

# Zitteliana

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für Paläontologie und Geologie

28



DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

**Flugsaurier: pterosaur papers in honour of  
Peter Wellnhofer**

München 2008

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## B28

DAVID W. E. HONE & ERIC BUFFETAUT (Eds)

### Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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**Cover Illustration:** Modell eines *Rhamphorhynchus* aus dem Oberjura von Eichstätt. Entwurf: P. Wellnhofer, Modell: R. Liebreich,  
Foto und Collage: M. Schellenberger, L. Geißler, BSPG München.

**Umschlagbild:** Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer;  
design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

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# Pterosaur distribution in time and space: an atlas

By

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## Abstract

Pterosaurs first appeared in the Late Triassic and persisted until the terminal Cretaceous: they achieved a global distribution during the Mesozoic. Here, we attempt to provide the first comprehensive summary of pterosaur distribution through time and space, including information on the taxonomic composition of pterosaur faunas and the lithostratigraphic units in which they occur. We hope that this compilation will be used as a primary research tool, permitting more detailed and rigorous analyses of pterosaur diversity and palaeobiogeography than have been possible to date.

**Key words:** distribution, biogeography, stratigraphy

## Zusammenfassung

In der Späten Trias erschienen Flugsaurier zum ersten Mal. Sie erreichen während des Mesozoikums bis zum Ende der Kreidezeit eine globale Verbreitung. Wir versuchen hier eine erste umfassende Zusammenfassung der Verbreitung der Flugsaurier sowie der lithostratigraphischen Einheiten in denen sie erscheinen zu liefern. Wir hoffen dass diese Aufstellung als grundlegendes wissenschaftliches Werkzeug genutzt werden wird, da es eine detailliertere und umfassendere Analyse der Diversität und Palaeobiogeographie der Flugsaurier bietet als bisher möglich gewesen ist.

**Schlüsselwörter:** Verbreitung, Biogeographie, Stratigraphie

## 1. Introduction

### 1.1 Pterosaurs in time and space

Recent compendia of dinosaur occurrences (WEISHAMPEL

1990; WEISHAMPEL et al. 2004) are greatly facilitating studies of dinosaur palaeobiogeography, macroecology and macroevolution (e.g. FASTOVSKY et al. 2004; WANG & DODSON 2006). These databases are (almost) exhaustive and provide accessible summaries of a vast literature, placing details of stratigraphical horizons and faunal composition in a geographical context. Consequently, they have become tools that allow researchers to rapidly locate basic site information and find relevant citations. Moreover, such compilations can help to focus future fieldwork efforts by highlighting regions that remain relatively undersampled.

To date, WELLNHOFER (1978) has provided the only comprehensive summary of the entire pterosaur fossil record, although several more recent popular accounts also exist (WELLNHOFER 1991a, UNWIN 2006). In addition, some reviews of pterosaurs from particular regions (e.g. BAKHURINA & UNWIN 1995; UNWIN et al. 2000; KNOLL & BOUVEUR 2001) or timeslices (e.g. UNWIN 1996a) have also been published. In the 30 years that have passed since the publication of WELLNHOFER's (1978) compendium, many new pterosaur taxa have been named (see WELLNHOFER 1991a and UNWIN 2006 for summaries) and several detailed reappraisals of historical taxa have also appeared (e.g. UNWIN 2001; BENNETT 2006). Consequently, a new compilation is required that incorporates these new discoveries. Moreover, few of the published summaries on pterosaur distribution deal with the data on a locality-by-locality basis: furthermore, they do not generally include sites that have yielded only fragmentary or indeterminate material.

Here, we present the first iteration of a global database for pterosaur occurrences. This new compilation should be viewed as a dynamic database that will need to be refined periodically in order to incorporate new localities and taxa as they are discovered, and to account for future changes to existing stratigraphical and taxonomic terminology. We hope that this database will provide a firm foundation for broader scale evolutionary studies on pterosaurs and Mesozoic ecosystems in general, including investigations into topics such as palaeobiogeography and controls on species-richness.

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## 1.2 Materials and methods

In general, we have followed the conventions used by WEISHAMPEL et al. (2004) in their survey of Mesozoic dinosaur distributions. Our aim is not to provide a complete bibliography of pterosaur research, but to provide key references that record all known pterosaur localities. Information on pterosaur occurrences was taken directly from searches of the primary literature. The resulting information has been arranged stratigraphically by sub-Period (Upper Triassic, Lower Jurassic, Middle Jurassic, Upper Jurassic, Lower Cretaceous and Upper Cretaceous). Where there is conflict over the dating of a particular deposit, it has been placed within the earliest suggested time period, with alternative dates appended. Within each time period, the data are sub-divided geographically on the basis of continent, country and administrative region: each of these listings is hierarchical and countries are listed alphabetically. The recent classification proposed by UNWIN (2003, 2006) has been used as a framework for the taxonomic lists. Ages for each deposit are given using Standard European Stages and the geological timescale of GRADSTEIN et al. (2004).

In order to visualise the spatial distribution of the data, maps have been provided to show each locality (with the exceptions of the single localities on Antarctica and Greenland) on a region by region basis: Africa and the Middle East (Fig. 1); Australia and New Zealand (Fig. 2); China and eastern Asia (Fig. 3); central Asia (Fig. 4); UK (Fig. 5); France (Fig. 6); central and eastern Europe (Fig. 7); the Iberian Peninsula (Fig. 8); North America (Figs 9-10); and South America and India (Fig. 11). Figures were created by plotting localities onto continental reconstructions in ESRI ArcMap 9.1; shapefiles were downloaded from [http://www.vdstech.com/map\\_data.htm](http://www.vdstech.com/map_data.htm).

## 1.3 Acknowledgements

We thank the editors for their invitation to contribute to this volume, L. STEEL (NHM, London) for commenting on an early version of this database and especially D. MARTILL (University of Portsmouth) and M. BENTON (University of Bristol) for their helpful comments on the manuscript.

## 2. Pterosaur distribution

### 2.1 Upper Triassic

#### 2.1.1 Europe

##### 1. Tirol, Austria

Seefeldler Schichten (Ankerschlag: DALLA VECCHIA et al. [2002]; Karwendal Mountains: WELLNHOFER [2003]).

'Rhamphorhynchoidea'; Campylognathoididae  
*Austriadactylus cristatus*  
*Eudimorphodon* cf. *E. ranzii*

Age: middle Norian (DALLA VECCHIA et al. 2002); late Norian (WELLNHOFER 2003).

##### 2. Gloucestershire, England

Unnamed unit of fissure fills (Cromhall Quarry: FRASER & WALKDEN [1983], FRASER & UNWIN [1990]).

Pterosauria indet.

Age: late Norian (WALKDEN & FRASER 1993).

##### 3. Département de la Meurthe-et-Moselle, France

Gres à *Avicula contorta* (Varangéville: GODEFROIT [1997]; St Nicholas-de-Port: GODEFROIT & CUNY [1997]).

?Pterosauria indet. (= '?*Eudimorphodon* sp.')

Age: late Norian–Rhaetian (SIGOGNEAU-RUSSELL & HAHN 1994).

##### 4. Lombardia, Italy

- i) Calcare di Zorzino (Cene: ZAMBELLI [1973], WILD [1978, 1994], DALLA VECCHIA [2003a, 2003b, 2003c]; Endenna/Zogno, Brucciatà Valley: PADIAN [1980], WILD [1984], DELLA VECCHIA [2003a, 2003b, 2003c]).

'Rhamphorhynchoidea'; Campylognathoididae  
*Eudimorphodon ranzii*  
cf. *Eudimorphodon* sp.  
'Rhamphorhynchoidea'; Dimorphodontidae  
*Peteinosaurus zambelli*  
*Peteinosaurus* sp. (= '*Preondactylus* sp.')

Pterosauria indet.

Age: late Norian (DALLA VECCHIA 2003c).

- ii) Argilliti di Riva di Solto (Ponte Giurino/Berbenno: WILD [1994], DELLA VECCHIA [2003a, 2003b, 2003c]).

'Rhamphorhynchoidea'; Campylognathoididae  
*Eudimorphodon ranzii*

Age: late Norian (JADOUL et al. 1994; DALLA VECCHIA 2003c).

##### 5. Friuli-Venezia Giulia, Italy

Dolomia di Forni (Seazza Creek, Preone Valley: WILD [1984], DALLA VECCHIA et al. [1989], DALLA VECCHIA [2002, 2003a, 2003b]; Forchiar Creek, Preone Valley: DALLA VECCHIA [1995]; Rovadia Creek, Preone Valley: DALLA VECCHIA [2003a, 2003b]; Purone Creek, Preone Valley: DALLA VECCHIA [2003a, 2003b]).

Basal Pterosauria

*Preondactylus buffarini*  
'Rhamphorhynchoidea'; Campylognathoididae  
*Eudimorphodon rosenfeldi*  
*Eudimorphodon* sp.

Pterosauria indet.

Age: late Norian (ROGHI et al. 1995; DALLA VECCHIA 2003c).

## 6. District de Luxembourg, Luxembourg

Unnamed unit 'Syren Bonebed' (Syren: GODEFROIT et al. [1998], DELSATE [2000]).

?Pterosauria indet. (= '*Eudimorphodon* sp.')

Age: early Rhaetian (GODEFROIT et al. 1998).

## 7. District de Diekirch, Luxembourg

Steinmergel Group (Medernach: CUNY et al. [1995], DELSATE [1999]).

?Pterosauria indet. (= '*Eudimorphodon* sp.')

Age: Norian–Rhaetian (DELSATE 1999).

## 8. Canton Graubünden, Switzerland

Kössen Formation (Mount Schesaplana: FRÖBISCH & FRÖBISCH [2006]).

Basal Pterosauria  
*Caviramus schesaplanensis*

Age: late Norian or early Rhaetian (FURRER 1993).

## 9. Canton Schaffhausen, Switzerland

Unnamed unit 'Hallau Bonebed' (Hallau: CLEMENS [1980], TATARINOV [1985]).

?Pterosauria indet. (= 'Eudimorphodontidae indet.')

Age: Rhaetian (CLEMENS 1980).

## 2.1.2 North America

### 10. Tunu, Greenland (not plotted)

Fleming Fjord Formation (Macknight Bjerg: JENKINS et al. [2001]).

'Rhamphorhynchoidea'; Campylognathoididae  
*Eudimorphodon cromptonellus*

Age: Norian–Rhaetian (CLEMMENSEN et al. 1998).

### 11. Arizona, United States of America

Bluewater Creek Formation/Petrified Forest Formation (*Placerias* Quarry, St Johns: LONG & MURRY [1995]).

?Pterosauria indet.

Age: late Carnian-early Norian (LUCAS et al. 1997).

## 12. New Mexico, United States of America

i) Santa Rosa Formation (Canada Colorado: HUNT et al. [1993], LONG & MURRY [1995]).

?Pterosauria indet.

Age: middle-late Carnian (HUNT et al. 1993; LONG & MURRY 1995).

ii) Sloan Canyon Formation (Sloan Canyon: HUNT & LUCAS [1993]).

?Pterosauria indet.

Age: early Norian–Rhaetian (HUNT & LUCAS 1989).

iii) Petrified Forest Formation (Chama Basin: ZIEGLER et al. [2004]).

?Pterosauria indet.

Age: early-middle Norian (ZIEGLER et al. 2004).

## 13. Texas, United States of America

Tecovas Formation (Kalgary: MURRY [1986], LUCAS & LUO [1993], ANDRES [2006]).

'Rhamphorhynchoidea'; Campylognathoididae  
*Eudimorphodon* sp.

Age: late Carnian (LUCAS & LUO 1993).

## 2.2 Lower Jurassic

### 2.2.1 Africa

#### 14. Free State, South Africa

Upper Elliot Formation (Spioenkop: BLACKBEARD & YATES [2007]).

Pterosauria indet.

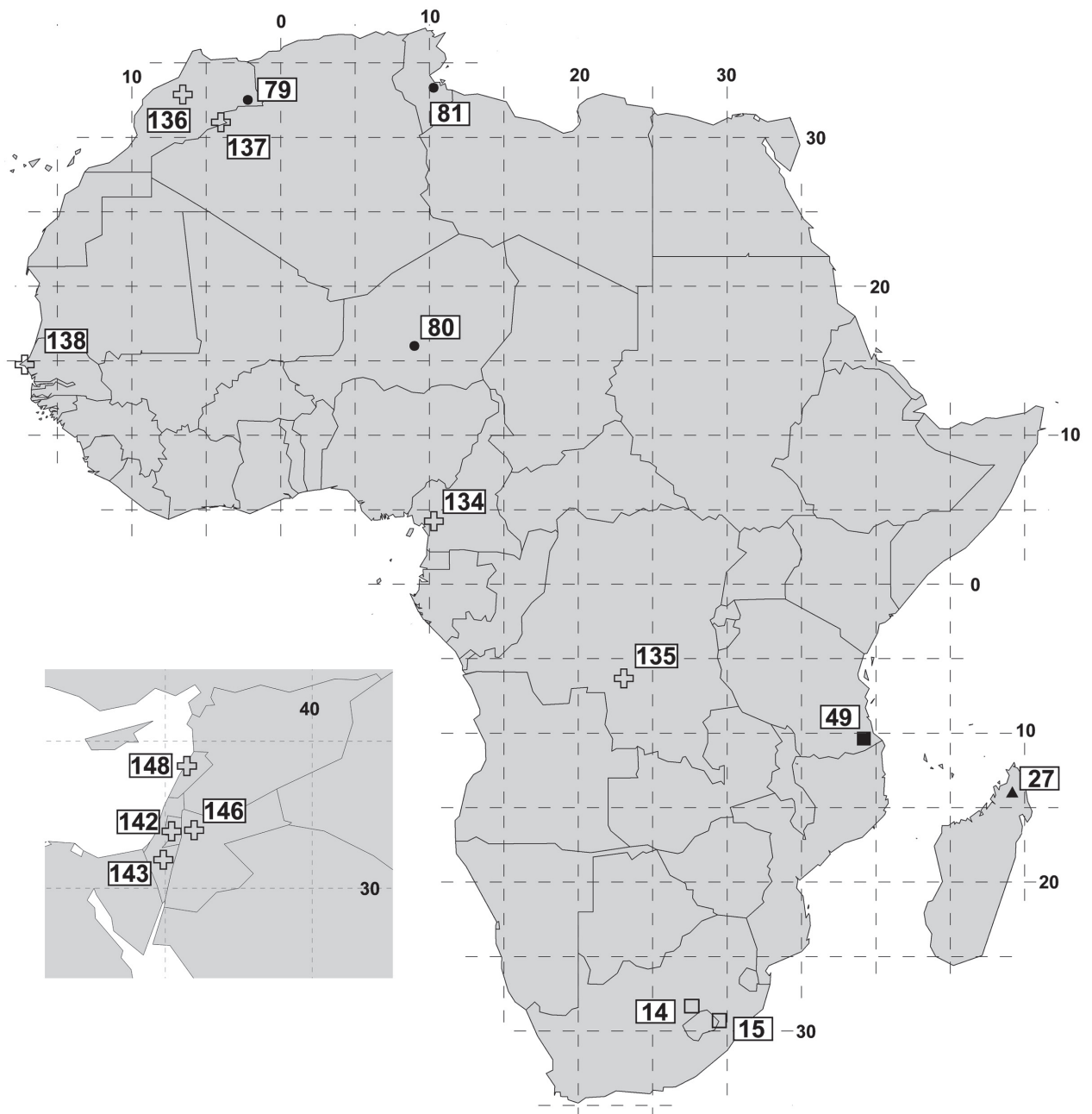
Age: Pliensbachian-Toarcian (YATES et al. 2004).

#### 15. Kwazulu-Natal, South Africa

Clarens Formation (Giant's Castle: VAN DIJK [1978], KNOLL [2005]).

?Pterosaur tracks (*Molapopentapodiscus supersalta* tor)

Age: Pliensbachian-Toarcian (YATES et al. 2004).



**Figure 1:** Pterosaur localities from the Lower Jurassic to Upper Cretaceous of Africa, Madagascar and the Middle East. Upper Triassic pterosaur localities are currently unknown in these regions. Key: open squares, Lower Jurassic localities; filled triangles, Middle Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

## 2.2.2 Antarctica

### 16. Central Transantarctic Mountains, Antarctica

Hanson Formation (Mount Kirkpatrick: HAMMER & HICKERSON [1994]).

'Rhamphorhynchoidea' indet.

Age: Lower Jurassic (SMITH et al. 2007).

