires complete prints, which are rather seldom observed.

Tambachichnium schmidti Müller 1954 or *Rhynchosauroides* Maidwell 1911. Many lacertoid footprints discovered in a disused quarry of St-Raphaël (Pradineaux Formation) were referred to *Tambachichnium schmidti* Müller 1954 by Gand *et al.* (1995) (Fig. 6e). This followed study by Gand in the Gotha Museum (Saxony, Germany) of the holotype and other lacertoid footprints, all coming from the Manebach Formation (Saale Basin). These last were represented by Pabst (1908, fig. 1, pl. XII).

The choice of *T. schmidti* was justified by the comparison of the manus traces, which have the same size and morphology in Saxony and France. Because he had only referred to the holotype, Haubold (1998a, p. 14) judged our determination as erroneous, which is far from being demonstrated. But, if the French lacertoid footprints are not *T. schmidti*, can they be referred to the ichnogenus *Rhynchosauroides*, which is known in the Val Gardena Sandstones and Bellerophon Formation (Italy), by two ichnospecies: *R. pallinii* Conti *et al.* 1977 and *R. palmatus* (Lull 1942)? The two sets of prints are close morphologically but are not of the same age: Artinskian for the German traces and Dzhulfian to Lower Dorashamian for those in Italy (Conti *et al.* 1986; Massari *et al.* 1999). Pending a statistical study, the answer remains open.

Protosauria

Pseudosynaptichnium esterelense Gand *et al.* 1995 was defined from a long trackway not seen elsewhere (Fig. 6h). Haubold (1998a, p. 14) suggested that these footprints are close to lacertoid traces that we have named *T. schmidti*, but we need more research to test this proposal.

At the end of this discussion, it appears that in each couple or triplet of taxa – *Batrachichnus salamandroides* / *B. delicatulus*, *Hyloidichnus bifurcatus* / *Hyloidichnus major*, *Erpetopus willistoni* / *Microsauripus acutipes* / *Varanopus curvidactylus*, *Hylopus hermitanus* = *Gilmoreichnus hermitanus* (*sensu* Haubold *et al.* 1995a) / *Varanopus rigidus*, and *Lunaepes ollierorum* / *Lunaepes fragilis* – the ichnospecies are so close that the first name could have nomenclatural priority.

But, with respect to the stability of nomenclature, possibly it is better to continue using these binomials in a 'regional' sense. Anyway, before selecting the name having priority, it will be necessary to complete the morphological and morphometrical study by using modern methods (discriminant, Fourier, Procrust analysis)

Most of the French taxa are ubiquitous in different formations of the Lodève, Provence, Saint-Affrique and Rodez (Sermels and Campagnac) basins. This is true for *Dromopus lacertoides*, *Dromopus didactylus*, *Limnopus zeileri*, *Amphisauropus latus*, *Batrachichnus salamandroides*, *Hyloidichnus major*, *Dimetropus leisnerianus*, and *Varanopus curvidactylus* / *Microsauripus acutipes*.

Stratigraphical inferences

The reference Lodève Basin

The most complete Permian sedimentary section in France crops out in the Lodève Basin (Languedoc), and it also yields the greatest variety of non-marine palaeontological elements, distributed irregularly through the entire succession: palynomorphs and macroflora, invertebrate trace and body fossils (insects, crustaceans, etc.), tetrapod footprints (numerous) and bones (rather scarce). The series is composed of two sedimentary cycles separated by an unconformity (Odin 1986). The first cycle consists of three formations: F1–F3 ('Autunian Group'), and the second of two: F4 and F5 ('Saxonian group') (Figs 2&3).

The ichnoassociations

The strata containing footprints have been precisely located in the lithostratigraphy, which is well-known from uranium prospecting. This has formed the basis of a palichnostratigraphical scale in which several local ichnoassociations have been identified (Gand 1987; Châteauneuf & Gand 1989; Gand 1993) (Fig. 3). Within the first cycle (Usclas-St.Privat, Les Tuillères-Loiras and Viala formations), two ichnoassociations (I and II) were distinguished initially. If we take into consideration the equivalencies of *Salichnium decessus* and *S. pectinatus* (undertracks) with *Gilmoreichnus brachydactylus* (*sensu* Gand 1987) = *Batrachichnus salamandroides*, the interpretation of *D. nicolasi* as an undertrack corresponding to *Dimetropus leisnerianus*, and the uncertain presence of *Ichniotherium* (in any case rather rare), it can be seen that the first sedimentary cycle contains:

Fig. 3. Vertical range of footprints in the Lodève Permian basin. Members: L.I., Lower Loiras; L.S., Upper Loiras; M.A., Mas d'Alary; V.I., Lower Viala; V.S., Upper Viala. Volcanic markers with roman numbers = 'cinérites' (dust-ash tuffs).

- (1) Ichnotaxa confined there (*Limnopus zeilleri*, *Dromopus lacertoides*, *Amphisauropus latus* and *Ichniotherium*); therefore, they characterize this part of the sedimentary succession.
- (2) Ichnotaxa that reach the basal part (Rabejac Formation) of the second cycle (*Batrachichnus salamandroides* and *Dimetropus leisnerianus*).

Above the unconformity, Association III (Rabejac) begins with the first appearance of *Varanopus curvidactylus* / *Microsauripus acutipes*, *Dromopus didactylus* and *Hyloidichnus major*. These two last ichnospecies, as well as *B. salamandroides*, are found up into a few levels of the F5 Salagou Formation, which is almost 2000 m thick. In the upper part of the Salagou Formation appears Association IV (La Lieude) with *Brontopus giganteus*, *B. circagiganteus*, *Planipes antecursor*, *Lunaepes ollierorum* and *Merifontichnus thalerius*. All are possibly therapsid traces except *Brontopus*, whose trackmaker could be a pelycosaurian (Gand *et al.* 2000).

