SENCKENBERG

REVIEW

Mesozoic and Palaeocene lissamphibian assemblages of North America: a comprehensive review

James D. Gardner · David G. DeMar Jr.

Abstract The Mesozoic and Palaeocene record of lissamphibians (i.e. anurans, caudates, gymnophionans and albanerpetontids) in North America is reviewed on the basis of over 400 published and unpublished occurrences from 61 geological formations. The record is heavily biased towards isolated bones, although some associated and articulated skeletons and rare tracks and trackways are known. Most of the localities are in the Western Interior: in central and southern Alberta and southern Saskatchewan, Canada, extending southwards through the USA and into northern Mexico. Outside of that region, records are limited to one Late Cretaceous age formation in Baja California and several Late Triassic and Cretaceous age formations in the eastern USA. Putative lissamphibians have been reported from the Late Triassic (middle Carnian and early Norian). Unambiguous lissamphibians are known from the Early Jurassic (Sinemurian–Pliensbachian), the Late Jurassic (Kimmeridgian–earliest Tithonian), the basal Cretaceous (late Berriasian–Valanginian) and a nearly continuous sequence extending from the Aptian through to the terminal Palaeocene. The Early Jurassic (Sinemurian–Pliensbachian) of Arizona documents the oldest global occurrences of an anuran (i.e. crown frog) and a stem caecilian; the latter also is the only North American fossil occurrence for Gymnophiona prior to the Quaternary. Late Jurassic (Kimmeridgian–earliest Tithonian) age deposits in Colorado, Utah and Wyoming contain a moderate diversity of anurans, urodeles (i.e. crown salamanders) and possibly stem salamanders. A basal Cretaceous locality (late Berriasian–Valanginian) in South Dakota contains a urodele and the first North American occurrence for Albanerpetontidae. Aptian/Albian age localities in Montana, Wyoming, Texas and Oklahoma contain a mixture of anurans, urodeles and albanerpetontids— that tripartite lissamphibian composition persists in North America through the remainder of the Cretaceous and intermittently through the Palaeocene. Most of the anurans are of uncertain familial affinities. The urodeles contain a mixture of extinct families (Scapherpetontidae and Batrachosauroididae) that were prominent through the Cretaceous into the early Palaeogene, along with the earliest appearances of several extant families, specifically sirenids in the Santonian, amphiumids and proteids in the late Maastrichtian and dicamptodontids and unequivocal cryptobranchids in the late Palaeocene. The albanerpetontid genus *Albanerpeton* was moderately diverse during the Cretaceous and Palaeocene, before vanishing from the North American record near the end of the Palaeocene. Temporal richness estimates of North American lissamphibians were calculated based on taxic and minimum lineage level occurrence data per 5 million year time interval beginning in the Early Jurassic and though to the end of the Palaeocene. The resulting richness curves demonstrate a general pattern of increasing richness leading up to the Cretaceous-Palaeogene (K-Pg) boundary, with peak values during the Campanian and Maastrichtian and a decline thereafter. The latter part of that pattern suggests higher extinction rates for lissamphibians across the K-Pg boundary compared to previous estimates,

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which we attribute to our coarser temporal binning, taxonomic additions and changes to some earlier taxonomic identifications. Although the overall richness pattern may at least partially reflect a true signal, it is heavily influenced by factors such as taphonomy, temporal gaps, fossil sampling and publication biases towards particular intervals and taxonomic groups; more detailed studies of all major lissamphibian clades are needed to corroborate these findings. This review highlights the strengths and weaknesses of the Mesozoic and Palaeocene portion of the North American lissamphibian record and provides a framework for future work.