## 2.2.3 Asia

### 17. Andhra Pradesh, India

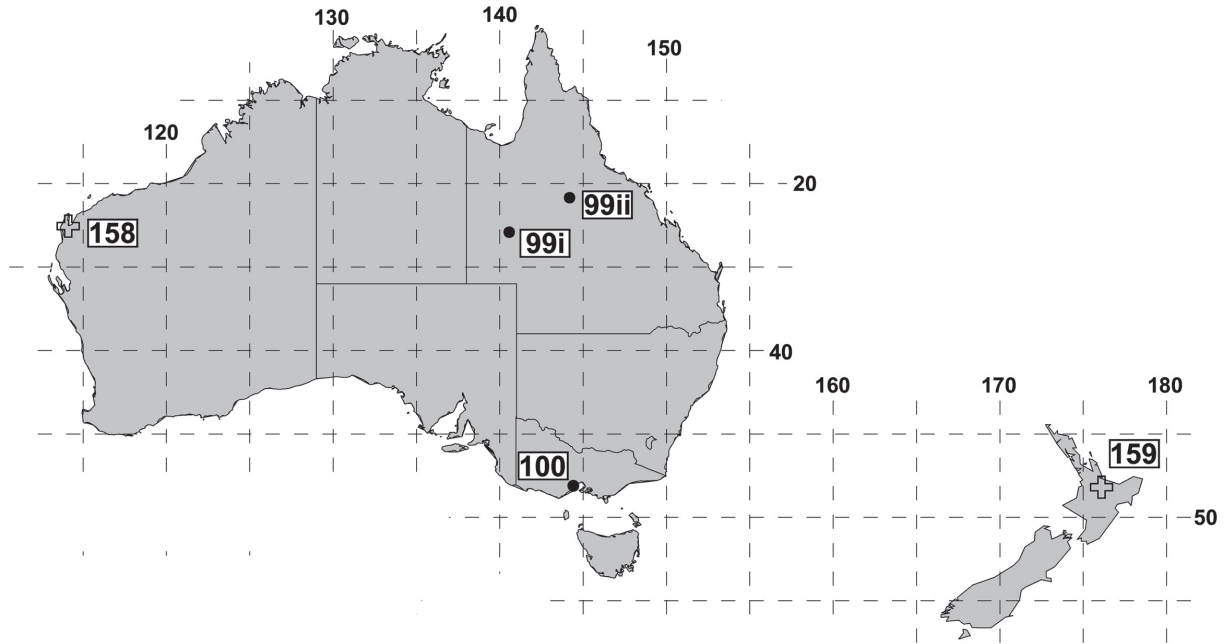
Kota Formation (Kota: JAIN [1974]; Chitpur: RAO & SHAH [1963]).

'Rhamphorhynchoidea'; Campylognathoididae

*Campylognathoides indicus*

Pterosauria indet. (= *Rhamphorhynchus* sp.)

Age: Pliensbachian-Toarcian (BANDYOPADHYAY 1999).



**Figure 2:** Pterosaur localities in Australia and New Zealand: note that all localities are restricted to the Cretaceous. Key: filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

## 2.2.4 Europe

### 18. Dorset, England

Lower Lias (Lyme Regis: BUCKLAND [1829], OWEN [1870, 1874], LYDEKKER [1888], UNWIN [1988a]; Charmouth: UNWIN [2003]).

'Rhamphorhynchoidea'; Dimorphodontidae  
*Dimorphodon macronyx* (including *Pterodactylus maderi*)  
Dimorphodontidae indet.

Age: late Sinemurian (COPE et al. 1980a).

### 19. Yorkshire, England

Alum Shales (Upper Lias) (Loftus: NEWTON [1888]).

'Rhamphorhynchoidea'; Rhamphorhynchidae;  
Rhamphorhynchinae  
*Dorygnathus* (= *Parapsicephalus*) *purdoni*

Age: early Toarcian (COPE et al. 1980a).

### 20. Département de la Meurthe-et-Moselle, France

Unnamed unit (Place Thiers: DELSATE & WILD [2000]).

'Rhamphorhynchoidea'; Rhamphorhynchidae;  
Rhamphorhynchinae

*Dorygnathus* cf. *D. banthensis*

Age: early Toarcian (DELSATE & WILD 2000).

### 21. Baden-Württemberg, Germany

Posidonienschiefer (Lias Epsilon) (Holzmaden, Ohmden and Zell: QUENSTEDT [1858], PLIENINGER [1895, 1906, 1907], WELLNHOFER [1974]; Erzingen: WILD [1975]).

'Rhamphorhynchoidea'; Campylognathoididae  
*Campylognathoides liasicus*  
*Campylognathoides* cf. *C. liasicus*  
*Campylognathoides zitteli*

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae  
*Dorygnathus banthensis*

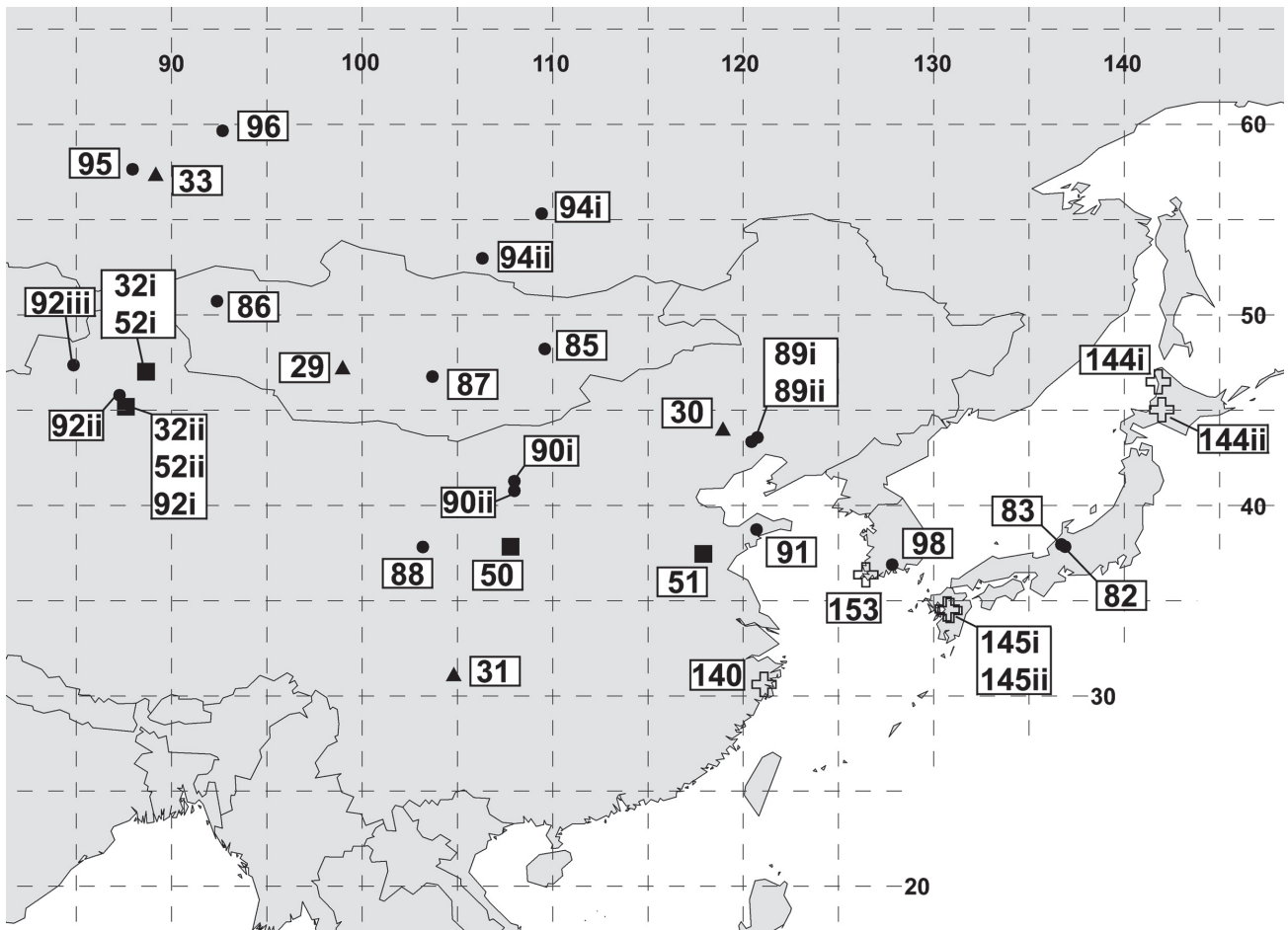
Age: early Toarcian (GEYER & GWINNER 1962).

### 22. Bayern, Germany

Posidonienschiefer (Lias Epsilon) (Banz: VON THEODORI [1830]; Mistelgau: WILD [1971]).

'Rhamphorhynchoidea'; Rhamphorhynchidae;  
Rhamphorhynchinae  
*Dorygnathus banthensis*  
*Dorygnathus mistelgauensis*





**Figure 3:** Pterosaur localities from the Middle Jurassic to Upper Cretaceous of eastern Asia, including China, Mongolia, far eastern Russia, South Korea and Japan. Upper Triassic and Lower Jurassic pterosaur localities are currently unknown in these regions. Key: filled triangles, Middle Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

Age: early Toarcian (GEYER & GWINNER 1962).

### 23. Niedersachsen, Germany

Posidonienschiefer (Lias Epsilon) (Flechtorf: WELLNHOFER [1978]; Schandelah: WELLNHOFER & VAHLDIK [1986]).

'Rhamphorhynchoidea'; Campylognathoididae  
*Campylognathoides* sp.  
 'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae  
*Dorygnathus banthensis*

Age: early Toarcian (GEYER & GWINNER 1962).

### 24. Glamorganshire, Wales

Unnamed unit of fissure fills (Pant and Pontalun: FRASER [1989], GILL et al. [2006]).

'Rhamphorhynchoidea'; Rhamphorhynchidae

Rhamphorhynchidae indet.

Age: Hettangian or Sinemurian (EVANS & KERMACK 1994).

### 2.2.5 North America

#### 25. Arizona, United States of America

Kayenta Formation (Foxtrot Mesa and Airhead West: PADIAN [1984a], CURTIS & PADIAN [1999]).

Pterosauria *incertae sedis*  
*Rhamphinion jenkinsi*  
 Pterosauria indet.

Age: Sinemurian-Pliensbachian (PETERSON & PIPIRINGOS 1979).

#### 26. Massachusetts, United States of America

Turners Falls Formation (Gill: RAINFORTH [2006]).

?Pterosaur tracks (*Antipus flexiloquus*)

Age: Lower Jurassic (RAINFORTH 2006).

## 2.3 Middle Jurassic

### 2.3.1 Africa

#### 27. Faritany Majunga, Madagascar

Isalo III Formation (Andranomamy: DAL SASSO & PASINI [2003]).

'Rhamphorhynchoidea' indet.

Age: Bathonian (TAQUET 1977).

### 2.3.2 Asia

#### 28. Jalal-Abad, Kyrgyzstan

Balabansai Svita (Tashkumyr: NESSOV [1990], BAKHURINA & UNWIN [1995], AVERIANOV et al. [2005a], MARTIN et al. [2006]).

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae

Rhamphorhynchinae indet.

?Pterosauria indet.

Age: Callovian (KAZNYSHKIN 1988).

#### 29. Bayan-Khongoraimak, Mongolia

Bakhar Svita (Bakhar: BAKHURINA & UNWIN [1995], UNWIN & BAKHURINA [2000]).

'Rhamphorhynchoidea'; Anurognathidae  
Anurognathidae indet.

Age: early Middle Jurassic (SHUVALOV 1982).

#### 30. Nei Mongol Zizhiqu, People's Republic of China

Jiulongshan Formation, Daohugou Formation, Haifangou Formation or Yixian Formation (Daohugou locality: CZERKAS & JI [2002], WANG et al. [2002], JI & YUAN [2002]).

'Rhamphorhynchoidea'; Anurognathidae

*Jeholopterus ningchengensis*

'Rhamphorhynchoidea'; Rhamphorhynchidae;  
Scaphognathinae

*Pterorhynchus wellnhoferi*

Pterodactyloidea

Undescribed taxon

Age: Bathonian-Callovian (JI et al. 2006), Oxfordian-Kimmeridgian (ZHANG 2002) or late Barremian-early Aptian (SWISHER et al. 1999)

#### 31. Sichuan, People's Republic of China

Lower Shaximiao Formation (Dashanpu: HE et al. [1983]).

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae

*Angustinarhipterus longicephalus*

Age: Bajocian (CHEN et al. 1982) or Bathonian-Callovian (DONG & TANG 1984).

#### 32. Xinjiang Uygur Zizhiqu, People's Republic of China

i) Lower Shishugou Formation (Wucuiwan: ANDRES & CLARK [2005]; CLARK et al. [2006]).

Pterodactyloidea indet.

Age: Bathonian-Callovian (CHEN et al. 1982; CLARK et al. 2004).

ii) Toutunhe Formation (Toutunhe: MAISCH et al. [2005]).

'Rhamphorhynchoidea' indet.

Age: Bathonian-Callovian (EBERTH et al. 2001).

#### 33. Krasnoyarsk, Russian Federation

Itat Formation (Berezovsk: SKUTCHAS [2006]).

Pterodactyloidea indet.

Age: Bathonian (SKUTCHAS 2006).

### 2.3.3 Europe

#### 34. Cambridgeshire, England

i) Lower Oxford Clay (Whittlesey and Peterborough: ANDREWS [1911-12], LEEDS [1956], UNWIN [1996a]).

'Rhamphorhynchoidea'; Rhamphorhynchidae  
Rhamphorhynchidae indet.

Age: middle Callovian (COPE et al. 1980b).

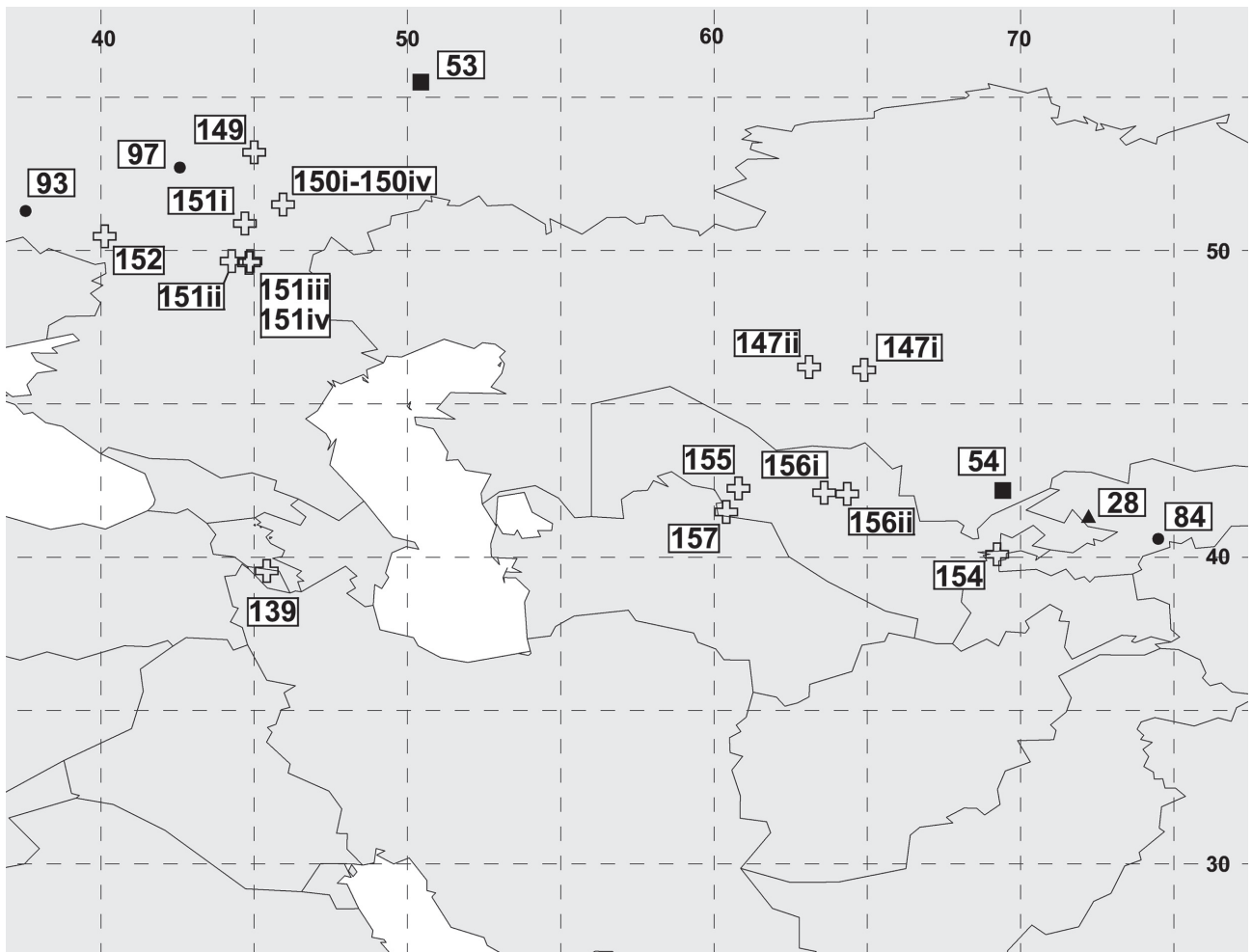
ii) Middle Oxford Clay (St Ives: LYDEKKER [1890], UNWIN [1996a]).