Chronostratigraphy

The floristic content of the F1–F2 formations suggests, after comparison with that of the Autunian of Autun, an age ranging between the uppermost Ghzelian and the lower Sakmarian (Broutin *et al.* 1999). From the insects and conchostracans collected in the Salagou Formation, Nel & Schneider (in Gand *et al.* 1997) put forward ‘a Kungurian to Tatarian age (Leonardian to Capitanian)’ for this unit. Since that time, the distribution of various Odonoptera (Nel *et al.* 1999) and Archaeorthoptera (Béthoux *et al.* 2001, 2002a,b, 2003a,b) suggested Artinskian, Ufimian and Kazanian ages. But, because of some undecided lithostratigraphical assignments and the fact that the stratigraphical range is not established for several taxa of reference, these age determinations are not consistent with one another. In a recent work, based on conchostracans, Schneider (in Gand *et al.* 2004a,b) modified slightly the age of the Salagou Formation, and included it between the Kungurian and the Changxingian.

Tentative correlations with others regions

The basins of Provence

The main stratigraphical marker through the Permian basins of Provence is the A7 Rhyolite (Fig. 4). In the central part of the Bas-Argens Basin (Le Muy area), it is composed of five successive flows. Radio-isotopic dating ($^{39}\text{A}/^{40}\text{A}$) gave an age of 272.5 ± 0.3 Ma (Zheng *et al.* 1992),

fitting well with the Artinskian–Kungurian boundary according to Jin *et al.* (1997).

Over a long time, footprints and tracks have been collected from formations overlying the A7 lava flow (Demathieu *et al.* 1992, Gand *et al.* 1995) (Fig. 5). *Batrachichnus salamandroides*, *Limnopus* sp., *Hyloidichnus major*, *Varanopus rigidus*, *Laoporus* sp., *Dimetropus* sp., *Dimetropus latus*, and cf. *Dromopus* were gathered mainly from the Pelitic Formation of the Luc Basin (i.e. La Motte Formation of the Bas-Argens Basin). *B. salamandroides* and *Limnopus zeilleri* came from the Muy and Mitau formations, and *Dromopus didactylus* from the Mitau Formation.

The Muy Formation yielded many plant remains (Visscher 1968; Germain 1968), among them coalified remnants, silicified woods (Vozenin-Serra *et al.* 1991) and various abundant palynomorphs. Such a floristic association, which is comparable to those found in the Zechstein (in the original sense), can be regarded as the youngest known currently in the French Permian (Broutin, in Toutin-Morin *et al.* 1994).

Other traces came from the Pradineaux Formation overlying the A7 Rhyolite. *B. salamandroides*, and *Varanopus curvidactylus* / *Microsauripus acutipes* were found in the Coulet-Redon quarry (Bas Argens). Numerous footprints were observed on a large slab belonging to the upper part near St-Raphaël town (Estérel): *B. salamandroides*, *Limnopus* sp., *Hyloidichnus major*, *Lunaepes fragilis*, *Planipes caudatus*, *Pseudosynaptichnium esterelense*, *Chelichnus incurvus*, and *Tambachichnium schmidtii* (Fig. 4).

The Pradineaux Formation has been the subject of various attempts at dating. It includes the last important acidic flow (A11) that clearly predates the Illawarra Reversal, since it is cut by a fluorite-barite vein with adularia giving an isotopic age of 264 ± 2 Ma (Zheng *et al.* 1992). Near Agay, a thick unit of grey, fine-grained, lacustrine siliciclastics yields the oldest biostratigraphical elements known in that part of the series. They are mainly macrofloral remains, with very few palynomorphs, which allowed Visscher (1968) to propose an ‘Early Thuringian’ age, that is earliest Tatarian according to Menning (1994). Higher, the Pra Baucous lacustrine limestone beds yielded an ostracod association. According to their known stratigraphical occurrences in Russia, these species indicate an earliest Tatarian age, which can be correlated with the Early Midian of the Tethyan marine scale (Lethiers *et al.* 1993).

Recently, and for the first time, footprints have been discovered below the lava flow A7. *Varanopus curvidactylus* / *Microsauripus acutipes* and *Dromopus didactylus* were found in the