Keywords Albanerpetontidae · Anura · Caudata · Gymnophiona · Mesozoic · North America · Palaeocene · Species richness curve

Introduction

Lissamphibia are a long-lived (Early Triassic to Recent) tetrapod clade that includes Salientia or frogs (Early Triassic–Recent), Caudata or salamanders (Middle Jurassic–Recent), Gymnophiona or caecilians (Early Jurassic–Recent) and the extinct, superficially salamander-like Albanerpetontidae (Middle Jurassic–late Pliocene). Extant lissamphibians have a near global distribution and consist of about 7,045 named species distributed among some 75 families (Frost 2013). Excluding introduced species, the North American continent (i.e. Canada, USA and Mexico) is home to about 8.3% of the known diversity of extant lissamphibians. The extant North American lissamphibian fauna is overwhelmingly dominated by an almost equal number of anurans (i.e. crown frogs: 294 species in 10 families) and urodeles (i.e. crown salamanders: 286 species in 9 families), plus at the southern end of Mexico a minor (2 species in 1 family) complement of apodans (i.e. crown caecilians) (AmphibiaWeb 2013). The North American lissamphibian fossil record extends back to at least the Early Jurassic, includes representatives of all four lissamphibian clades and adds about another 100 named species and a half dozen families to the continental inventory (e.g. Gardner and Böhme 2008; Holman 2003, 2006). The North American fossil record also is notable for having produced some morphologically and phylogenetically significant specimens (e.g. the stem caecilian *Eocaecilia* and the oldest known crown frog *Prosalirus*, both from the Early Jurassic of Arizona, USA) and for containing the most stratigraphically continuous late Early Cretaceous to Palaeocene record for lissamphibians anywhere in the world. This temporally extensive and taxonomically diverse fossil record is important for interpreting the evolutionary history of lissamphibians, both within North America and globally.

The Mesozoic and earliest Cenozoic (Palaeocene) portions of the North American lissamphibian record are particularly interesting because these document (1) the origins, radiations

and extinctions of groups prior to the establishment of the more modern aspect lissamphibian fauna on the continent and (2) the initial phases of this modernisation, which began in the latest Cretaceous and continued into the Neogene. The first report of pre-Eocene lissamphibians in North America dates back to Cope's (1876) description of five fossil salamander species (only one of which is currently recognised) from the Late Cretaceous (Campanian) of Montana, USA. Since then, numerous additional Mesozoic and Palaeocene lissamphibian localities, fossils (e.g. Figs. 1, 2) and taxa have been discovered in North America (e.g. Estes 1981; Gardner and Böhme 2008; Holman 2003, 2006; Roček et al. 2010). Although many of those discoveries have been reported, the literature is scattered and the quality of the accounts varies. Other discoveries have yet to be published. In an attempt to consolidate these records and to provide a springboard for future research, here we present the first comprehensive review of the North American Mesozoic and Palaeocene lissamphibian record. Based on occurrence data presented here, we also construct the first Mesozoic and Palaeocene species richness curve for Lissamphibia in North America.

Methodology and conventions

Introductory remarks

Our review of the North American Mesozoic and Palaeocene lissamphibian record is founded on a combination of published reports and unpublished occurrences known to us. While we were diligent in our review of the literature, it is almost certain that we have overlooked some relevant accounts, especially those in more obscure publications, such as graduate theses and dissertations, conference abstract volumes, fieldtrip guide books and less readily available regional or in-house scientific journals. We also have intentionally excluded a small number of unpublished and recently discovered localities that are known to contain lissamphibian fossils, either because the material has not yet been prepared or studied in adequate detail or because the localities are being studied by other colleagues. None of those excluded localities occurs in regions or intervals that are poorly sampled, meaning their exclusion likely will not significantly compromise our findings. Finally, we note that there undoubtedly are fossils unknown to us residing in institutional collections that document additional occurrences. Despite the limitations of our data gathering, our review is the most comprehensive to date for Mesozoic and Palaeocene lissamphibians from North America.