'Rhamphorhynchoidea'; Rhamphorhynchidae  
Rhamphorhynchidae indet. (= *Rhamphorhynchus jessoni*)

Age: late Callovian (COPE et al. 1980b).

#### 35. Dorset, England

Forest Marble Formation (Watton Cliff and Swyre)



**Figure 4:** Pterosaur localities from the Middle Jurassic to Upper Cretaceous of central Asia, including Russia, Kazakhstan, Uzbekistan and Kyrgyzstan. Upper Triassic and Lower Jurassic pterosaur localities are currently unknown from these regions. Key: filled triangles, Middle Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

EVANS & MILNER [1994]).

Pterosauria indet.

Age: late Bathonian (COPE et al. 1980b).

### 36. Gloucestershire, England

- i) Chipping Norton Formation (Hornsleasow: EVANS & MILNER [1994], METCALF & WALKER [1994], UNWIN [1996a]).

‘Rhamphorhynchoidea’; Rhamphorhynchidae; Rhamphorhynchinae  
*Rhamphocephalus* sp.

Age: early Bathonian (COPE et al. 1980b).

- ii) Cotswold Slate Formation (Eyford Hill, Huntsman’s and Kinton Thorns Quarries: EVANS & MILNER [1994], UNWIN [1996a]).

‘Rhamphorhynchoidea’; Rhamphorhynchidae; Rham-

phorhynchinae

*Rhamphocephalus* sp.

Age: middle Bathonian (COPE et al. 1980b).

### 37. Rutland, England

‘Great Oolite’ (Essendine/Banthorpe: BENTON & SPENCER [1995], UNWIN [1996a]).

Pterosauria indet.

Age: late Bathonian (COPE et al. 1980b).

### 38. Oxfordshire, England

- i) Chipping Norton Formation (Smith’s Quarry: HUXLEY [1859], UNWIN [1996a, 2003]).

‘Rhamphorhynchoidea’; Rhamphorhynchidae; Rhamphorhynchinae

*Rhamphocephalus bucklandi* (including *Rhamphocephalus depressirostris*)

Age: early Bathonian (COPE et al. 1980b).

- ii) Sharp's Hill Formation (Sharp's Hill: EVANS & MILNER [1994]).

Pterosauria indet.

Age: early Bathonian (COPE et al. 1980b).

- iii) Taynton Limestone Formation (Stonesfield Slates: BUCKLAND [1829], HUXLEY [1859], PHILLIPS [1871], OWEN [1874], SEELEY [1880], LYDEKKER [1888], UNWIN [1996a]).

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae

*Rhamphocephalus bucklandi* (including *Pterodactylus aclandi*, *Pterodactylus duncani*, *Pterodactylus kiddi*)

Age: middle Bathonian (COPE et al. 1980b; BONEHAM & WYATT 1993).

- iv) Hampen Marly Formation (Woodeaton: EVANS & MILNER [1994]).

Pterosauria indet.

Age: middle Bathonian (COPE et al. 1980b).

- v) Forest Marble Formation (Kirtlington: EVANS & MILNER [1994], UNWIN [1996a]).

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae

*Rhamphocephalus* sp.

Age: late Bathonian (COPE et al. 1980b).

- vi) Middle Oxford Clay (St Clements: PHILLIPS [1871], UNWIN [1996a]).

Rhamphorhynchoidea'; Rhamphorhynchidae  
?Rhamphorhynchidae indet.

Age: late Callovian (COPE et al. 1980b).

### 39. Département du Calvados, France

Marne des Dives (Villers: KNOLL & BOUVEUR [2001]).

'Rhamphorhynchoidea' indet.

Age: late Callovian (TAQUET & WELLS 1977).

### 40. Distrito do Leiria, Portugal

Unnamed unit (THULBORN 1973)

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rham-

phorhynchinae

*Rhamphorhynchus* sp.

Age: late Callovian (THULBORN 1973).

### 41. Isle of Eigg, Scotland

Lealt Shale Formation (Kildonnan and Eilean Thuilim: BARROW [1908], BENTON & SPENCER [1995]).

Pterosauria indet.

Age: early Bathonian (HARRIS & HUDSON 1980).

### 42. Isle of Skye, Scotland

Kilmaluag Formation (Cladach a'Glinne: EVANS & MILNER [1994], EVANS et al. [2006]).

Pterosauria indet.

Age: late Bathonian (HARRIS & HUDSON 1980).

### 2.3.4 North America

#### 43. Estado de Tamaulipas, Mexico

La Boca Formation (Huizachal Canyon: CLARK et al. [1994, 1998]).

Pterosauria *incertae sedis*

'*Dimorphodon*' *weintraubi*

Age: early Middle Jurassic (FASTOVSKY et al. 1995).

#### 44. Arizona, United States of America

Undifferentiated Summerville-Bluff Formation (Carrizo Mountains: LOCKLEY & MICKELSON [1997]).

Pterosaur tracks

Age: Callovian-Oxfordian (ANDERSON & LUCAS 1992).

#### 45. Colorado, United States of America

Summerville Formation (Cactus Park: LOCKLEY & WRIGHT [2003]; Furnish Canyon: LOCKLEY et al. [1996, 2001]).

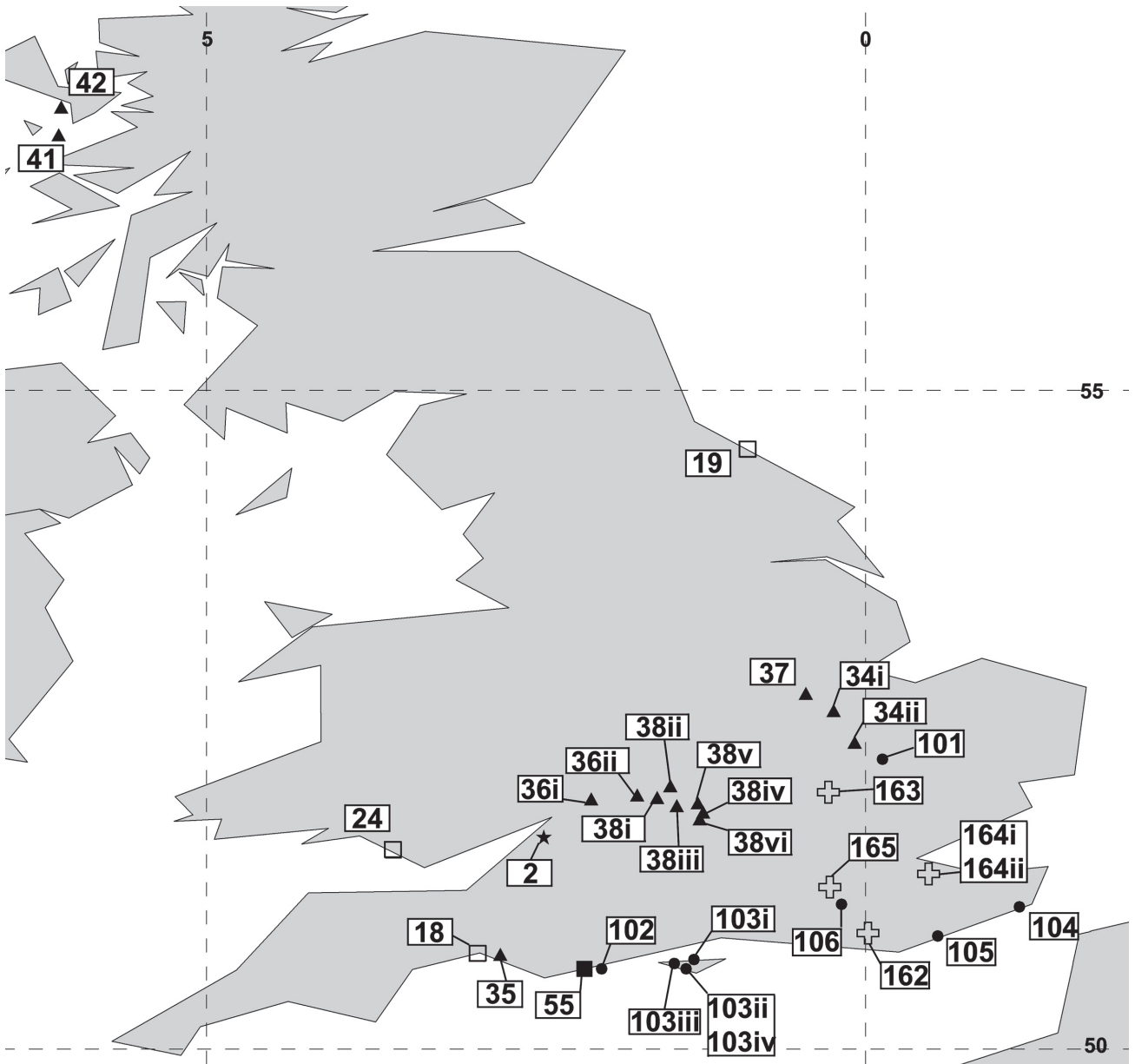
Pterosaur tracks (*Pteraichnus* sp.)

Age: Callovian-Oxfordian (ANDERSON & LUCAS 1992).

#### 46. Utah, United States of America

- i) Curtis/Stump Formation (Flaming Gorge: HAYDEN [2002]).

Pterosaur tracks



**Figure 5:** Pterosaur localities from the Upper Triassic to Upper Cretaceous of the UK. Key: filled star, Upper Triassic; open squares, Lower Jurassic localities; filled triangles, Middle Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

Age: middle Callovian (HAYDEN 2002).

- ii) Summerville Formation (Del Monte Mines: LOCKLEY et al. [1995], LOCKLEY & WRIGHT [2003]; Ferron: LOCKLEY & WRIGHT [2003], MICKELSON et al. [2004]).

Pterosaur tracks (*Pteraichnus* sp.)

Age: Callovian-Oxfordian (ANDERSON & LUCAS 1992).

#### 47. Wyoming, United States of America

Sundance Formation (Alcova Lake: LOCKLEY et al. [1995], LOCKLEY & WRIGHT [2003]; Como Bluff: UNWIN [1996b]).

Pterosaur tracks (including *Pteraichnus stokesi*)

Age: middle-late Bathonian (KVALE et al. 2001).

#### 2.3.5 South America

##### 48. Chubut Province, Argentina

Cañadon Asfalto Formation (Cerro Cóndor, Las Chacritas: RAUHUT et al. [2001], CODORNIÚ & GASPARINI [2007]).

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae

?Rhamphorhynchinae indet.

Rhamphorhynchoidea'; Rhamphorhynchidae; Scaphognathinae

?Scaphognathinae indet.

Age: Callovian-Oxfordian (TASCH & VOLKHEIMER 1970).

## 2.4 Upper Jurassic

### 2.4.1 Africa

#### 49. Mtwara, Tanzania

Tendaguru Formation (Middle and Upper Saurian beds, Tendaguru: RECK [1931], GALTON [1980], UNWIN & HEINRICH [1999], SAYAO & KELLNER [2001]).

‘Rhamphorhynchoidea’ indet. (= *Rhamphorhynchus tendagurensis*)

Pterodactyloidea indet. (including *Pterodactylus maximus*, ?Archaeopterodactyloidea indet.)

Pterodactyloidea; Dsungaripteroidea  
*Tendaguripterus recki*

Dsungaripteroidea indet. (= *Pterodactylus brancai*)

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Pterosauria indet. (= *Pterodactylus arningi*)

Age: late Kimmeridgian-Tithonian (ABERHAN et al. 2002).

### 2.4.2 Asia

#### 50. Gansu, People’s Republic of China

Huachihuanhe Formation (Sanshilipu: DONG 1982).

Pterodactyloidea; Ctenochasmatoidea;

Ctenochasmatidae

*Huanhepterus quingyangensis*

Age: Upper Jurassic (DONG 1982).

#### 51. Shandong, People’s Republic of China

Meng-Yin Formation (Mengyin: YOUNG [1964]).

Pterodactyloidea; Dsungaripteroidea;

Dsungaripteridae

?Dsungaripteridae indet.

Age: early Tithonian (CHEN et al. 1982) or Kimmeridgian (DONG pers. comm. in WEISHAMPEL et al. 2004).

#### 52. Xinjiang Uygur Zizhiqu, People’s Republic of China

- i) Upper Shishugou Formation (Wucaiwai: ANDRES & CLARK [2005], CLARK et al. [2006]).

Undescribed ‘rhamphorhynchoid’

Age: Oxfordian (EBERTH et al. 2001).

- ii) Qigu Formation (Lihuanguo: MARTIN et al. 2006).

‘Rhamphorhynchoidea’; Rhamphorhynchidae  
Rhamphorhynchidae indet.

Age: Oxfordian (ASHRAF cited in MARTIN et al. 2006).

#### 53. Volga Region, Russia

Unknown locality (BAKHURINA & UNWIN 1995).

Pterosauria indet.

Age: Upper Jurassic (BAKHURINA & UNWIN 1995).

#### 54. South Kazakhstan Province, Kazakhstan

Karabastau Svita (Karatau ridge: RYABININ [1948], SHAROV [1971], BAKHURINA & UNWIN [1995], UNWIN & BAKHURINA [2000]).

‘Rhamphorhynchoidea’; Anurognathidae

*Batrachognathus volans*

‘Rhamphorhynchoidea’; Rhamphorhynchidae; Rhamphorhynchinae

*Sordes pilosus*

Age: Oxfordian-Kimmeridgian (DOLUDENKO & ORLOSKAYA 1976).

### 2.4.3 Europe

#### 55. Dorset, England

Kimmeridge Clay (Encombe Bay: BENTON & SPENCER [1995]; Kimmeridge Bay: UNWIN [1988b], BENTON & SPENCER [1995]; Weymouth: OWEN [1874], LYDEKKER [1888], BENTON & SPENCER [1995]).

Pterodactyloidea; Dsungaripteroidea

*Germanodactylus* sp.

Unnamed pterosaur

Pterosauria indet. (includes *Rhamphorhynchus* sp.,

*Pterodactylus manseli*, *Pterodactylus pleydelli*,

*Pterodactylus* sp.)

Age: Kimmeridgian (COPE et al. 1980b).