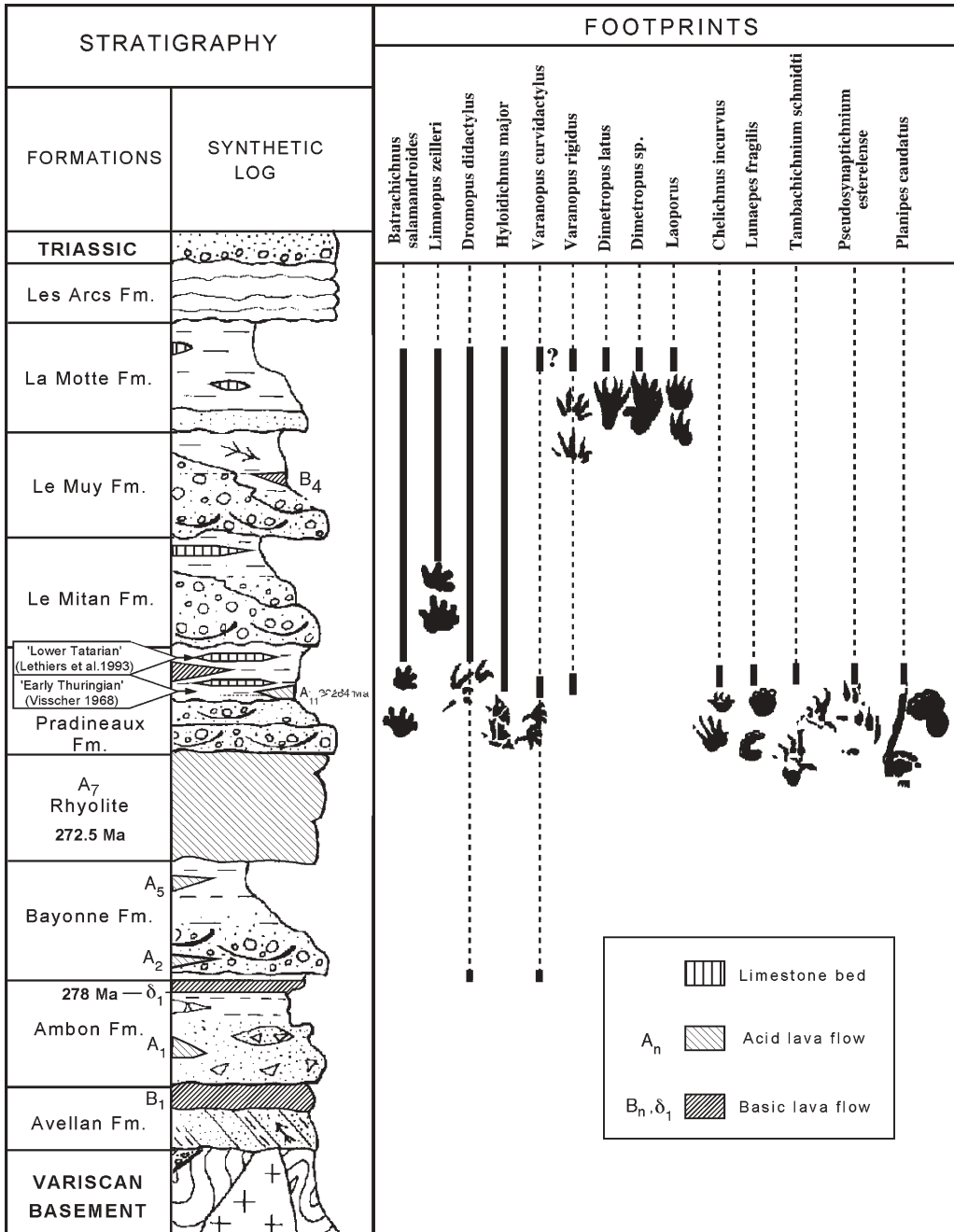


Fig. 4. Stratigraphical distribution of footprints in the Permian of Provence (Estérel-Bas Argens Basin).

Boson quarry in the Bayonne Formation (Durand *et al.* 2002). The ichnites are located above the δ 1 doleritic basalt, which represents the uppermost part of the Ambon Formation (Fig. 4). It was sampled for a ³⁹Ar /⁴⁰Ar dating,

yielding an age of 278 ± 2 Ma (Zheng *et al.* 1992). According to Menning (1994) and Jin *et al.* (1997), this date is Artinskian.

As far as correlations are concerned, except for isolated ichnites such as *Laoporus* sp.,

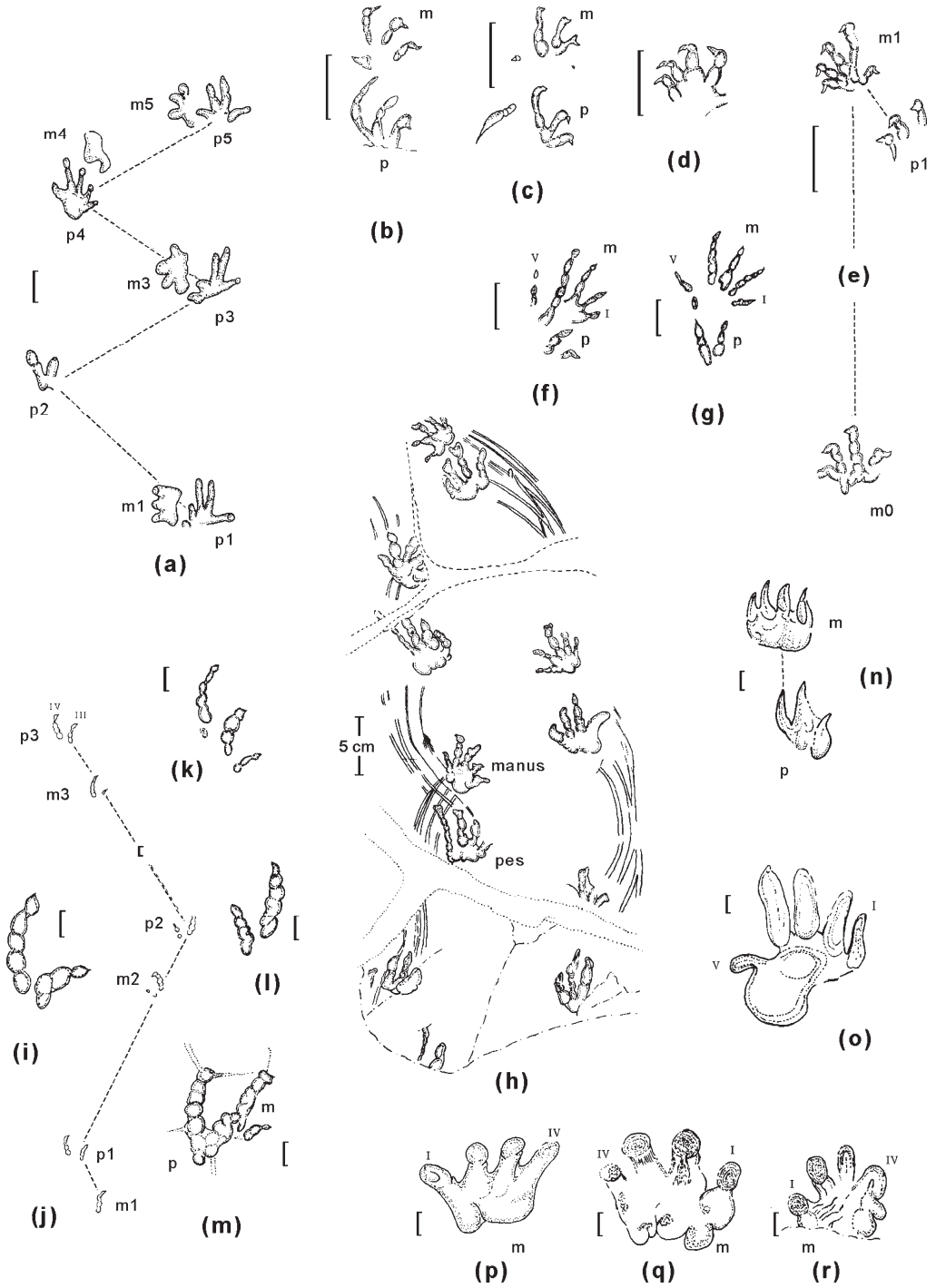


Fig. 5. Footprints from the Permian series of Provence. (a) *Batrachichnus salamandroides*, (b-e) *Varanopus curvidactylus*, (f&g) *Varanopus rigidus*, (h) *Hylodichnus major*, (i-m) *Dromopus didactylus*, (n) '*Laoporus*' sp., (o) *Dimetropus* sp., (p-r) *Limnopus zeilleri*. Scale bar: 1 cm.