#### 56. Département de l’Ain, France

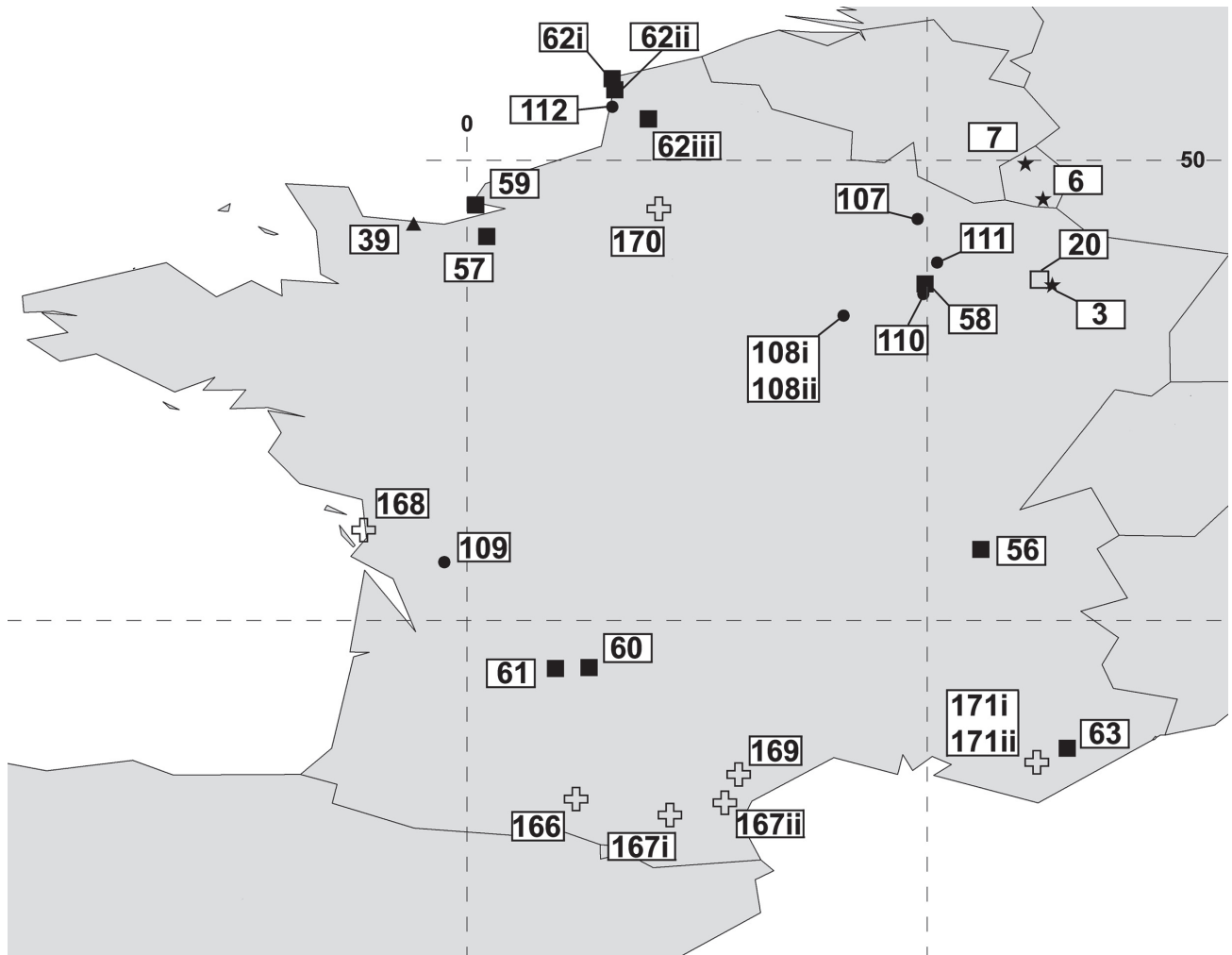
“Lithographic limestones” (Cerin: VON MEYER [1860], BUFFETAUT et al. [1990]).

Pterosauria indet. (includes *Pterodactylus cerinensis*)

Age: Kimmeridgian (BUFFETAUT et al. 1990).

#### 57. Département du Calvados, France

Upper Sables de Glos (Lisieux: BUFFETAUT et al.



**Figure 6:** Pterosaur localities from the Upper Triassic to Upper Cretaceous of France and Luxembourg. Key: filled star, Upper Triassic; open squares, Lower Jurassic localities; filled triangles, Middle Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

[1985], KNOLL & BOUVEUR [2001], BUFFETAUT & GUIBERT [2001]).

Pterosauria indet.

Age: late Oxfordian (BUFFETAUT et al. 1985).

#### 58. Département de la Haute-Marne, France

Calcaires tâchetés (Saint-Dizier: TAQUET [1972], JOUVE [2004], BENNETT [2007a]).

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmataidae

*Ctenochasma taqueti*

Age: early Tithonian (TAQUET 1972).

#### 59. Département de la Haute-Normandie, France

Argiles d'Ecqueville (Cap de la Hève: LENNIER [1887], BUFFETAUT et al. [1998]).

Pterodactyloidea; Dsungaripteroidea

*Normannognathus wellnhoferi*

Pterosauria indet. (including *Pterodactylus* sp.)

Age: late Kimmeridgian (BUFFETAUT et al. 1998).

#### 60. Département du Lot, France

Unnamed unit (Crayssac: MAZIN et al. [1997, 2003]).

Pterodactyloidea indet.

Pterosaur tracks (*Pteraichnus* sp.)

Age: early Tithonian (MAZIN et al. 1997).

#### 61. Département du Lot-et-Garonne, France

Unnamed unit (Fumel: SAUVAGE [1902]).

Pterosauria indet.

Age: late Kimmeridgian (KNOLL & BOUVEUR 2001).

## 62. Département du Pas-de-Calais, France

- i) Grès de la Crèche inférieurs (Boulogne-sur-Mer: KNOLL & BOUVEUR [2001]).

?‘Rhamphorhynchoidea’ indet.  
Pterodactyloidea indet.  
Pterosauria indet.

Age: early Tithonian (KNOLL & BOUVEUR 2001).

- ii) Unnamed unit (Boulogne-sur-Mer: SAUVAGE [1872], WELLNHOFER [1978], KNOLL & BOUVEUR [2001]).

Pterosauria indet. (including *Pterodactylus suprajurensis*)

Age: late Kimmeridgian (WELLNHOFER 1978).

- iii) Unnamed unit (Montrouge: KNOLL & BOUVEUR [2001]).

Pterosauria indet.

Age: late Tithonian (KNOLL & BOUVEUR 2001).

## 63. Département du Var, France

Gisement des Bessons (Canjuers: FABRE [1976], BENNETT [1996a]).

Pterodactyloidea; Ctenochasmatoidea  
*Cycnorhamphus canjuersensis*

Age: early Tithonian (KNOLL & BOUVEUR 2001).

## 64. Baden-Württemberg, Germany

Nusplingen Limestone, Malm Zeta 1 (Nusplingen: VON MEYER [1854], WELLNHOFER [1978], BENNETT [1995, 1996a, 1996b]).

‘Rhamphorhynchoidea’; Rhamphorhynchidae;  
Rhamphorhynchinae  
*Rhamphorhynchus muensteri*  
Pterodactyloidea; Ctenochasmatoidea  
*Cycnorhamphus suevicus*  
Pterodactyloidea; Ctenochasmatoidea;  
Ctenochasmatidae  
*‘Pterodactylus’ longicollum*

Age: late Kimmeridgian (DIETL & SCHWEIGERT 2001).

## 65. Bayern, Germany

- i) Mornsheimer Limestone, Malm Zeta 3 (Daiting and Kelheim: WAGNER [1851], WELLNHOFER [1978], BENNETT [1995, 2006]).

‘Rhamphorhynchoidea’; Rhamphorhynchidae;

Rhamphorhynchinae

?*Rhamphorhynchus muensteri* (= *Rhamphorhynchus longicaudus*)

Pterodactyloidea; Dsungaripteroidea

*Germanodactylus rhamphastinus*

Pterodactyloidea; Ctenochasmatoidea

*Pterodactylus antiquus* (= *Pterodactylus kochi*)

Pterodactyloidea; Ctenochasmatoidea;

Ctenochasmatidae

*‘Pterodactylus’ longicollum*

Age: Tithonian (WELLNHOFER 1978).

- ii) Solnhofen Limestone, Malm Zeta 2 (Eichstätt, Solnhofen and Workerszell: CUVIER [1809], GOLDFUSS [1831], WAGNER [1837], VON MEYER [1846, 1847], DÖDERLEIN [1923], WELLNHOFER [1978], BENNETT [1995, 1996a, 1996b, 2006, 2007a, 2007b], JOUVE [2004]).

‘Rhamphorhynchoidea’; Anurognathidae

*Anurognathus ammoni*

‘Rhamphorhynchoidea’; Rhamphorhynchidae;

Rhamphorhynchinae

*Rhamphorhynchus muensteri* (including *Rhamphorhynchus longicaudus*, *Rhamphorhynchus intermedius*, *Rhamphorhynchus gemmingi*, *Rhamphorhynchus longiceps*)

‘Rhamphorhynchoidea’; Rhamphorhynchidae;

Scaphognathinae

*Scaphognathus crassirostris*

Pterodactyloidea; Ctenochasmatoidea

*Cycnorhamphus suevicus*

*Pterodactylus antiquus* (including *Pterodactylus kochi*)

*‘Pterodactylus’ micronyx*

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmatidae

*Ctenochasma elegans* (including *Ctenochasma gracile* and *Ctenochasma porocristata*)

*Gnathosaurus subulatus*

*‘Pterodactylus’ longicollum*

Pterodactyloidea; Dsungaripteroidea

*Germanodactylus cristatus*

*Germanodactylus rhamphastinus*

Pterodactyloidea; Azhdarchoidea; Azhdarchidae

?Azhdarchidae (unnamed taxon)

Age: Tithonian (BARTHEL 1978).

## 66. Niedersachsen, Germany

Lower Kimmeridgian mudstones (Langenberg Quarry, Oker: FASTNACHT [2005]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae  
Dsungaripteridae indet.

Age: Kimmeridgian (FASTNACHT 2005).

## 67. Województwo mazowieckie, Poland



'Wierzbica Oolite and Platy Limestones' (Wierzbica: PIENKOWSKI & NIEDZWIEDZKI [2005]).

Pterosaur tracks (*Pteraichnus* sp.)

Age: early Kimmeridgian (GUTOWSKI 1998).

#### 68. Distrito do Leiria, Portugal

Camadas de Guimarota (Guimarota: WIECHMANN & GLOY [2000]).

'Rhamphorhynchoidea' indet.  
Pterodactyloidea indet.

Age: Kimmeridgian (SCHUDACK 2000).

#### 69. Provincia de Asturias, Spain

Lastres Formation (La Costa de los Dinosaurios: VALENZUELA et al. [1988], LOCKLEY et al. [1995], GARCÍA-RAMOS et al. [2006]).

Pterosaur tracks (*Pteraichnus* sp.)

Age: Kimmeridgian (GARCÍA-RAMOS et al. 2006).

#### 70. Kanton Bern, Switzerland

Unspecified unit (Biel: BILLON-BRUYAT [2005]).

Pterosauria indet.

Age: Late Oxfordian (BILLON-BRUYAT 2005).

#### 71. Kanton Jura, Switzerland

Reuchenette Formation (Porrentruy: BILLON-BRUYAT [2005]).

'Rhamphorhynchoidea'; Rhamphorhynchidae; Rhamphorhynchinae  
Rhamphorhynchinae indet.

Age: late Kimmeridgian (BILLON-BRUYAT 2005)

#### 72. Kanton Solothurn, Switzerland

i) Unspecified unit (Olten: BILLON-BRUYAT [2005]).

Pterosauria indet.

Age: Late Oxfordian (BILLON-BRUYAT 2005).

ii) Solothurn Turtle Limestone (St. Niklaus: MEYER & HUNT [1999]).

Pterosauria indet.

Age: late Kimmeridgian (MEYER & HUNT 1999).

### 2.4.4 North America

#### 73. Pinar del Rio Province, Cuba

Jagua Formation (Viñales: COLBERT [1969], GASPARINI et al. [2004]).

'Rhamphorhynchoidea'; Rhamphorhynchidae;  
Rhamphorhynchinae  
*Nesodactylus hesperius*  
'Rhamphorhynchoidea'; Rhamphorhynchidae;  
Scaphognathinae  
*Cacibupteryx caribensis*

Age: middle-late Oxfordian (ITURRALDE-VINENT & NORELL 1996).

#### 74. Arizona, United States of America

Morrison Formation (Carrizo Mountains: STOKES [1957]).

Pterosaur tracks (*Pteraichnus saltwashensis*)

Age: Kimmeridgian-Tithonian (KOWALLIS et al. 1998).

#### 75. Colorado, United States of America

Morrison Formation (Dry Mesa Quarry: JENSEN & OSTROM [1977], JENSEN & PADIAN [1989], SMITH et al. [2004], BENNETT [2007c]; Small Quarry, Garden Park: HARRIS & CARPENTER [1996]; Kings View Quarry, Fruita: KING et al. [2006]; Mygatt-Moore Quarry: KING et al. [2006]; Uravan locality: KING et al. [2006]).

'Rhamphorhynchoidea'; Anurognathidae  
?'*Mesadactylus ornithosphyos*' partim (may be a chimera: BENNETT [2007a])  
Pterodactyloidea *incertae sedis*  
?'*Mesadactylus ornithosphyos*' partim (may be a chimera: BENNETT [2007a])  
?Pterodactyloidea indet.  
Pterodactyloidea; Dsungaripteroidea  
*Kepodactylus insperatus*  
Pterosauria indet.

Age: Kimmeridgian-Tithonian (KOWALLIS et al. 1998).

#### 76. Oklahoma, United States of America

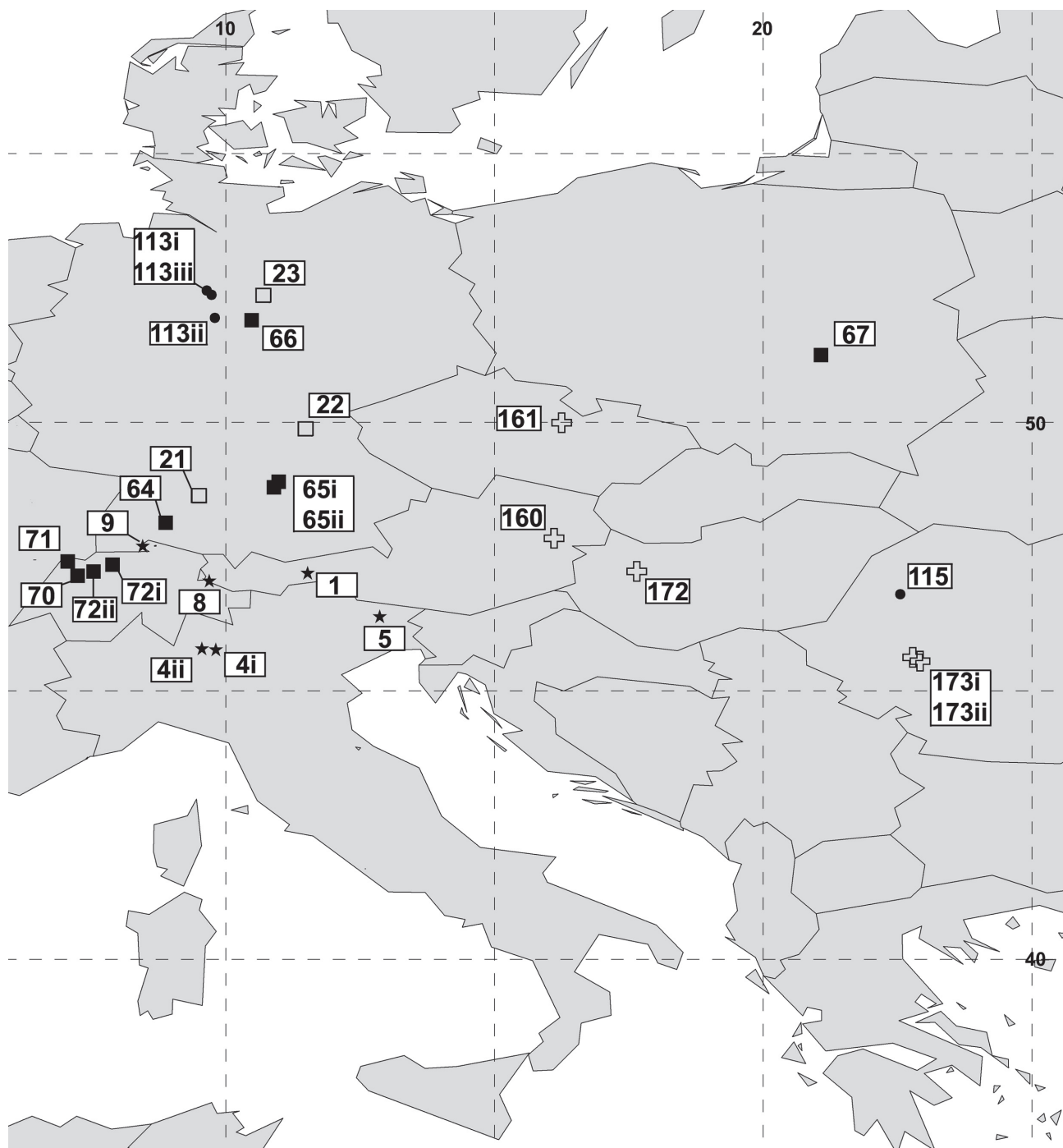
Morrison Formation (Panhandle: LOCKLEY et al. [2001]).

Pterosaur tracks (*Pteraichnus* sp.)

Age: Kimmeridgian-Tithonian (KOWALLIS et al. 1998).

#### 77. Wyoming, United States of America

Morrison Formation (Alcova Reservoir: CONNELLY [2006]; ?Big Al Quarry: KING et al. [2006]; Bone



**Figure 7:** Pterosaur localities from the Upper Triassic to Upper Cretaceous of central and eastern Europe, including Germany, Italy, Austria, Switzerland, Poland, Romania, Hungary and the Czech Republic. Note that no Middle Jurassic pterosaur localities are currently known from these regions. Key: filled star, Upper Triassic; open squares, Lower Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

Cabin Quarry: CARPENTER et al. [2003]; Como Bluff: MARSH [1878, 1881a, 1881b], GALTON [1981], OSTROM [1986]).

‘Rhamphorhynchoidea’; Rhamphorhynchidae; Sca-phognathinae

*Harpactognathus gentryii*

‘Rhamphorhynchoidea’ indet. (= *Comodactylus*

*ostromi*)

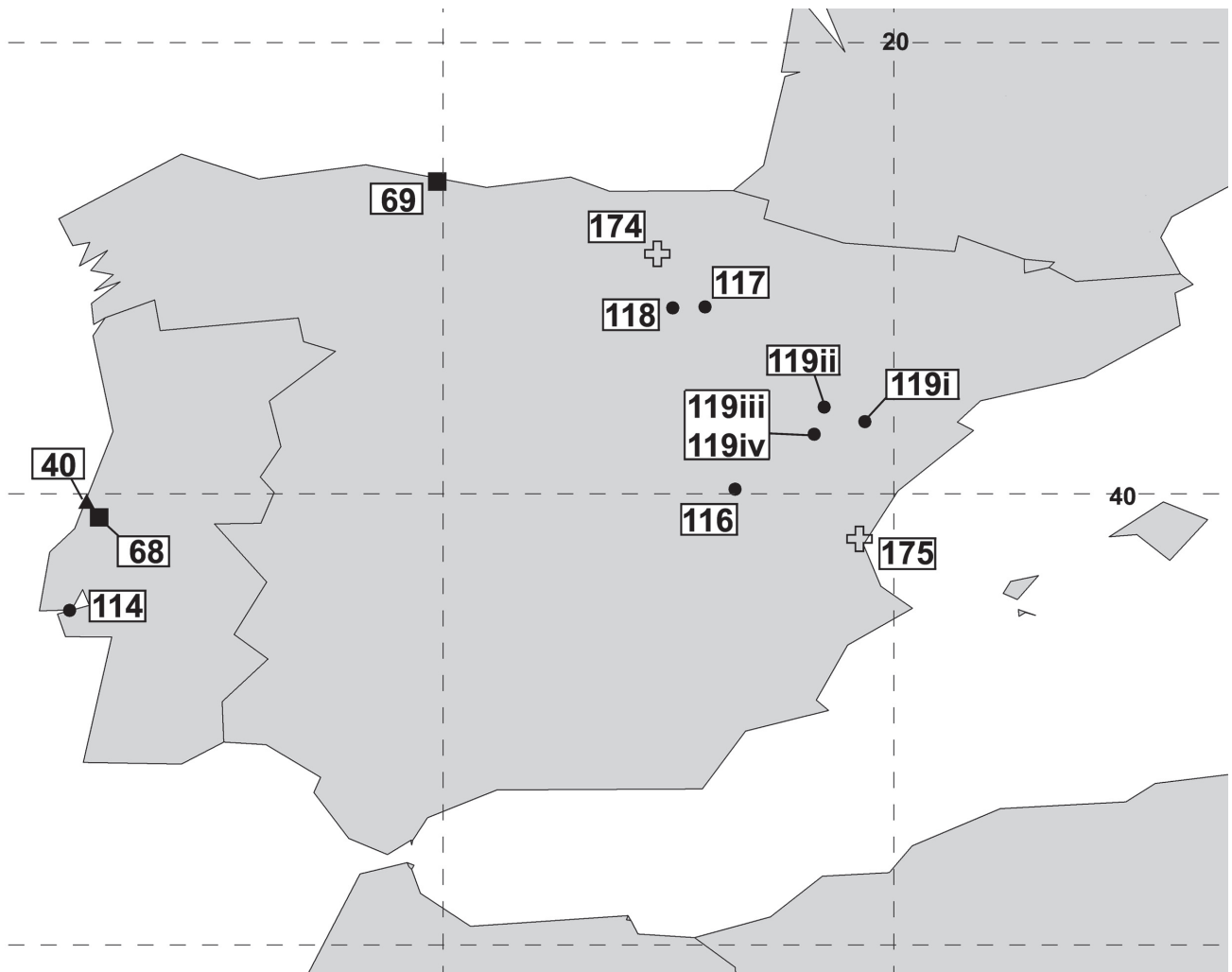
Pterodactyloidea indet. (= *Dermodactylus montanus*)

Pterosauria indet. (= *Laopteryx priscus*)

Pterosaur tracks (*Pteraichnus* sp.)

Age: Kimmeridgian-Tithonian (KOWALLIS et al. 1998).

#### 2.4.5 South America



**Figure 8:** Pterosaur localities from the Middle Jurassic to Upper Cretaceous of the Iberian Peninsula, including Spain and Portugal. Note that no Upper Triassic or Lower Jurassic pterosaur localities are currently known from this region. Key: filled triangles, Middle Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

## 78. Neuquén Province, Argentina

Vaca Muerta Formation (Arroyo Picún Leufú anticline: CASAMIQUELA [1975], CODORNIÚ & GASPARINI [2007]; Los Catutos: GASPARINI et al. [1987], CODORNIÚ et al. [2006], CODORNIÚ & GASPARINI [2007]).

Pterodactyloidea *incertae sedis*

*Herbstosaurus pigmaeus*

Pterodactyloidea; Euctenochasmia

?Euctenochasmia indet. (= Archaeopterodactyloidea indet.)

Pterodactyloidea indet.

Age: middle-late Tithonian (LEANZA & ZEISS 1992).

## 2.5 Lower Cretaceous

### 2.5.1 Africa

#### 79. Oriental, Morocco

Unnamed unit, 'Couches Rouges' (Anoual: SIGOGNEAU-RUSSELL et al. [1998], KNOLL [2000]).

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmataidae; Gnathosaurinae

?Gnathosaurinae indet.

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae

?Ornithocheiridae indet.

Age: Berriasian (SIGOGNEAU-RUSSELL et al. 1990).

#### 80. Département d'Agadez, Niger

Elrhaz Formation (Unnamed locality and Gadoufaoua: SERENO et al. [1998], BLACKBURN [2002]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae

Undescribed ornithocheirid

Pterodactyloidea; Azhdarchoidea

Undescribed ?azhdarchoid

Pterodactyloidea; Azhdarchoidea; Azhdarchidae

?Azhdarchidae indet.

Age: late Aptian (MOODY & SUTCLIFFE 1991).

### 81. Gouvernorat de Tatouine, Tunisia

Chenini Formation (unnamed locality: BENTON et al. [2000]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: early Albian (BENTON et al. 2000).

### 2.5.2 Asia

#### 82. Gifu Prefecture, Japan

Okurodani Formation (Kobudani Valley, Shokawa: UNWIN et al. [1996], EVANS et al. [1998]).

Pterodactyloidea indet.  
Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae  
Dsungaripteridae indet.

Age: Berriasian (EVANS et al. 1998).

#### 83. Ishikawa Prefecture, Japan

Kuwajima Formation (Kuwajima: UNWIN et al. [2000], ISAJI et al. [2005]).

Pterodactyloidea; Ornithocheiroidea  
Ornithocheiridae indet.  
Pterodactyloidea; Ctenochasmatoidea; Ctenochasmata-  
tidae; Gnathosaurinae  
Gnathosaurinae indet.  
Pterodactyloidea; Dsungaripteroidea  
?Dsungaripteroidea indet.

Age: Valanginian (ISAJI et al. 2005).

#### 84. Osh, Kyrgyzstan

Alamyshik Formation (Kylodzhun: NESSOV [1990], BAKHURINA & UNWIN [1995], AVERIANOV [2004]).

Pterodactyloidea indet.

Age: early-middle Albian (AVERIANOV 2004).

#### 85. Dornogovi, Mongolia

Züünbayan Formation (Hüren Dukh: BAKHURINA & UNWIN [1995], UNWIN & BAKHURINA [2000]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Undescribed taxon (*Coloborhynchus?*)

Age: Aptian-Albian (SHUVALOV 1974).

#### 86. Khovd, Mongolia

Tsagaantsav Svita (Tatal: BAKHURINA [1982, 1986], BAKHURINA & UNWIN [1995], UNWIN & BAKHURINA [2000]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae  
*'Phobator' parvus*

Age: Berriasian-Valanginian (SHUVALOV 2000).

#### 87. Övörkhangai, Mongolia

Öösh Formation (Öösh: ANDRES & NORELL [2005]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae  
?Dsungaripteridae indet.

Age: Berriasian-Valanginian (SHUVALOV 2000).

#### 88. Gansu, People's Republic of China

Hekou Formation (Yellow River valley: LI et al. [2002]).

Pterosaur tracks (cf. *Pteraichnus*)

Age: Lower Cretaceous (LI et al. 2002).

#### 89. Liaoning, People's Republic of China

i) Yixian Formation (Beipiao, Jinzhou, Lujiatun, Sihetun and others: JI & JI [1997, 1998], JI et al. [1999, 2004], UNWIN et al. [2000], WANG & LÜ [2001], LÜ [2003], LÜ & JI [2005a], WANG & ZHOU [2004, 2006a, 2006b], WANG et al. [2005, 2007], KELLNER et al. [2007a]).

'Rhamphorhynchoidea'; Anurognathidae  
*Dendrorhynchoides curvidentatus*

Pterodactyloidea *incertae sedis*

*Feilongus youngi*

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmata-  
tidae

*Beipiaopterus chenianus*

*Eosipterus yangi*

*Cathayopterus grabaui*

*Gegepterus changi*

Pterodactyloidea; Ornithocheiroidea; Ornithocheiri-  
dae

*Boreopterus cuiiae*

*Haopterus gracilis*

Pterodactyloidea; Azdarchoidea; Tapejaridae

Unnamed tapejarid

Pterosaur eggs (Ornithocheiridae indet.)

Age: late Barremian – early Aptian (SWISHER et al. 1999).

ii) Jiufotang Formation (Chaoyang and nearby localities: DONG et al. [2003], LI et al. [2003], WANG & ZHOU

[2003a, 2003b, 2006a], DONG & LÜ [2005], LÜ & JI [2005b], LÜ & YUAN [2005], LÜ & ZHANG [2005], WANG et al. [2005, 2008], ANDRES & JI [2006], KELLNER et al. [2006], LÜ et al. [2006a, 2006b, 2007]).

Pterodactyloidea; Ornithocheiroidea; Istiodactylidae

*Istiodactylus sinensis*

*Nurbachius ignaciobrito*

Pterodactyloidea; Azdarchoidea; Tapejaridae

*Chaoyangopterus zhang* (= *Eoazhdarcho liaoxiensis*, *Eopteranodon lii*)

'*Huaxipterus*' *benxiensis*

'*Huaxipterus*' *corollatus*

*Jidapterus edentus*

*Sinopterus dongi* (= *Huaxipterus jii*)

*Sinopterus gui*

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae

*Liaoningopterus gui*

*Liaoxipterus brachyognathus*

Pterodactyloidea; Dsungaripteroidea

*Nemicolopterus crypticus*

Age: Aptian (HE et al. 2004).

## 90. Nei Mongol Zizhiqu, People's Republic of China

- i) Ejinhor Formation (Muhuaxiao Village: DONG [1993]).

Pterosauria indet.

Age: Lower Cretaceous (DONG 1993).

- ii) Luohangdong Formation (Laolonghuo: BRINKMAN & PENG [1993], RUSSELL & DONG [1993]).

Pterosauria indet.

Age: ?Valanginian-?Albian (RUSSELL & ZHAO 1996).

## 91. Shandong, People's Republic of China

Qingshan Formation (Laiyang: YOUNG [1958, 1964]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae  
?Dsungaripteridae indet.

Age: Aptian-Albian (MATEER pers. comm. in WEISHAMPEL et al. 2004).

## 92. Xinjiang Uygur Zizhiqu, People's Republic of China

- i) Lianmuxin Formation, Upper Tugulu Group (Lihonggou: MAISCH et al. [2004]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae

*Lonchognathosaurus acutirostris*

Age: ?Aptian-Albian (MAISCH et al. 2004).

- ii) Tugulu Group, unspecified horizon (Changchi:

YOUNG [1964], BUFFETAUT [1996]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae  
Dsungaripteridae indet.

Age: ?Valanginian-Albian (SHEN & MATEER 1992).

- iii) Upper Tugulu Group (Wuerho: YOUNG [1964, 1973]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae

*Dsungaripterus weii*

*Noriopterus complicidens*

Age: ?Valanginian-Albian (SHEN & MATEER 1992).

## 93. Belgorod Oblast, Russia

Sekmenevka Formation or Paramonovo and Polpino Formations (Lebedi and Stoilo quarries: NESSOV [1990], BAKHURINA & UNWIN [1995], AVERIANOV [2004, 2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: Aptian (AVERIANOV 2007a).

## 94. Republic Buryatia, Russia

- i) Khilok Formation (Krasnyi Yar: AVERIANOV [2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: Aptian (AVERIANOV 2007a).

- ii) Murtoi Formation (Mogoito: AVERIANOV [2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: late Barremian-middle Aptian (AVERIANOV 2007a).

## 95. Kemerovo Oblast, Russia

Ilek Formation (Shestakovo 1: AVERIANOV [2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: Aptian-Albian (AVERIANOV 2007a).

## 96. Krasnoyarsk Krai, Russia

Ilek Formation (Bol'shoi Kemchug 3: AVERIANOV [2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: ?Hauterivian-Barremian (AVERIANOV 2007a).

## 97. Tambov Oblast, Russia

Unnamed unit (Kobyaki: BAKHURINA & UNWIN [1995]).

?Pterosauria indet.

Age: Albian-Cenomanian (BAKHURINA & UNWIN 1995) or early Cenomanian (AVERIANOV et al. 2005b).

## 98. Gyeongsangnam-do, South Korea

Hasandong Formation (no locality data: LIM et al. [2002], LEE & LEE [2006]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae  
?Dsungaripteridae indet.  
Pterosaur trackways

Age: Hauterivian-Barremian (LIM et al. 2002).

### 2.5.3 Australia

#### 99. Queensland, Australia

- i) Toolebuc Formation (Warra Station: MOLNAR & THULBORN [1980], MOLNAR [1987]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Anhanguera ?cuvieri*

Age: Albian (MOLNAR 1980).

- ii) Allaru Formation (Hughenden: LONG [1998]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
cf. *Anhanguera* sp.

Age: Albian (MOLNAR 1982).

#### 100. Victoria, Australia

Eumeralla Formation (Dinosaur Cove: RICH & RICH [1989]).

Pterosauria indet.

Age: early Albian (RICH & RICH 1989).

### 2.5.4 Europe

#### 101. Cambridgeshire, England

Cambridge Greensand (numerous localities, including Barton, Cambridge, Ditton, Grantchester and Haslingfield: OWEN [1859, 1874], SEELEY [1869a, 1870], LYDEKKER [1888], HOOLEY [1914], UNWIN et al. [2000], UNWIN [2001]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae

*Anhanguera cuvieri* (including *Lonchodectes scaporrhynchus*, *Ornithocheirus brachrhinus*, *Ornithocheirus colorhinus*, *Ornithocheirus cuvieri*, *Ornithocheirus dentatus*, *Ornithocheirus denticulatus*, *Ornithocheirus enchorhynchus*, *Ornithocheirus xyphorrhynchus*, *Ptenodactylus cuvieri*, *Pterodactylus cuvieri*)

*Anhanguera fittoni* (including *Ornithocheirus fittoni*, *Ornithocheirus nasutus*, *Ornithocheirus polyodon*, *Ptenodactylus fittoni*, *Pterodactylus fittoni*) *Coloborhynchus capito* (including *Amblydectes eurygnathus*, *Criorhynchus capito*, *Ornithocheirus capito*, *Ornithocheirus readi*)

*Coloborhynchus sedgwickii* (including *Amblydectes crassidens*, *Criorhynchus crassidens*, *Criorhynchus woodwardi*, *Ornithocheirus crassidens*, *Ornithocheirus sedgwickii*, *Ornithostoma seeleyi*, *Ptenodactylus sedgwicki*, *Ptenodactylus woodwardi*, *Pterodactylus sedgwickii*, *Pterodactylus woodwardi*)

*Ornithocheirus simus* (including *Criorhynchus carteri*, *Criorhynchus platyrhinus*, *Criorhynchus simus*, *Ornithocheirus carteri*, *Ornithocheirus platyrhinus*, *Pterodactylus simus*)  
*Ornithocheirus* sp.