Dimetropus sp. and *Dimetropus latus*, the series of Provence contains traces also recorded from the Lodève Basin, but only in the second cycle (F4 and F5 formations). The Bayonne Formation yielded only *Varanopus curvidactylus* / *Microsauripus acutipes* and *Dromopus didactylus*, two taxa appearing in Association III. From common footprints, such as *Hyloidichnus major*, *Lunaepes* and *Planipes*, it is possible to correlate the formations located above the A7 Rhyolite with the Salagou Formation of Lodévois, containing Association IV. It should be noted that *Limmopus zeilleri* has a greater vertical distribution in the whole French Permian series than is observed in the Saint-Affrique and Lodève basins alone, ranking it close to that of *Batrachichnus salamandroides*.

Thus, the Permian series of Provence could be about the same age as that of Lodève: namely, between Artinskian and Lopingian. The Pradineaux Formation levels bearing *Lunaepes* and *Planipes* could be Tatarian with reference to the precise location of these ichnogenera in the Lodève Basin.

In a recent work, Haubold & Lucas (2001a), using the Late Artinskian age of the *Erpetopus willistoni*, *V. curvidactylus*, *Dromopus palmatus* association from the Choza Formation (Texas), assign the same age to the Pradineaux Formation, which contains the same ichnospecies. But, the recent discovery of *V. curvidactylus* / *Microsauripus acutipes* in the Bayonne Formation shows that the vertical range of the latter taxa is so large that it cannot be used as a good marker. So, the 'Artinskian' age of the Pradineaux Formation is not demonstrated by footprints. On the other hand, a review of all the other dating elements concludes that the Pradineaux Formation is of Wordian age (Durand, 2006).

The United States basins

The Permian palichnofauna of the United States has been the subject of an active revision in recent years (Haubold *et al.* 1995a,b; Haubold 1996; Haubold & Lucas 2001a,b, 2003), which leads to several correlations between the United States and Europe (Haubold 2000; Haubold & Lucas 2001b; Lucas 2002a,b).

In their work of 2001a, Haubold & Lucas refer to the Choza Formation of Texas and to the Robledo Mountains Formation of New Mexico, which have layers bearing footprints inserted in marine beds dated by fossils. The ichnofauna of the Choza Formation, with *Erpetopus willisti*, *Microsauripus acutipes*, *Varanopus curvidactylus*, and *Dromopus palmatus* (*sensu* Haubold & Lucas 2001a) = (*D. didactylus sensu* Gand & Haubold

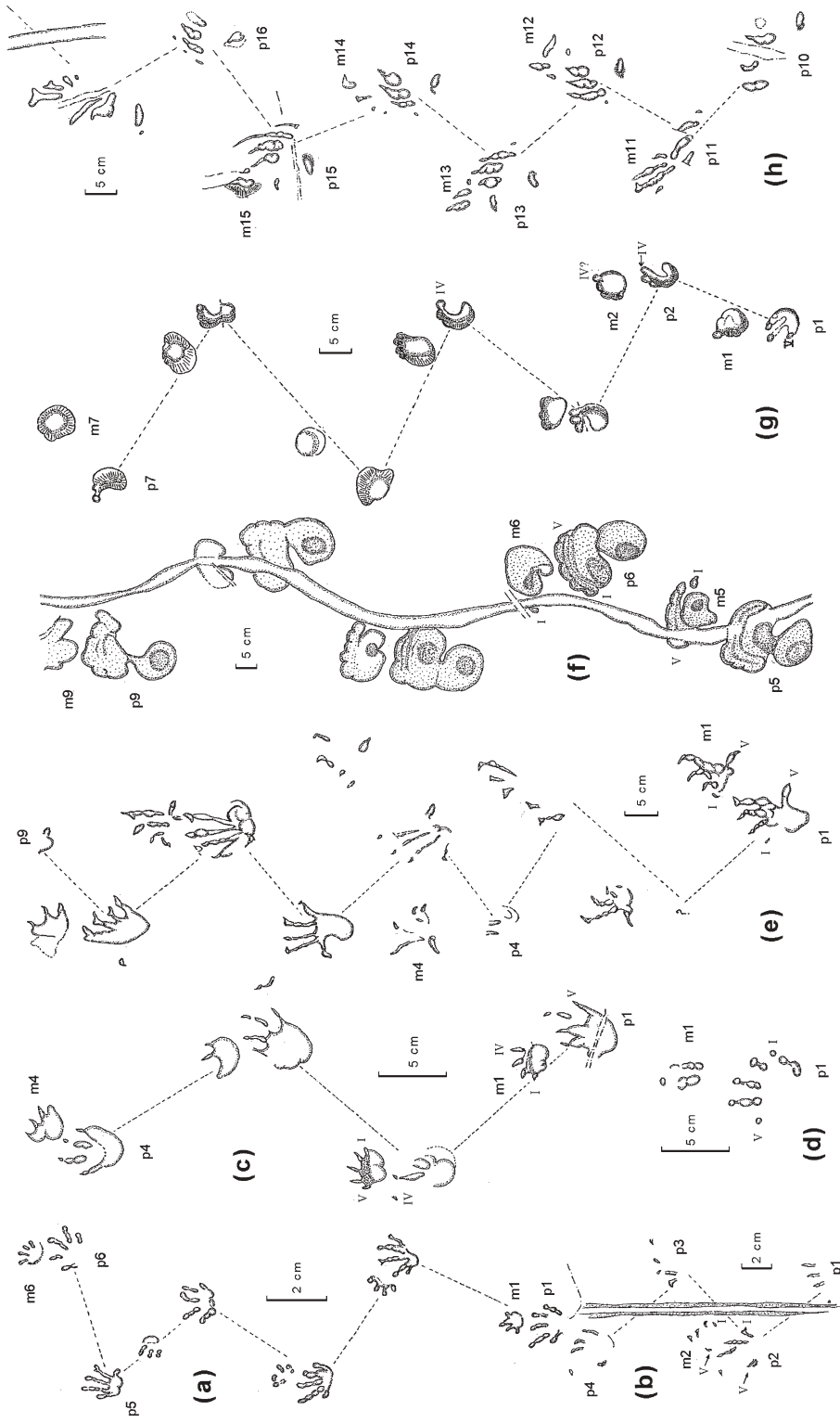
1984), is the youngest, with a Late Artinskian age. This association is underlain by the Robledo Mountains Formation which, is dated as Early Artinskian. It comprises *Batrachichnus delicatulus*, *Dromopus agilis/lacertoides*, *Amphisauropus*, and *Dimetropus nicolasi*. As 'an identical composition and vertical succession are shown by the ichnofaunas of the red bed formations of the Lower Permian in Europe', the authors conclude 'The same geological age, Late Artinskian, is evident, e.g. for the Rabejac, Pradineaux-Mitan and Collio formations of some Permian basins in southern Europe'. Such a dating for the European formations can be accepted only if the vertical distribution of the ichnospecies of the Choza Formation does not exceed its stratigraphical limits. However, it is not the case since two of its ichnotaxa – *Varanopus curvidactylus* and *Dromopus palmatus* (*sensu* Haubold & Lucas 2001a) = *Varanopus palmatus* Moodie 1930 – appear in the Upper Asselian (Lucas 2002a).

When comparing the vertical range of the ichnospecies closest morphologically (*Batrachichnus delicatulus* ≈ *B. salamandroides*, *Dimetropus nicolasi* ≈ *D. leisnerianus*, *Gilmoreichnus hermitanus* ≈ *Varanopus rigidus*, *Hyloidichnus bifurcatus* ≈ *H. major*, and *Varanopus curvidactylus* ≈ *Microsauripus acutipes*), it is clear that there is not 'an identical composition and vertical succession' in every basin (Fig. 7), which prohibits any certainty concerning the correlations made from footprints. The results depend on the ichnospecies and the basin which are taken as reference. Thus, the comparison of the footprint vertical distributions of the United States basins (in Lucas 2002a,b) with that of the Provence basins (Fig. 4) would result in dating the American formations from lower Artinskian to Tatarian if one considers the *Varanopus curvidactylus* / *Microsauripus acutipes* distribution, and only equating Tatarian with *H. major* and *V. rigidus* (≈ *Gilmoreichnus hermitanus*).

Such a result underlines the importance of the palaeontological gaps within each basin, demonstrated in those of Lodève and Provence, and the great stratigraphical range of certain footprints: *H. major*, *Limmopus*, *B. salamandroides*, *V. curvidactylus* / *M. acutipes*, and *D. didactylus*.

Lombardy: Orobic and Trompia basins (northern Italy)

The palichnofauna of the Collio Formation was collected and studied at many sites in the Lombardy basins by Conti *et al.* (1977, 1991, 1997, 1999), Nicosia *et al.* (1999, 2000, 2001), Santi & Krieger (1999, 2001), Avanzini *et al.* (2001), Santi (2001, 2003), and Arduini *et al.* (2003). These last authors present a list by basin, including the



following taxa: '*Batrachichnus salamandroides*, *B. sp.*, *Camunipes cassinisi*, *Amphisauropus latus*, *A. imminutus*, *V. curvidactylus*, *Dromopus lacertoides*, *D. didactylus* and *Ichniotherium cottae*.

After examination of the material in April 1999 in the Sapienza University (Rome), G.G. confirms the existence of *B. salamandroides*. While referring to its description and illustration in Ceoloni *et al.* (1987), *C. cassinisi* seems to be *Microsauropus acutipes*, but some footprints ascribed to this ichnogenus are clearly *B. salamandroides*. Thus, on a slab illustrated by Santi (2003, pl.Ic), the existence of digital scratches and the well marked metacarpal I results in recognizing a pentadactyl clawed hand, which is not the case for *M. acutipes*. Conversely, in Nicosia *et al.* (2000, p. 762), the '*A. imminutus*' trackway with a tetradactyl manus trace is not characteristic of the ichnogenus *Amphisauropus* in which the manus is pentadactyl.

All these ichnospecies are distributed in the Collio Formation, which rests on a volcanic member and is covered by the Verrucano. Isotopic studies make it possible to date it between 286/283 and 278/273 Ma (Cassinis *et al.* 1999). It is thus Artinskian based on the time scale of Menning (2001).

The Dolomites: Bolzano Basin (northern Italy)

Among the 24 taxa identified in the section of the Val Gardena Sandstone and Bellerophon Formation in the canyon of Butterloch-Bletterbach (Conti *et al.* 1977; Ceoloni *et al.* 1988), Avanzini *et al.* (2001) retained only the following ichnotaxa, which are common to other areas: Chirotheridae, *Rhynchosauroides sp.*, *R. aff. palmatus*, *R. pallinii*, *Dicynodontipus sp.*, *Ichniotherium aff. cottae*, *Ichniotherium accordii* and *Pachypes dolomiticus*. In this canyon, the Italian authors also identified: *Hylodichnus tirolensis*, '*Chelichnus tazelwuermi*', *?Paradoxichnium radeinensis* and *Janusichnus bifrons*.

During the study of the material by G.G., in 1999, Umberto Nicosia specified that *Tridactylum* and *Phalangichnus perwangeri* had been invalidated, and that many footprints named *Dromopus*, *Phalangichnus*, *Varanopus curvidactylus* had been assigned to *Rhynchosauroides*. It is a fact that this ichnogenus is present and abundant in the Bolzano basin; and, we

wondered whether the lacertoid trackways of St-Raphaël (France) could not comprise part of it. Another Italian ichnospecies, *Ichniotherium accordii*, suggests also a unification with *Merifontichnus thalerius* of the Lodève Basin. There is in both cases homopody and rather digitigrade manus traces, but the pes of *I. accordii* is generally plantigrade, whereas that of *M. thalerius* is digitigrade. More abundant material would thus be necessary to validate the assumption of a possible common ichnospecies between the Lodève and Bolzano basins. The comparison between *Pachypes dolomiticus* and *Brontopus giganteus*, both large round traces with indistinct digits, was made in Gand *et al.* (2000, p. 50). These ichnospecies differ in the size of the digits, which increase from the I to the IV in the first one, while the order is reversed in the second.

The association of the Bolzano Basin is well dated. It is indeed framed by levels with fusulinids and sporomorphs that make it possible to allot to it an age ranging from nearly 259 to 255 Ma (Avanzini *et al.* 2001), and is therefore Wuchiapingian.