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*Ornithostoma sedgwicki* (including *Ornithostoma seeleyi*)

Pterodactyloidea; Azhdarchoidea; Lonchodectidae  
*Lonchodectes compressirostris* (including *Lonchodectes tenuirostris*, *Ornithocheirus tenuirostris*)  
*Lonchodectes machaerorhynchus* (including *Ornithocheirus machaerorhynchus*)

*Lonchodectes microdon* (including *Lonchodectes oweni*, *Ornithocheirus huxleyi*, *Ornithocheirus microdon*, *Ornithocheirus oweni*)

*Lonchodectes platystomus* (including *Amblydectes platystomus*, *Criorhynchus platystomus*, *Ornithocheirus platystomus*)

*Lonchodectes* sp.

Age: late Albian (RAWSON et al. 1978).

#### 102. Dorset, England

Middle Purbeck Beds (Langton Matravers: SEELEY [1869b, 1875], OWEN [1870], DELAIR [1958], HOWSE & MILNER [1995], WRIGHT et al. [1997]).

Pterodactyloidea indet.

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmatoidea; Ctenochasmatinae

*Gnathosaurus macrurus*

*Plataleorhynchus streptorhodon*

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmatoidea

Ctenochasmatidae indet. (= *Doratorhynchus validus*)

Pterosaur trackways (*Purbeckopus pentadactylus*)

Age: Berriasian (ALLEN & WIMBLEDON 1991).

**103. Isle of Wight, England**

- i) Wessex Formation (various localities including Barnes High and Yaverland: LYDEKKER [1888], MARTILL et al. [1996], HOWSE et al. [2001], STEEL et al. [2005], SWEETMAN [2006]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Caulkicephalus trimicrodon*  
 Ornithocheiridae indet.  
 Pterosauria indet.

Age: Barremian (RAWSON et al. 1978).

- ii) Vectis Formation (Atherfield Point: HOOLEY [1913], MARTILL et al. [1996], HOWSE et al. [2001]).

Pterodactyloidea; Ornithocheiroidea; Istiodactylidae  
*Istiodactylus latidens*  
 Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
 Ornithocheiridae indet.  
 Pterosauria indet.

Age: Barremian (RAWSON et al. 1978).

- iii) “Wealden” (No locality data: OWEN [1870], LYDEKKER [1888], MARTILL et al. [1996], HOWSE et al. [2001]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
 Ornithocheiridae indet. (= ‘*Ornithocheirus nobilis*’)  
 Pterosauria indet.

Age: Barremian (RAWSON et al. 1978).

- iv) Upper Greensand (Atherfield Point: UNWIN et al. [2000]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Ornithocheirus* sp.

Age: Albian (RAWSON et al. 1978).

**104. Kent, England**

Gault Clay (Folkestone: OWEN [1874], UNWIN et al. [2000])

Pterodactyloidea; Azhdarchoidea; Lonchodectidae  
*Lonchodectes platystomus*  
 Pterodactyloidea indet. (= *Ornithocheirus daviesii*)

Age: Albian (RAWSON et al. 1978)

**105. East Sussex, England**

Hastings Beds (Hastings: MANTELL [1827, 1844], OWEN [1870, 1874], LYDEKKER [1888], HOWSE et al. [2001]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae

*Coloborhynchus clavirostris*  
 Pterodactyloidea; Azhdarchoidea; Lonchodectidae  
*Lonchodectes sagittirostris*  
 Pterosauria indet.

Age: late Berriasian – Valanginian (RAWSON et al. 1978).

**106. West Sussex, England**

Hastings Beds (Tilgate Forest: MANTELL [1827, 1844], Owen [1870, 1874], HOWSE et al. [2001]).

Pterosauria indet. (= *Ornithocheirus clifti*, *Ornithocheirus curtus*)

Age: late Berriasian – Valanginian (RAWSON et al. 1978).

**107. Département des Ardennes, France**

Unnamed unit (Grandpré: BUFFETAUT & WELLNHOFER [1983], KNOLL & BOUVEUR [2001]).

?Pterosauria indet.

Age: early Albian (KNOLL & BOUVEUR 2001).

**108. Département de l’Aube, France**

- i) *Toxaster* Limestone (exact provenance unknown: BUFFETAUT [2004]).

Pterodactyloidea; Ornithocheiroidea  
 Ornithocheiroidea indet.

Age: Hauterivian (LAPPARENT & STCZEPINSKY 1968).

- ii) Unnamed unit “Sables verts de l’Albien” (Le Gaty: BUFFETAUT et al. [1989], UNWIN et al. [2000]).

Pterodactyloidea; Ornithocheiroidea  
 Ornithocheiroidea indet.

Age: Albian (BUFFETAUT et al. 1989).

**109. Département du Charante, France**

Unnamed unit ‘Purbeckien’ (Chevres-de-Cognac: MAZIN et al. [2006]).

Pterodactyloidea indet.

Age: early – middle Berriasian (COLIN et al. 2004).

**110. Département de Haute-Marne, France**

*Toxaster* Limestone (= “Calcaire à Spatangues”) (Attancourt: BUFFETAUT & WELLNHOFER [1983], UNWIN et al. [2000]).

Pterosauria indet.

Age: Hauterivian (LAPPARENT & STCSTEPINSKY 1968).

#### 111. Département de la Meuse, France

Unnamed unit 'Gault' (Louppy-Le-Chateau: UNWIN et al. [2000], KNOLL & BOUVEUR [2001]).

Pterosauria indet.

Age: early Albian (KNOLL & BOUVEUR 2001).

#### 112. Département du Pas-du-Calais, France

Unnamed unit (Boulogne-sur-Mer: KNOLL & BOUVEUR [2001]).

Pterosauria indet. (?Ornithocheiridae indet.)

Age: Albian (KNOLL & BOUVEUR 2001).

#### 113. Niedersachsen, Germany

- i) "Purbeck" (Deister Hills: VON MEYER [1851], BENNETT [2007a]).

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmatidae  
*Ctenochasma roemeri*

Age: Berriasian (BENNETT 2007a).

- ii) Elligerbrink Shale (Delligsen: KOKEN [1885]; WELLNHOFER [1991a]).

?Pterosauria indet. (= *Ornithocheirus hilsensis*)

Age: early Lower Cretaceous (Neocomian: KOKEN 1885).

- iii) Unnamed unit (Engelbostel: WILD [1990], UNWIN et al. [2000]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet. (= *Ornithocheirus wiedenrothi*)

Age: Hauterivian (WILD 1990).

#### 114. Distrito de Lisboa, Portugal

Unnamed unit "Ptérocérien marls and sandstones" (Serra Tiago dos Velhos: GALTON [1994]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
cf. *Ornithocheirus* sp.

Age: early Barremian (GALTON 1994).

#### 115. Judetul Bihor, Romania

Cornet bauxite (Cornet: BENTON et al. [1997]).

Pterodactyloidea; Dsungaripteroidea  
?Dsungaripteroidea indet.

Age: Berriasian – Hauterivian (PATRULIUS et al. 1983).

#### 116. Provincia de Cuenca, Spain

Calizas de La Huergina Formation (Las Hoyas: LOCKLEY et al. [1995], UNWIN [1996b]).

?Pterosaur tracks

Age: late Barremian (FREGENAL-MARTINEZ & MÉLÉNDEZ 1995).

#### 117. Comunidad Autónoma de La Rioja, Spain

Enciso Group (Los Cayos: MORATALLA [1993], LOCKLEY et al. [1995], UNWIN [1996b], MORATALLA & HERNÁN [2005]).

Pterosaur tracks (*Pterichnus* sp.)

Age: early Aptian (MORATALLA & HERNÁN 2005).

#### 118. Provincia de Soria, Spain

Oncala Formation (Santa Cruz de Yanguas and Villar del Río: MORATALLA [1993], LOCKLEY et al. [1995], UNWIN [1996b], FUENTES-VIDARTE & MEIJIDE-CALVO [1996], MEIJIDE-CALVO & FUENTES-VIDARTE [2001]).

Pterosauria indet.

Pterosaur tracks (*Pteraichnus manuelyi*, *Pteraichnus palacieisaenzi*)

Age: Berriasian (LOCKLEY et al. 1995).

#### 119. Provincia de Teruel, Spain

- i) Artoles Formation (Vallipón: RUIZ-OMEÑACA et al. [1998]).

Pterodactyloidea indet.

Age: Barremian (RUIZ-OMEÑACA et al. 1998).

- ii) Blesa Formation (La Cantalera: RUIZ-OMEÑACA & CANUDO [2001]).

Pterosauria indet.

Age: early Barremian (RUIZ-OMEÑACA et al. 1997).

- iii) El Castillar Formation (Galve: CANUDO et al. [1997]), SANZ et al. [1990]).

Pterodactyloidea; Dsungaripteroidea



?Dsungaripteroidea indet.  
Pterosauria indet.

Age: Berriasian-early Barremian (SÁNCHEZ-HERNÁNDEZ et al. 2007).

iv) Camarillas Formation (Galve: SÁNCHEZ-HERNÁNDEZ et al. [2007]).

Pterodactyloidea; Ornithocheiroidea  
Ornithocheiroidea indet.

Age: early Barremian (SÁNCHEZ-HERNÁNDEZ et al. 2007).

### 2.5.5 North America

#### 120. Estado de Puebla, Mexico

Tepexi Formation (Tlayúa: CABRAL-PERDOMO & AP-  
PLEGATE [1994], UNWIN et al. [2000], FREY et al. [2006]).

Pterodactyloidea indet.  
Pterodactyloidea; Ornithocheiroidea  
Ornithocheiroidea indet. (= *Pteranodon* sp.,  
*Nyctosaurus* sp.)

Age: Aptian-Albian (FREY et al. 2006).

#### 121. California, United States of America

Budden Canyon Formation (Shasta County: HILTON  
et al. [1999]).

Pterosauria indet.

Age: late Aptian (HILTON et al. 1999).

#### 122. Maryland, United States of America

Patuxent Formation (unnamed locality: KRANZ [1998],  
STANFORD & LOCKLEY [2004], STANFORD et al. [2007]).

Pterosaur tracks

Age: Aptian (DOYLE 1992).

#### 123. Oregon, United States of America

Hudspeth Formation (Wheeler County: GILMORE  
[1928], NESSOV [1991], BENNETT [1994], UNWIN et al.  
[2000]).

Pterodactyloidea; Azhdarchoidea  
?Azhdarchoidea indet. (= *Bennettazhia*  
[*Pteranodon*] *oregonensis*)

Age: Albian (GILMORE 1928).

#### 124. Texas, United States of America

i) Glen Rose Formation (Glen Rose and Seco Creek:  
LANGSTON [1974], MURRY et al. [1991], UNWIN et al.  
[2000]).

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
?Azhdarchidae indet.

?Pterosaur tracks

Age: late Aptian – early Albian (LANGSTON 1974).

ii) Antlers Formation (Forestburg: ZANGERL & DENISON  
[1950], UNWIN et al. [2000]).

?Pterosauria indet.

Age: late Aptian – middle Albian (LANGSTON 1974).

iii) Paw Paw Formation (Tarrant County: LEE [1994]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Coloborhynchus wadleighi*

Age: late Albian (JACOBS et al. 1991).

### 2.5.6 South America

#### 125. Neuquén Province, Argentina

i) Candeleros Formation (Ezequiel Ramos Mexía: CALVO  
& LOCKLEY [2001]).

Pterosaur tracks

Age: Albian (CALVO 1991) or Cenomanian (LEANZA et  
al. 2004).

ii) La Amarga Formation (Arroyo La Amarga: MONTA-  
NELLI [1987], BONAPARTE [1996]).

Pterodactyloidea indet.

Age: Hauterivian-Barremian (MONTANELLI 1987),  
Hauterivian (BONAPARTE 1996), Barremian-early  
Aptian (LEANZA et al. 2004).

iii) Cullín Grande Member, Lohan Cura Formation  
(Cerro de Los Leones: MARTINELLI et al. [2007]).

Pterosauria indet.

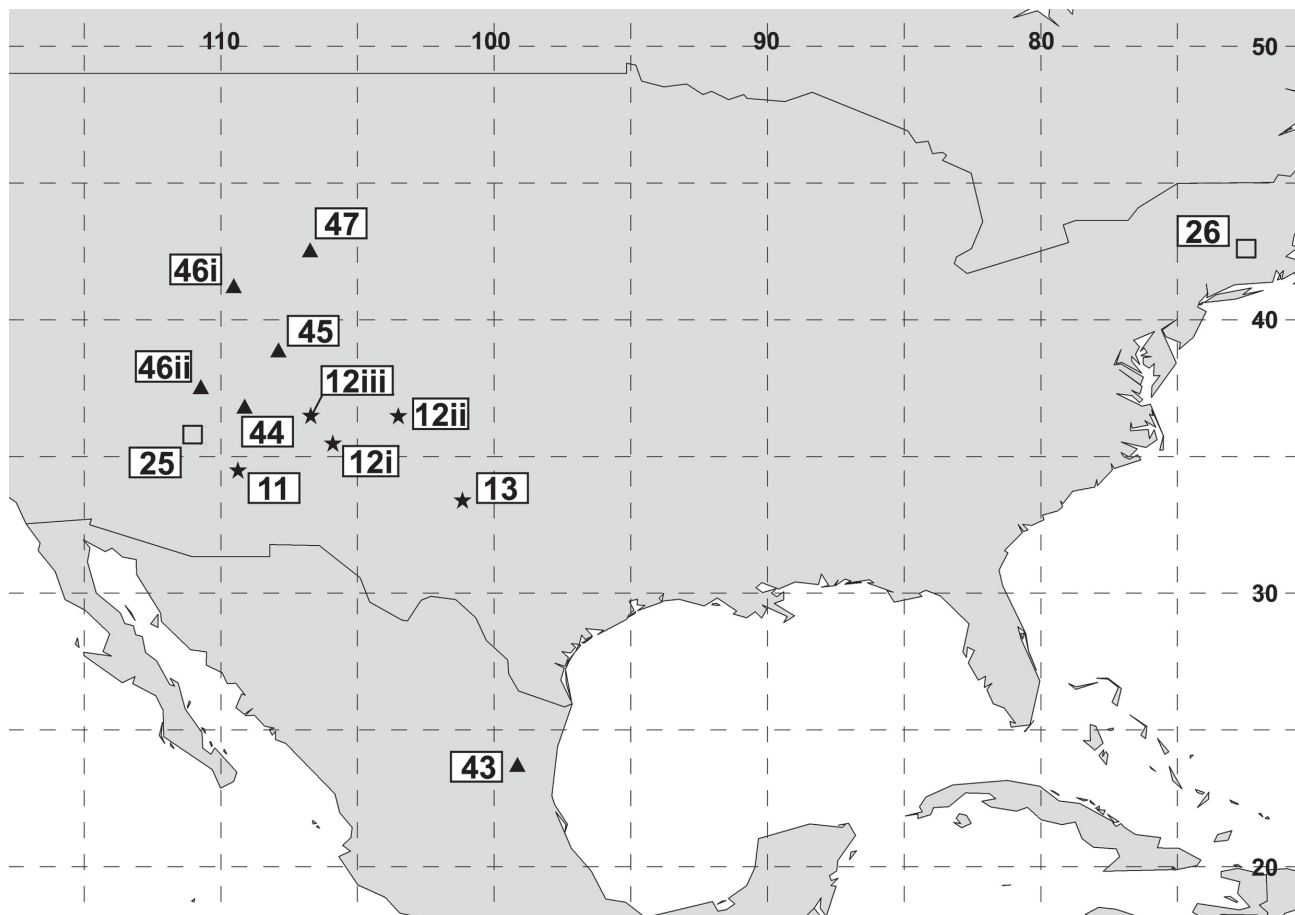
Age: early Albian (LEANZA 2002).

#### 126. San Luis Province, Argentina

i) La Cruz Formation (Hultarán: BONAPARTE & SÁNCHEZ  
[1975], CODORNIÚ & GASPARINI [2007]).

Pterodactyloidea; Ctenochasmatoidea; Ctenochasma-  
tidae; Ctenochasmatinae

*Pterodaustro guinazui* (= *Puntanipterus globosus*)



**Figure 9:** Pterosaur localities from the Upper Triassic to Middle Jurassic of North America. Key: filled star, Upper Triassic; open squares, Lower Jurassic localities; filled triangles, Middle Jurassic localities; Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

Age: Aptian (RIVAROLA 1999).