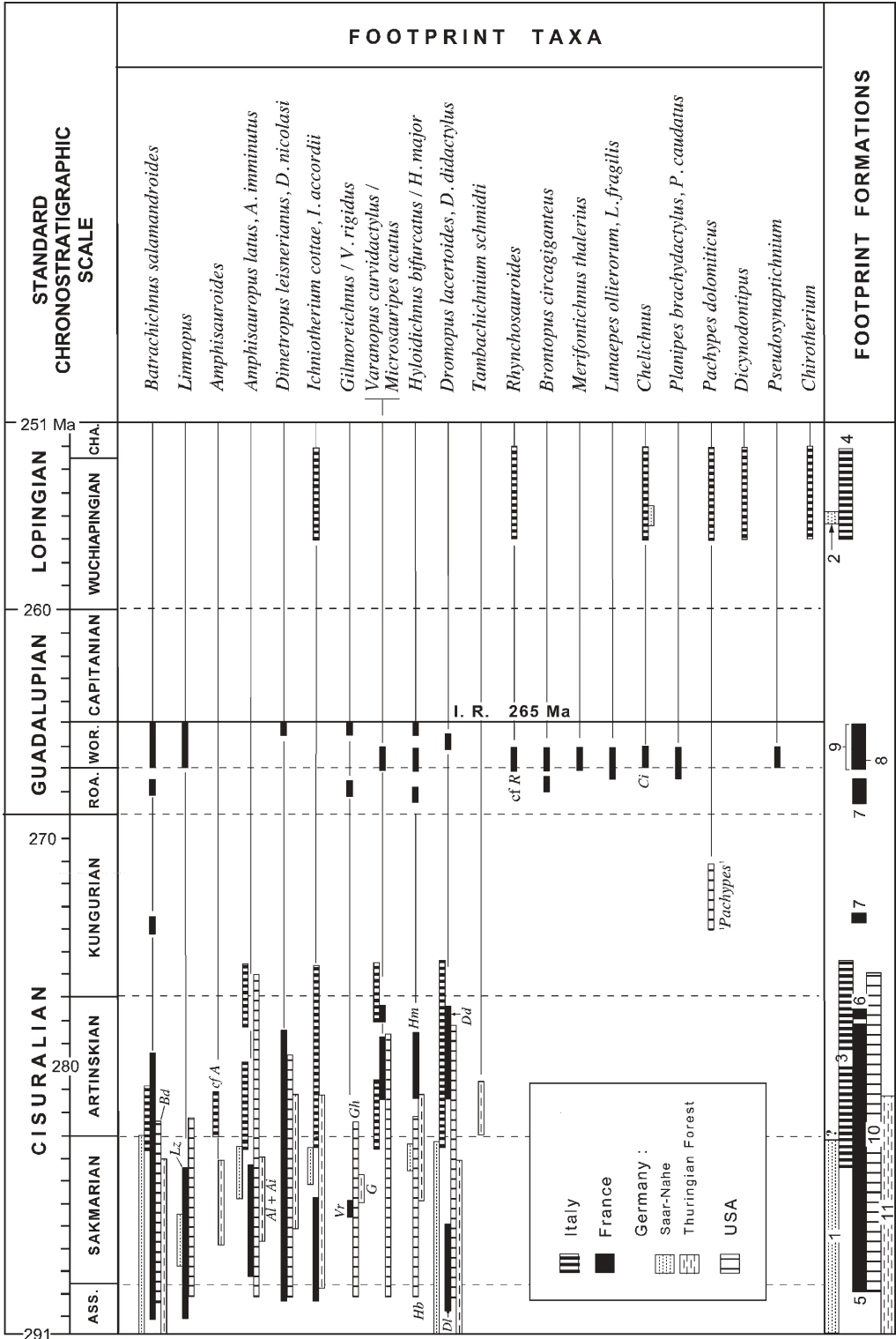
The Thuringian Forest Basin (Germany)

Numerous footprints have been found in three regions in Germany: the Thuringian Forest, the Cornberg area, and the Saar-Nahe Basin.

In Thuringia, footprints were studied and named by Pabst (1908), and their nomenclature was re-examined by Haubold (1971, 1973, 1996, 1998a,b). The palichnofauna was collected in the Lower Rotliegend, for a long time referred to the Autunian and Lower Saxonian (Haubold 1984). In the 'Autunian' part, Haubold listed the following characteristic footprints: *Batrachichnus salamandroides*, *Gracilichnium jacobii*, *Jacobiiichnus caudifer*, *Amphisauroides conrectus*, *A. discessus*, *Amphisauropus latus*, *A. imminutus*, *Hylodichnus arnhardti*, *Varanopus microdactylus*, *Gilmoreichnus brachydactylus*, *G. kablikae*, *G. minimus*, *Dromopus lacertoides*, *Ichniotherium cottae* and *Dimetropus leisnerianus*. *Palmichnus tambachensis* and *Tambachichnium schmidti* are only found in the Tambach Formation of the 'Lower Saxonian'.

In his revision, Haubold (1998a) regards *P. tambachensis* as an extramorphologic form of *Varanopus microdactylus*. This latter ichnogenus is written between quotation marks; Gand (1987, p. 155) has suggested replacing it with *Hylodichnus*. As in the French Lower Permian, *Folipes*, *Serripes* and *Acutipes* (Heyler & Lessertisseur 1963), *Gracilichnium* and *Jacobiiichnus* of the Thuringian Forest have only a regional interest because these taxa indicate slipped shapes of *B. salamandroides*. In our

Fig. 6. Trackways of the Saint-Sébastien slab (Pradineaux Formation, Estérel Basin, Provence). (a) *Batrachichnus salamandroides*, (b) *Varanopus rigidus*, (c) *Chelichnus incurvus*, (d) *Limnopus sp.*, (e) *Tambachichnium schmidti*, (f) *Planipes caudatus*, (g) *Lunaepes fragilis*, (h) *Pseudosynaptichnium esterelense*.



opinion, the taxa *G. minimus*, *G. kablikae* and *Hyloidichnus arnhardti* are not characteristic enough to be preserved.

The vertical distribution of these ichnospecies, well localized stratigraphically, led Haubold (1984) to distinguish the Autunian from the Saxonian. But, given the impossibility of defining the Saxonian as a stage, his scale lost its chronostratigraphic utility. The 'Saxonian' of the Thuringian Forest Basin is restricted to the Tambach Formation, which produced, in addition to a beautiful ichnofauna (Pabst 1908), vertebrate remains that were studied by Sumida *et al.* (1996). From the bones, the footprint association is dated as Wolfcampian. Menning (1995) placed the Tambach Formation in the lower Artinskian; other subjacent formations (Manebach to Rotterode Formations) are dated from Asselian to Sakmarian. This age assignment is close to that which can be given based on the typical 'Autunian' palaeoflora, which is to say Asselian to early Sakmarian.

The Cornberg Sandstein (Hessian Depression, Germany)

The footprints at this locality were made on the surface of aeolian dune deposits. Schmidt (1959) studied them and distinguished several ichnospecies of *Phalangichnus*, *Akropus*, *Palmichnus*, *Chelichnus*, *Barypodus* and *Harpagichnus*, these last three ichnogenera being attributed to therapsids. Haubold (1971, 1984) synonymized the nomenclature a little, maintaining only *Laoporus* and *Chelichnus* at first, then *Chelichnus* alone in his last revision (Haubold 1996). The ichnogenetic differences introduced by Schmidt are due, for Morales and Haubold (1995), to 'certain

preservational dunes facies influences, which are without taxonomic value'. This is, in our opinion, too simplified. The problem was also discussed by Fichter (1994).

The Cornberg Sandstein Formation was dated as Tatarian by Menning (1995). In the stratigraphical scale, this formation is above the 'Illawara reversal', which indicates an age younger than 265 Ma.

The Saar-Nahe and Wetterau basin (Germany)

The Saar-Nahe palichnofaunas were collected by Boy, Fichter and Stapf, then studied with much meticulousness by Fichter (1976, 1982, 1983a,b, 1984) and Fichter & Kowalczyk (1983). From the study of the French Permian palichnofauna and that of the Thuringian Forest (Gand 1987), G.G. studied in 1994 the Fichter collection preserved at Mainz University and that of the Stapf family stored at the Nierstein Museum. Many traces were collected in the Nahe and Lebach Groups, and some others in the Kusel Group, which rests on the 'C Stephanian'. The ichnospecies are well located in lithostratigraphies established by Stapf (1992, 2003) and then by Boy & Fichter (1982, 1988). The last authors divided the Kusel Group into 7 formations (R-Lo3), the Lebach Group into 19 formations (Lo3-Lo10, D1-D2), and the upper Nahe Group into 8 formations (N1-N8). Based on the 'Autunian flora' (Kerp & Fichter 1985) and the varied vertebrate fauna, methodically described by Boy (1972, 1987a,b, 1988, 1989, 1993, 1995, 2003), the Kusel and Lebach Groups were assigned to the 'Autunian' and most of the Nahe Group (N2-N5 Formation) to the 'Saxonian'.

In the Kusel and Lebach groups, Fichter (1976, 1982, 1983a,b, 1984) identified all the ichnospecies recorded from the Thuringian Forest Formation, plus *Limnopus palatinus* and *Foliipes abscissus*, the latter also mentioned in France. Without entering into details, our determinations were different. We thus established the presence of *Batrachichnus salamandroides* (= *Saurichnites salamandroides* of Fichter) but also referred to *B. salamandroides* the specimens described by Fichter as *Foliipes abscissus*, *Jacobichnus caudifer*, *Amphisauroides imminutus*, *Saurichnites incurvatus*, *Gilmoreichnus brachydactylus*, *G. kablikae*, *G. minimus*, *Varanopus microdactylus* and *Hyloidichnus arnhardti*. All these footprints show, indeed, at best, a tetradactyl manus without claw impressions. To determine *Gilmoreichnus*, for example, it is necessary to recognize pentadactyl and clawed footprints. The tail mark is not enough because it is irregular in the trackways of *B. salamandroides*. But, it is the true that, in this last ichnospecies,

Fig. 7. European and American stratigraphical ranges of footprint taxa. I.R., Illawarra Reversal. Stages: ASS, Asselian; ROA, Roadian; WOR, Wordian; CHA, Changhsingian. Footprint taxa: Bd, *Batrachichnus delicatulus*; Lz, *Limnopus zeileri*; cf. A, cf. *Amphisauroides*; Al + AI, *Amphisauropus latus* and *A. imminutus*; Vr, *Varanopus rigidus*; Gh, *Gilmoreichnus hermitanus*; G, *Gilmoreichnus*; Hb, *Hyloidichnus bifurcatus*; Hm, *Hyloidichnus major*; DI, *Dromopus lacertoides*; Dd, *Dromopus didactylus*; cf. R, cf. *Rhynchosauroides*; Ci = *Chelichnus incurvus*. Footprint formations: 1, Saar-Nahe basins, Kusel to Nahe Groups; 2, Cornberg Sandstone Fm.; 3, Lombardy basins, Collio Fm.; 4, Bolzano Basin, Val Gardena Sandstone and Bellerophon Fms; 5, Lodève Basin, Usclas-St-Privat to Rabecjac Fms; 6, Estérel Basin, Bayonne Formation; 7, Lodève Basin, lower Salagou Fm.; 8, Salagou Fm., La Lieude Mb.; 9, Provence basins, Pradineaux to La Motte Fms; 10, USA basins; 11, Thuringian Forest Basin, Manebach to Tambach Fms.

distal digital scratches and a deep print of the metacarpal I may be mistaken for prints of the claws and digit I; thus, such extramorphological *B. salamandroides* could be assigned to *Gilmoreichnus*. *Amphisauroides* sp. with a tetradactyl manus and broad digits (Fichter 1983a, p. 56; 1983b, p. 25) are better assigned to *Limnopus palatinus*, but many *L. palatinus* are *B. salamandroides*. The presence of *Dromopus lacertoides*, *Amphisauropus latus* (= *Saurichnites intermedius* in Fichter 1983a) and *Limnopus zeilleri* is confirmed. These last ichnospecies were seen in the Stapf collection (Nierstein museum) and in that of Fichter (Mainz University), but *L. zeilleri* was named *Dimetropus leisnerianus* (Fichter 1976, p. 100; 1983b, p. 155) or *Ichniotherium cottae* (Fichter 1983b, p. 47). Actually, we never observed these two ichnotaxa in the Kusel and Lebach groups. Nevertheless, the sample PIM K 217 from the Wahnwegen Formation suggests the last one by its size and its plantigrady, but it is clearly lacertoid. Let us add to this list the presence of *Amphisauropus imminutus*, well characterized by only one trackway from the Stapf collection.