- ii) Lagarcito Formation (Loma del Pterodaustro: BONAPARTE [1970], CHIAPPE & CHINSAMY [1996], CHIAPPE et al. [1998], CHIAPPE et al. [2004], CODORNIÚ & CHIAPPE [2004], CODORNIÚ & GASPARINI [2007]).

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmatidae; Ctenochasmatinae

*Pterodaustro guinazui*

Age: Albian (CHIAPPE et al. 1998).

#### 127. Santa Cruz Province, Argentina

Río Belgrano Formation (Lake Belgrano: KELLNER et al. [2003]).

Pterodactyloidea; Ornithocheiroidea  
Ornithocheiroidea indet. (= ‘?Anhangueridae indet.’)

Age: early-middle Barremian (RICCARDI 1983).

#### 128. Bahia, Brazil

Bahia Series (Bahia: MAWSON & WOODWARD [1907]: the majority of specimens attributed to pterosaurs from this locality have now been referred to the coelacanth *Mawsonia*).

?Pterosauria indet.

Age: Aptian (TAQUET 1977).

#### 129. Ceará, Brazil

- i) Nova Olinda Member, Crato Formation (Araripe Basin: FREY & MARTILL [1994], CAMPOS & KELLNER [1997], MARTILL & FREY [1998, 1999], SAYAO & KELLNER [1998, 2000], FREY et al. [2003a, 2003b], KELLNER & CAMPOS [2007], UNWIN & MARTILL [2007]).

Pterodactyloidea; Ornithocheiroidea  
Ornithocheiroidea indet. (= ‘*Brasileodactylus* cf. *araripensis*’)

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Arthurdactylus conandoylei*  
*Ludodactylus sibbicki*

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
?Azhdarchidae indet.

Pterodactyloidea; Azhdarchoidea; Tapejaridae

*Tupundactylus imperator*

*Tupundactylus navigans*

Age: late Aptian-early Albian (BATTEN 2007).

- ii) Romualdo Member, Santana Formation (Araripe Basin: PRICE [1971], WELLNHOFER [1977, 1985, 1987, 1991b], BUISONJE [1980], WELLNHOFER et al. [1983], KELLNER [1984, 1996], CAMPOS & KELLNER [1985], LEONARDI & BORGOMANERO [1985], KELLNER & CAMPOS [1988, 1994, 2002], UNWIN [1988c, 2002], MARTILL & UNWIN [1989], BENNETT [1990], DALLA VECCHIA [1993], KELLNER & TOMIDA [2000], FASTNACHT [2001], VELDMEIJER [2003]).

Pterodactyloidea indet.

Pterodactyloidea *incertae sedis* (including ‘*Araripesaurus castilhoi*’, ‘*Araripedactylus dehmi*’, ‘*Santanadactylus brasiliensis*’, ‘*Santanadactylus araripensis*’, ‘*Anhanguera araripensis*’, ‘*Santanadactylus pricei*’, ‘*Santanadactylus spixi*’, ‘*Ceardactylus ligabuei*’)

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae

*Anhanguera blittersdorffi*

*Anhanguera santanae* (= *Araripesaurus santanae*)

*Brasileodactylus araripensis*

*Coloborhynchus robustus* (= *Tropeognathus robustus*; including *Anhanguera piscator*)

*Coloborhynchus spielburgi*

*Ornithocheirus mesembrinus* (= *Tropeognathus mesembrinus*)

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmatoidea; Gnathosaurinae

*Cearadactylus atrox*

Pterodactyloidea; Azhdarchoidea; Tapejaridae

*Tapejara wellnhoferi*

Pterodactyloidea; Azhdarchoidea; Neoazhdarchia

*Thalassodromeus sethi*

*Tupuxuara longicristatus*

*Tupuxaura leonardi*

Age: Aptian-Albian (PONS et al. 1990).

### 130. Región de Antofagasta, Chile

Santa Ana Formation (Quebrada La Carreta: CASAMIQUELA & DIAZ [1978], MARTILL et al. [2000]).

Pterodactyloidea; Dsungaripteroidea; Dsungaripteridae

*Domeykodactylus ceciliae*

Age: probably Lower Cretaceous (CHONG 1976; CASAMIQUELA & DIAZ 1978; MARTILL et al. 2000), possibly Upper Jurassic (CASAMIQUELA & DIAZ 1978).

### 131. Región de Atacama, Chile

Quebrada Monardes Formation (Cerro la Isla: BELL & PADIAN [1995], RUBILAR et al. [2002], MARTILL et al. [2006]).

Pterodactyloidea; Ctenochasmatoidea; Ctenochasmatoidea; Ctenochasmatoidea

Ctenochasmatoidea indet.

Age: Lower Cretaceous (BELL & PADIAN 1995).

### 132. Huánuco, Peru

Chulec Formation (Huanzala Mine: BENNETT [1989]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae; Pteranodontidae indet.

Age: Albian (BENNETT 1989).

### 133. Estado Zulia, Venezuela

Apón Formation (Rosarito Quarry, Villa de Rosario: KELLNER & MOODY [2003]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae; Ornithocheiridae indet. (= ‘?Anhangueridae indet.’)

Age: Aptian (RENZ 1982).

## 2.6 Upper Cretaceous

### 2.6.1 Africa

#### 134. Littoral Province, Cameroon

Logbadjeck Formation (unnamed locality: NTAMAK-NIDA et al. [2006]).

Pterosauria indet.

Age: early Campanian (NTAMAK-NIDA et al. 2006).

#### 135. Kasai-Oriental, Democratic Republic of the Congo

Unnamed unit (Bibanga: SWINTON [1948]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae; ?Ornithocheiridae indet. (= ‘cf. *Ornithocheirus*’)

Age: Cenomanian-Turonian (MADER & KELLNER 1999).

#### 136. Chaouia-Ouardigha, Morocco

Upper ‘couche III’, phosphate deposits (Oued Zem, Oulad Abdoun Basin, Khouribga: PEREDA SUBERBIOLA et al. [2003]).

Pterodactyloidea; Azhdarchoidea; Azhdarchidae; *Phosphatodraco mauritanicus*

Age: Maastrichtian (PEREDA SUBERBIOLA et al. 2003).

**137. Meknès-Tafilalt, Morocco**

Unnamed unit (Beg'aa, Kem-Kem region, Hamada du Guir: KELLNER & MADER [1996, 1997], MADER & KELLNER [1997, 1999], WELLNHOFER & BUFFETAUT [1999], RODRIGUES et al. [2006]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Coloborhynchus moroccensis* (= *Siroccopteryx moroccensis*)  
?Ornithocheiridae indet.

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
?Pteranodontidae indet.

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Pterodactyloidea; Azhdarchoidea; Tapejaridae  
Tapejaridae indet.

?Pterosauria indet.

Age: early Cenomanian (WELLNHOFER & BUFFETAUT 1999).

**138. Thiès, Senegal**

Unnamed unit (Paki: MONTEILLET et al. [1982]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: Campanian-Maastrichtian (MADER & KELLNER 1999).

**2.6.2 Asia****139. Vayots Dzor, Armenia**

Unnamed formation (Khidzorut: AVERIANOV & ATABEKYAN [2005]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Turonian (AVERIANOV & ATABEKYAN 2005).

**140. Zhejiang Province, People's Republic of China**

Tangshang Formation (Linhai: CAI & WEI [1994], UNWIN & LÜ [1997]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
*Zhejiangopterus linhaiensis*

Age: early Campanian (MU & CAI 1992).

**141. Rajasthan, India**

Intertrappean Beds (Sirolkhal: DUBEY & NARAIN [1946]).

Pterosauria indet.

Age: late Maastrichtian (PRASAD 1989).

**142. Judea and Samaria Area/West Bank, Israel**

Amminadav Formation or Bet-Meir Formation ('Ein Yabrud: TCHERNOV et al. [1996]).

Undescribed pterodactyloid

Age: early Cenomanian (RIEPEL et al. 2003).

**143. Southern District, Israel**

Mishash Formation (Oron: LEWY et al. [1992]).

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
Azhdarchidae indet. (= '*Titanopteryx* sp.')

Age: late Campanian (REISS et al. 1985).

**144. Hokkaido Prefecture, Japan**

i) Hakobuchi Group (Enbetsu: CHITOKO [1996]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
?Ornithocheiridae indet.

Age: late Campanian (CHITOKO 1996).

ii) Upper Yezo Group (Mikasa: OBATA et al. [1972]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
?Pteranodontidae indet. ('*Pteranodon* sp.')

Age: Santonian-early Campanian (UNWIN et al. 1996).

**145. Kumamoto Prefecture, Japan**

i) Himenoura Group (UNWIN et al. 1996).

Pterosauria indet.

Age: Santonian (UNWIN et al. 1996).

ii) "Upper" Formation, Mifune Group (Mifune: IKEGAMI & TAMURA [1996], OKAZAKI & KITAMURA [1996], IKEGAMI et al. [2000]).

Pterodactyloidea indet.

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Cenomanian-early Turonian (MATSUMOTO et al. 1982).

**146. Amman, Jordan**

Unnamed formation (Ruseifa: ARAMBOURG [1959], FREY & MARTILL [1996], MARTILL et al. [1998]).



Azhdarchidae indet. (includes '*Bogolubovia orientalis*')

Age: early Campanian (AVERIANOV 2007b).

#### 150. Saratov Oblast, Russia

- i) Pudovinko Formation (Saratov: AVERIANOV et al. [2005b], AVERIANOV [2007b]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Campanian (AVERIANOV et al. 2005b).

- ii) Rybushka Formation (Beloe Ozero, Shyrokii Karamysh: AVERIANOV [2007b]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Campanian (AVERIANOV 2007b).

- iii) Unnamed formation (Sinen'kie: AVERIANOV [2004]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
?Ornithocheiridae indet.

Age: early Cenomanian (AVERIANOV 2004).

- iv) Unnamed formation (Saratov: GLIKMAN [1953], UNWIN & BAKHURINA [2000], AVERIANOV [2004, 2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
cf. *Coloborbhynchus* sp.  
Ornithocheiridae indet.

Age: late Cenomanian (AVERIANOV 2004).

#### 151. Volgograd Oblast, Russia

- i) Melovatka Formation (Melovatka: UNWIN & BAKHURINA [2000], AVERIANOV et al. [2005c], AVERIANOV [2007a]).

Pterodactyloidea; Ornithocheiroidea  
Ornithocheiroidea indet.

Age: late Cenomanian (AVERIANOV et al. 2005b).

- ii) Unnamed formation (Solodcha: AVERIANOV et al. [2005c], AVERIANOV [2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: late Cenomanian (AVERIANOV et al. 2007a).

- iii) Unnamed formation (Polunino 2: AVERIANOV & YARKOV [2004]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: Campanian (AVERIANOV & YARKOV 2004).

- iv) Unnamed formation (Polunino 1: AVERIANOV & YARKOV [2004]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
?Azhdarchidae indet.

Age: Maastrichtian, redeposited in Paleocene (AVERIANOV & YARKOV 2004).

#### 152. Voronezh Oblast, Russia

Unnamed unit (Pavlovsk: AVERIANOV [2004]).

Pterodactyloidea indet.

Age: Cenomanian (AVERIANOV 2004).

#### 153. Jeollanam-do, South Korea

Uhangri Formation (Haenam Bay: HWANG et al. [2002]).

Pterosaur tracks (= *Haenamichnus uhangriensis*,  
*Haenamichnus* sp.)

Age: Santonian-early Campanian (KIM et al. 2003).

#### 154. Sughd Province, Tadjikistan

Yalovach Formation (Kansai: NESSOV [1990], BAKHURINA & UNWIN [1995], AVERIANOV [2007b]; Zamuratscho & Kyzylpilyal: NESSOV [1990], BAKHURINA & UNWIN [1995]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
?Azhdarcho sp.  
Azhdarchidae indet.  
?Pterosauria indet.

Age: early Santonian (AVERIANOV 2007b).

#### 155. Karakalpakistan, Uzbekistan

Khodzhakul Formation (Khodzhakul, Sheikhdzheili, Khodzhakulsai, Chelpyk & Karachadalysai: NESSOV [1990], BAKHURINA & UNWIN [1995], AVERIANOV [2007a, 2007b]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Ornithocheirus* sp.  
Ornithocheiridae indet.  
Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: early Cenomanian (AVERIANOV [2007b]).

**156. Navoiy Province, Uzbekistan**

- i) Bissekty Formation (Dzharakuduk 2: NESSOV [1984], BAKHURINA & UNWIN [1995], UNWIN & BAKHURINA [2000], AVERIANOV [2007b]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
*Azhdarcho lancicollis*

Age: middle-late Turonian (AVERIANOV 2007b).

- ii) Dzharakuduk Formation (Itemir: AVERIANOV [2007a]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet.

Age: Cenomanian (AVERIANOV [2007a]).

**157. Xorazm Province, Uzbekistan**

?Bissekty Formation (Zenge Kurgan 3: AVERIANOV [2007b]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: middle-late Turonian (AVERIANOV 2007b).

**2.6.3 Australasia****158. Western Australia, Australia**

Miria Formation (Toothawarra Creek: BENNETT & LONG [1991]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
?Azhdarchidae indet.

Age: Maastrichtian (BENNETT & LONG 1991).

**159. North Island, New Zealand**

Tahora Formation (Mangahouanga Stream: WIFFEN & MOLNAR [1988], MOLNAR & WIFFEN [1994]).

Pterodactyloidea indet.

Age: Campanian (MOORE 1987).

**2.6.4 Europe****160. Niederösterreich, Austria**

Gosau Formation (Muthmannsdorf: SEELEY [1881]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
Ornithocheiridae indet. (= '*Ornithocheirus bunzeli*')

Age: Campanian (JELETZKY 1960; THENIUS 1974).

**161. Pardubický, Czech Republic**

Middle Iser Shales (Zárecká Lhota, Chocen: FRITSCH [1881], WELLNHOFER [1978]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
?Ornithocheiridae indet. (= '*Ornithocheirus blavat schi*')

Age: Turonian (WELLNHOFER 1978).

**162. East Sussex, England**

Lower-Middle Chalk (Southerham Grey Pit, Lewes: BENTON & SPENCER [1995]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
?Ornithocheiridae indet. (= '*Ornithocheirus*')

Age: Cenomanian-Turonian (BENTON & SPENCER 1995).

**163. Hertfordshire, England**

Lower Chalk (Hitchin: BENTON & SPENCER [1995]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
?Ornithocheiridae indet. (= '*Ornithocheirus*')

Age: early Cenomanian (RAWSON et al. 1978).

**164. Kent, England**

- i) Lower-Upper Chalk (Burham: BOWERBANK [1846, 1848, 1852], OWEN [1851]; Halling, Maidstone and Snodland: BENTON & SPENCER [1995], UNWIN [2001]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
*Anhanguera cvvieri*

?Ornithocheiridae indet.

Pterodactyloidea; Azhdarchoidea; Lonchodectidae  
*Lonchodectes compressirostris*  
*Lonchodectes giganteus*

Age: Cenomanian-Turonian (BENTON & SPENCER 1995).

- ii) White Chalk Formation (Hope Point: MARTILL et al. [2008]).

Pterodactyloidea; Azhdarchoidea  
?Azhdarchoidea indet.

Age: Coniacian (JENKYN et al. 1994).

**165. Surrey, England**

Lower Chalk (Betchworth: BENTON & SPENCER [1995]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
?Ornithocheiridae indet. (= '*Ornithocheirus*')

Age: early Cenomanian (RAWSON et al. 1978).

#### 166. Département de l'Ariège, France

Marnes d'Auzas Formation (Mérigon: BUFFETAUT et al. [1997], BUFFETAUT [2008]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Maastrichtian (BUFFETAUT et al. 1997).

#### 167. Département de l'Aude, France

i) Marnes Rouges Inférieures Formation (Bellevue, C3: BUFFETAUT [1998, 2008], LE LOEUFF [2005]).

Pterosauria indet.

Age: Maastrichtian (BILOTTE 1985) or late Campanian (BILOTTE cited in LE LOEUFF 2005).

ii) Marnes rouges de Roquelongue (Montplaisir: BUFFETAUT et al. [1996], BUFFETAUT 2008).

Pterosauria indet.

Age: late Maastrichtian (BUFFETAUT et al. 1996).

#### 168. Département de la Charente-Maritime, France

Unnamed formation (Fouras Peninsula: NÉRAUDEAU et al. [2003], BUFFETAUT [2008]).

Pterosauria indet.

Age: early Cenomanian (NÉRAUDEAU et al. 2003).