In the Nahe Group (N1–N8), which begins with a rhyolitic complex, red formations seldom produced complete traces. Fichter (1983a,b, 1984) identified in this group almost all the ichnospecies collected in the Kusel and Lebach groups, to which it is necessary to add *Phalangichnus alternans*, *Chelichnus*, *Laoporus* and *Anhomoiichnium*. We confirm *Dromopus lacertoides*, *Amphisauropus imminutus*, *A. latus* and *V. microdactylus*, whereas cf. *Chelichnus*, cf. *Laoporus*, *Phalangichnus* are doubtful, and *Anhomoiichnium* represents *D. didactylus*. *Varanopus curvidactylus* is a possible identification for only one specimen. Other rather common traces are represented only by the digital impressions with ends rounded like balls; they can be assigned to *Limnopus* or *A. latus*.

The ichnofauna discovered in the Wetterau (eastern extension of the Saar–Nahe Basin) comes from the Bleichenbach Formation. From the footprints, it was correlated 'with the upper part of the Nahe Group of the Saar–Nahe Basin'. Based on the figures of Fichter & Kowalczyk (1983), we recognized *B. salamandroides*, *Limnopus*, *A. latus* and *A. discensus*, but the footprints named *Dimetropus leisnerianus* and *G. kablikae* are not really determinable. *Ichniotherium cottae* does not seem characteristic of this ichnofauna, but the existence of this ichnotaxon is certain in the Sponheim (N4) Formation, since it is represented by a trackway preserved at Pollichia Natural History Museum of Bad Dürkheim. Certain *I. cottae* forms from the

Wetterau suggest large *H. major* from the Lodève Basin (Gand 1987).

At the end of this revision, which was carried out by G.G. in 1994 (unpublished but communicated to Haubold and Fichter), the following ichnospecies were identified in the Saar–Nahe Basin: *Batrachichnus salamandroides*, *Limnopus zeilleri*, *L. palatinus*, *Amphisauropus latus*, *A. discensus*, *Varanopus microdactylus*, *Dromopus lacertoides*, *D. didactylus*, *Ichniotherium cottae* and cf. *H. major*. Such a result naturally modifies the palichnostratigraphy that was worked out by Boy & Fichter (1982) based on ichnospecies that we did not identify (see Fig. 7).

The majority of the footprints collected in the Kusel and Lebach Groups were associated with an 'Autunian' palaeoflora and a vertebrate fauna, both forming characteristic associations of this 'stage' (Boy 1987a). Following Broutin *et al.* (1999) it is possible to assign a latest Gzhelian to Early Sakmarian age to the footprint-bearing levels ranging between the base of the Kusel Group and the top of the N3 Formation of the Nahe Group. These results are in rather good agreement with isotopic data. On the one hand, just below the base of the Kusel Group, a tuff yielded a $^{40}\text{Ar}/^{39}\text{Ar}$ age of 300.3 ± 1.2 Ma (Burger *et al.* 1997), which can be compared with that of the Gzhelian–Asselian boundary (299.0 Ma) on the last geological time scale (Gradstein *et al.* 2004). On the other hand, the isotopic ages of volcanites at the base of the Nahe Group, in the Donnersberg N3 Formation, ranges from 298.7 ± 5.3 to 294.6 ± 4.3 Ma by the $^{40}\text{Ar}/^{39}\text{Ar}$ method, and from 292.1 ± 3.4 to 291 ± 1.3 Ma by the Rb/Sr method (Lippolt & Hess 1989).

Conclusions

At the end of these analyses, summarized in Figure 7, we can conclude that many ichnospecies, such as *B. salamandroides*, *Limnopus zeilleri*, *Dromopus lacertoides*, *D. didactylus*, and even *Amphisauropus latus*, have a great vertical distribution. They are thus not good biostratigraphical markers for inter-basin correlations. It is, of course, also the case for taxa whose geographical range is restricted, such as *Amphisauroides* and *Ichniotherium cottae*, which are not found in the United States and are little represented in France, or *Hyloidichnus*, which was not observed in the Lower Permian of Lombardy.

When considering the ichnospecies common to several basins, their vertical distribution differs so much that it is impossible to use them individually, nor even the ichnoassociations observed locally, in order to establish fine

correlations between the footprint-bearing formations. It is nevertheless seen that the Lower Permian (Cisuralian) corresponds to a single 'ichnofaunal unit' (Avanzini *et al.* 2001; Haubold & Lucas 2001) characterized by some ichnotaxa: *Amphisauroides*, *Amphisauropus imminutus*, *A. latus* and *Dimetropus leisnerianus* / *D. nicolasi*.

After an important palichnological gap, corresponding at least partially with 'Olson's gap' (Lucas & Heckert 2001), a second 'ichnofaunal unit' can be recognized in the Lodève and Estérel (Provence) basins, in which one finds new ichnospecies. Many of them are attributable to therapsids, but one (*Brontopus giganteus*) is attributed to a late pelycosaurian or a pareiasaurian (Gand *et al.* 1995, 2000). The following ichnospecies seem to characterize this unit: *Lunaepes fragilis*, *L. ollierorum*, *Pachypes brachydactylus*, *P. caudatus*, *Merifontichnus thalerius*, *Brontopus giganteus*, *Chelichnus incurvus* and *Pseudosynaptichnium esterelense*. But it should be noticed that the French basins have in common only the ichnogenera *Lunaepes* and *Planipes*. Moreover, in these areas, the vertical distribution of most ichnospecies is not known conclusively: *B. giganteus* was recently discovered at a second level, 100 m lower than that of La Lieude. Since palaeontological and isotopic data make it possible to date the Estérel supra-A7 footprint association (\approx Lodève Association IV) as Wordian (Durand, 2006), the second Permian 'ichnofaunal unit' seems typical of the Middle Permian (Guadalupian).

It is then necessary to consider the Italian basin of Bolzano, where a third 'ichnofaunal unit', dated as Wuchiapingian, contains some ichnospecies with Triassic features: chirotheroid forms and *Rhynchosaurooides*. It characterizes the Upper Permian (Lopingian). Thus, the French palaeoichnologic record allows us to discriminate three time intervals of Permian time in northern Pangaea, as do the skeletal remains (Lozovsky 2003).

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