#### 169. Département de l'Hérault, France

Unnamed formation (Sainte-Foy, Cruzy: BUFFETAUT [2001, 2008]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Campanian-early Maastrichtian (BUFFETAUT 2001).

#### 170. Département de l'Oise, France

White Chalk (Notre-Dame-du-Thil: KNOLL & BOUVEUR [2001]).

?Pterosauria indet. (This material may represent a bird: BUFFETAUT 2008).

Age: early Campanian (KNOLL & BOUVEUR 2001).

#### 171. Département du Var, France

i) Unnamed unit (Fox-Amphoux: BUFFETAUT et al. [2006], BUFFETAUT [2008]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Campanian-early Maastrichtian (BUFFETAUT et al. 2006).

ii) Unnamed unit (Pourrières: BUFFETAUT [2008]).

Unnamed pterosaur

Age: late Campanian-early Maastrichtian (BUFFETAUT 2008).

#### 172. Veszprém, Hungary

Csehbánya Formation (Iharkút: OSI et al. [2005]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
*Bakonydraco galaczi*  
Azhdarchidae indet.

Age: Santonian (KNAUER & SIEGL-FARKAS 1992).

#### 173. Hunedoara, Romania

i) Densus-Ciula Formation (Valioara & Tustea: BUFFETAUT et al. [2002, 2003]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
*Hatzegopteryx thambema*  
?Azhdarchidae indet.

Age: ?late Maastrichtian (GRIGORESCU 1992).

ii) Sânpetru Formation (Sânpetru: NOPCSA [1914], JIANU et al. [1997]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
?Pteranodontidae indet.

Age: ?late Maastrichtian (GRIGORESCU 1992).

#### 174. Burgos, Spain

Unnamed formation (Laño, levels L1A, L1B: ASTIBIA et al. [1990], BUFFETAUT [1999]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet. (= 'cf. *Azdarcho* sp.')

Age: late Campanian (PEREDA-SUBERBIOLA et al. 2000).

#### 175. Valencia, Spain

Calizas y Margas de Sierra Perenchiza Formation (La Solana: COMPANY et al. [1999, 2001]; Chera Region: RODRÍGUEZ et al. [2005]).



Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: Campanian-Maastrichtian (GUTIERREZ et al. 1984).

### 2.6.5 North America

#### 176. Alberta, Canada

- i) Dinosaur Park Formation (Dinosaur Provincial Park: RUSSELL [1972], CURRIE & RUSSELL [1982], CURRIE & PADIAN [1983], CURRIE & JACOBSON [1995], GODFREY & CURRIE [2005]).

Pterodactyloidea indet.  
Pterodactyloidea; Azdarchoidea; Azhdarchidae  
Azhdarchidae indet.  
Pterosauria indet.

Age: late Campanian (EBERTH 2005).

- ii) Dunvegan Formation (Pouce Coupe River: CURRIE [1989], LOCKLEY et al. [1995], UNWIN [1996b]).

?Pterosaur trackways

Age: Cenomanian (PLINT et al. 2001).

#### 177. Baja California, Mexico

El Gallo Formation (Tijuana: ARANDA-MANTECA, pers. comm. in FREY et al. [2006]).

Pterosauria indet.

Age: Maastrichtian (FREY et al. 2006).

#### 178. Coahuila de Zaragoza, Mexico

- i) Austin Group (El Rosario, Múzquiz County: STINNESBECK et al. [2005], FREY et al. [2006]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontia  
*Muzquizopterix coahuilensis*

Age: early Coniacian (STINNESBECK et al. 2005).

- ii) Cerro del Pueblo Formation (El Pelillal: RODRIQUEZ-DE LA ROSA & CEVALLOS-FERRIZ [1998], RODRIQUEZ-DE LA ROSA [2003]).

Pterodactyloidea indet.  
Pterosaur tracks (*Pteraichnus* sp.)

Age: late Campanian (VEGA-VERA et al. 1990).

#### 179. Alabama, United States of America

Mooreville Chalk (no locality data: LAWSON [1975], BENNETT [1994]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*?Pteranodon* sp.

Age: late Santonian-early Campanian (PUCKETT 1994).

#### 180. California, United States of America

Chico Formation (Butte County: HILTON et al. [1999]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*?Pteranodontidae* indet.

Age: Campanian (EMBREE cited in WEISHAMPEL et al. 2004).

#### 181. Delaware, United States of America

Merchantville Formation (New Castle County: BAIRD & GALTON [1981], BENNETT [1994]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*?Pteranodon* sp.

Age: early Campanian (OWENS 1983).

#### 182. Georgia, United States of America

Eutaw Formation (Ochilee Creek: SCHWIMMER et al. [1985]).

Pterosauria indet.

Age: late Santonian (KAYE & RUSSELL 1973).

#### 183. Kansas, United States of America

- i) Greenhorn Limestone (northwestern Russell County: LIGGETT et al. [2005]).

Pterosauria indet.

Age: Cenomanian (MIGGINS 2004).

- ii) Niobrara Chalk, Lower Smoky Hill Chalk Member (numerous localities: MARSH [1881b], HARKSON [1966], MILLER [1972], BENNETT [1994, 2003]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*Pteranodon sternbergi* (including *P. eatoni*)  
Pterodactyloidea; Ornithocheiroidea; Nyctosauridae  
*Nyctosaurus nanus*  
*Nyctosaurus* sp.

Age: late Coniacian-early Santonian (BENNETT 1994).

- iii) Niobrara Chalk, Upper Smoky Hill Chalk Member (numerous localities: COPE [1872], MARSH [1872, 1876], EATON [1910], MILLER [1972], BENNETT [1994]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae



**Figure 11:** Pterosaur localities from the Middle Jurassic to Upper Cretaceous of South America, including Argentina, Brazil, Chile, Peru and Venezuela, and from the Lower Jurassic and Upper Cretaceous of India. Upper Triassic pterosaur localities are unknown in both regions: in addition, Lower Jurassic localities are absent from South America and Middle Jurassic to Lower Cretaceous localities are absent from India. Key: Lower Jurassic localities; filled triangles, Middle Jurassic localities; filled squares, Upper Jurassic localities; filled circles, Lower Cretaceous localities; open crosses, Upper Cretaceous localities. Numbers in boxes refer to numbered localities in the text; other numbers refer to latitude and longitude.

Pteranodontidae indet. (= '*Pteranodon occidentalis*', '*P. ingens*', '*P. velox*', '*P. umbrosus*', '*P. harpyia*' and '*P. comptus*').

*Pteranodon longiceps* (including *P. marshi* and *P. walkeri*)

Pterodactyloidea; Ornithocheiroidea; Nyctosauridae  
*Nyctosaurus gracilis* (including *N. bonneri*)

Age: late Santonian–early Campanian (BENNETT 1994).

iv) Pierre Shale (no locality data: BENNETT [1994]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*Pteranodon longiceps*

Age: early Campanian (BENNETT 1994).

#### 184. Montana, United States of America

- i) Mowry Shale (Teigen: BENNETT [1989], UNWIN et al. [2000]).

Pterodactyloidea; Ornithocheiroidea  
Ornithocheiroidea indet. (= Pteranodontidae indet.)

Age: Cenomanian (KIRSCHBAUM & ROBERTS 2005).

- ii) Hell Creek Formation (northwestern Carter County: HENDERSON & PETERSON [2006]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
cf. *Quetzalcoatlus* sp.

Age: late Maastrichtian (BAADSGAARD & LERBEKMO 1980).

- iii) Upper Two Medicine Formation (Choteau & Glacier County: PADIAN [1984b], PADIAN & SMITH [1992], PADIAN et al. [1995], MCGOWAN et al. [2002]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
*Montanazhdarcho minor*  
Azhdarchidae indet.

Age: middle-late Campanian (HORNER cited in WEIS-HAMPEL et al. 2004).

#### 185. North Dakota, United States of America

Hell Creek Formation (no locality data: PEARSON et al. [2002]).

Pterosauria indet.

Age: late Maastrichtian (BAADSGAARD & LERBEKMO 1980).

#### 186. South Dakota, United States of America

- i) Greenhorn Limestone (VON LOH & BELL [1998]).

Pterosauria indet.

Age: late Cenomanian (LIGGETT et al. 2005).

- ii) Gammon Ferruginous Formation, Pierre Shale Group (Henderson Ranch, Wallace Ranch, Conger Ranch & Alum Creek [Fall River County]: LAWSON [1975], BENNETT [1994], ROBERTS [2004], HARGRAVE [2007]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*Pteranodon longiceps*

Age: early Campanian (BENNETT 1994).

- iii) Sharon Springs Formation, Pierre Shale Group (Brown Ranch [Pennington County], *Hesperornis* locality [Custer County], Henderson Ranch, Slurp Flats, Whitley's Wash & Conger Ranch [Fall River County]: HARGRAVE [2007]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*Pteranodon longiceps*

Age: early Campanian (BENNETT 1994).

#### 187. Texas, United States of America

- i) Aguja Formation (Big Bend National Park: GASAWAY et al. [2007]).

Pterosauria indet.

Age: early-late Campanian (LEHMAN 1985).

- ii) Buda Limestone (Hays County: LANGSTON [1974]).

Pterodactyloidea; Ornithocheiroidea; Ornithocheiridae  
?Ornithocheiridae indet.

Age: Cenomanian (LOVEJOY 1976).

- iii) Eagle Ford Formation (GILMORE 1935; BENNETT 1994).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
Pteranodontidae indet.

Age: late Turonian (MCNULTY 1966).

- iv) Javelina Formation (Big Bend National Park: LAWSON [1975], KELLNER & LANGSTON [1996]).

Pterodactyloidea; Azdarchoidea; Azhdarchidae  
*Quetzalcoatlus northropi*  
*Quetzalcoatlus* sp.

Age: late Maastrichtian (LEHMAN 1985).

#### 188. Utah, United States of America

- i) Blackhawk Formation (Emery County: LOCKLEY et al. [1995], UNWIN [1996b], LOCKLEY [1999]).

Pterosaur tracks (*Pteraichnus* sp.)

Age: early Campanian (CARPENTER 1992).

- ii) Mesaverde Group (Helper: LOCKLEY et al. [1995], UNWIN [1996b], LIGGETT et al. [2005]).

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
Azhdarchidae indet.  
?Pterosaur tracks

Age: Campanian (CARPENTER 1992).

iii) North Horn Formation (Emery County: LOCKLEY [1999]).

Pterosaur tracks (*Pteraichnus* sp.)

Age: late Maastrichtian (HINTZE 1973).

### 189. Wyoming, United States of America

i) Lance Formation (Niobrara County: ESTES [1964]).

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Maastrichtian (COBBAN & REESIDE 1952).

ii) Mesaverde Group (no locality data: LIGGETT et al. [2005]).

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: Campanian (CARPENTER 1992).

iii) Sharon Springs Formation, Pierre Shale Group (Mule Creek [Niobrara County]: BENNETT [1994], HARGRAVE [2007]).

Pterodactyloidea; Ornithocheiroidea; Pteranodontidae  
*Pteranodon longiceps*

Age: early Campanian (BENNETT 1994).

#### 2.6.6 South America

### 190. Neuquén, Argentina

i) Portezuelo Formation (Loma de la Lata, Barreales Lake: KELLNER et al. [2004, 2007b], CALVO et al. [2007], CODORNIÚ & GASPARINI [2007]).

Pterodactyloidea; Azhdarchoidea; Azhdarchidae  
Azhdarchidae indet.

Age: late Turonian-early Coniacian (CALVO & GRILL 2003).

### 191. Ceará, Brazil

Exu Formation (Simões: MARTILL [2008]).

Pterodactyloidea; Lophocratia  
Lophocratia indet.

Age: Upper Cretaceous (MARTILL 2008).

### 192. Paraíba, Brazil

Gramme Formation (Fazenda do Congo: WELLNHOFER [1978]).

Pterodactyloidea; Ornithocheiroidea; Nyctosauridae  
*Nyctosaurus lamegoi*

Age: Maastrichtian (WELLNHOFER 1978).

## 3. Revised records

Several reports of pterosaur occurrences have been recently reappraised and shown to represent other vertebrate taxa: they are listed here as a supplement to the foregoing list. Some records of Triassic pterosaurs from localities in England, Germany and the USA (based largely on isolated hollow bones) have been reviewed and rejected by DALLA VECCHIA (2003B) and these are omitted from this compilation. A possible pterosaur long bone was reported from the „Craie blanche“ (Coniacian) of Lezennes-Lez-Lille, Département du Nord, France and referred to ‘*Pterodactylus giganteus*’ (BARROIS 1875). However, this element is now regarded as the phalanx of a marine turtle (BUFFETAUT 2008). In addition, pterosaur remains reported in the gut contents of a metriorhynchid crocodile from the Lower Oxford Clay (middle Callovian) of Cambridgeshire, UK (MARTILL 1986) are currently thought to represent fish remains (UNWIN cited in FORREST 2003). Finally, although several of the pterosaur specimens reported from Bahía, Brazil are now regarded as coelacanth quadrates (MAWSON & WOODWARD 1907; D. M. MARTILL and P. L. FOREY, pers. comms.), one tooth from this locality may represent a pterosaur (MAWSON & WOODWARD 1907: Natural History Museum specimen number R8662) and this locality (locality 128, see above) is provisionally retained herein.

## 4. Discussion

Detailed analyses of the pterosaur fossil record lie outside of the scope of this contribution. Nevertheless, a brief survey of data presented herein does reveal some potentially interesting patterns that are worthy of additional investigation (Tab. 1). The most productive part of the pterosaur record (based on the number of localities) is currently the Upper Cretaceous period, with the Lower Cretaceous a close second. In total, the Cretaceous accounts for >60% of the total number of pterosaur-bearing localities (PBLs). In contrast, the Upper Triassic and Lower Jurassic are the poorest-sampled sections of the stratigraphic column with ~6% and ~5% of the total number of PBLs, respectively. The Middle and Upper Jurassic each have similar numbers of PBLs, which is perhaps surprising given the increase in pterosaur species-richness that occurs across the boundary between these intervals. Strong geographical biases are also evident in the data, with Europe comprising almost 40% of the total record and being the most productive region for pterosaur localities in all sub-Periods, with the exception of the Upper Cretaceous. North America and Asia each make substantial contributions to the total number of PBLs, but Africa, Antarctica, Australia and South America are markedly undersampled: these four continents combined account for only 12% of PBLs. Further work is needed to investigate the relative importance of different factors in generating these patterns, including genuine palaeobiological signals (e.g. ef-

fects of vicariance, changes in species-richness through time), geological biases (e.g. effects of different environments on preservation potential, influence of geological megabiases on

the number of pterosaur-bearing formations through time) and collection biases (e.g. intensity of collection efforts through time and in different regions).

**Table 1.** Pterosaur localities listed by continent and stratigraphic interval: the total number of localities for all areas and time intervals is 260. Numerals on the upper line represent the raw number of localities on each continent during each time interval. The figure in parentheses represents the percentage of localities that each continent contributes to the total number from that time interval (so, for example, 53.8% of Lower Jurassic localities are found in Europe). In the final column, the upper line displays the total number of localities reported for each time interval; the number in parentheses is a percentage that represents the contribution that each time period makes to the total number of pterosaur localities. The final row shows the contribution each continent makes to the number of pterosaur localities as a percentage of the total. Abbreviations: AFR, Africa; ANT, Antarctica; AUS, Australia; EUR, Europe; L, Lower; M, Middle; NAm, North America; SAm, South America; U, Upper.

	AFR	ANT	AUS	ASIA	EUR	NAm	SAm	Totals
U Triassic	-	-	-	-	10	6	-	16
	-	-	-	-	(62.5)	(37.5)	-	(6.2)
L Jurassic	2	1	-	1	7	2	-	13
	(15.4)	(7.7)	-	(7.7)	(53.8)	(15.4)	-	(5.0)
M Jurassic	1	-	-	7	16	6	1	31
	(3.2)	-	-	(22.6)	(51.6)	(19.4)	(3.2)	(11.9)
U Jurassic	1	-	-	6	22	5	1	35
	(2.9)	-	-	(17.1)	(62.8)	(14.3)	(2.9)	(13.5)
L Cretaceous	3	-	3	22	28	7	13	76
	(4.0)	-	(4.0)	(28.9)	(36.8)	(9.2)	(17.1)	(29.2)
U Cretaceous	5	-	2	29	20	30	3	89
	(5.6)	-	(2.2)	(32.6)	(22.5)	(33.7)	(3.4)	(34.2)
Totals	(4.6)	(0.4)	(1.9)	(25.0)	(39.7)	(21.5)	(6.9)	

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