The format and organisation of our review is based on those presented by Clemens et al. (1979) and Kielan-Jaworowska et al. (2004) in their respective reviews of global occurrences of Mesozoic mammals. As in those publications, here we review the lissamphibian record chronologically by

major time intervals (occurrences within each interval are grouped by some combination of age, formation and localities) and provide faunal lists and locality maps for each interval. Our presentation is enhanced by three additional attributes. First, our locality maps are augmented by time scales showing the approximate temporal occurrences of localities—this pairing of maps and time scales serves to visually summarise both the geographic and temporal distributions of localities, and it also highlights both clusters and gaps in those distributions (Figs. 3, 4, 5, 6, 7, 8, 9, and10). Second, we indicate relative levels of confidence for taxonomic identifications by using notations in the faunal lists (Tables 1, 2, 3, 4, 5, 6, 7, 8, and 9) contained in the print version of our paper, by providing more detailed explanations for our taxonomic decisions and by listing voucher specimens in the corresponding Appendices 1–9 within the on-line Electronic Supplementary Material (ESM) that accompanies our paper. Third, as an aid to cross-referencing among corresponding faunal lists, figures and appendices within each section, we use the same Arabic number to denote each occurrence; for example, in the Triassic and Jurassic section, Arabic number "1" always denotes the Tomahawk locality (see, for example, Fig. 3; Table 1; ESM Appendix 1).

Temporal, geographic and stratigraphic context of localities

For our temporal framework, we follow the geological time scale and absolute age estimates of Walker and Geissmann (2009), rather than the newer version of Walker et al. (2013) because the age estimates of Walker and Geissmann (2009) are more compatible with other studies and papers used for our review. Where appropriate, we also use North American Land Mammal Ages (NALMAs), following recent treatments and age estimates by Cifelli et al. (2004) and Kielan-Jaworowska et al. (2004) for the latest Cretaceous (late Santonian–latest Maastrichtian) and by Lofgren et al. (2004) for the Palaeocene. Because Late Cretaceous and Palaeocene NALMAs are based on age-diagnostic, mammalian taxa from non-marine deposits in the North American Western Interior, they have the advantage of providing a regional basis for establishing the relative ages of those deposits. NALMAs are independent of—but can be correlated with (e.g. Figs. 5, 6, 7, 8, 9, and 10)—European marine stages and epochs. NALMAs are especially relevant to our review because many (but not all) of the latest Cretaceous and Palaeocene lissamphibian-bearing formations reported here can be assigned to a NALMA. In those formations, fossils of age-diagnostic mammalian taxa often co-occur in the same locality(ies) with lissamphibian fossils. Although the Cenozoic NALMAs form a relatively continuous sequence, it is important to emphasise that the latest Cretaceous NALMAs are separated by temporal gaps of varying lengths (on the order of several millions of years) that correspond to intervals of restricted terrigenous deposition in the Western

Interior. Radiometric dates provide another basis for geological age determinations and can be used to calibrate NALMAs; however, such dates are available for only a fraction of the localities and geological formations included in our report.

As is typical for much of the Mesozoic and Palaeocene record of small-bodied, non-marine vertebrates in North America, lissamphibian occurrences on the continent are geographically and temporally discontinuous. Geographically, much of the lissamphibian record is concentrated in the Western Interior, which for the purpose of this paper is loosely defined as the region extending from the foothills of the Rocky Mountains eastwards into the Great Plains, from Canada southwards through the USA and into northern Mexico. Here a thick, clastic wedge of terrestrial and freshwater sediments, mostly derived from the then-emerging Rocky Mountains and carried eastward by rivers across a broad alluvial plain, provided appropriate palaeoenvironments and depositional conditions for preserving non-marine vertebrates. Within that region and interval, lissamphibians have been reported from 55 geological formations that collectively encompass the Early Jurassic (Sinemurian–Pliensbachian), the Late Jurassic (Kimmeridgian–earliest Tithonian), the basal Cretaceous (late Berriasian–Valanginian) and a nearly continuous sequence from the Aptian through to the terminal Palaeocene (Figs. 3, 4, 5, 6, 7, 8, 9, 10, and 11). The pre-Santonian portion of this record is limited to the USA, whereas the Santonian through to the late (but not latest) Palaeocene portion also extends into two provinces in western Canada, specifically the central and southern portions of Alberta and the southern portion of Saskatchewan. Farther south, there is one Campanian age occurrence in northern Mexico (Fig. 7). Outside of the Western Interior, lissamphibian occurrences are restricted to three or four Cretaceous formations: one each in the Campanian of Baja California, New Jersey and North Carolina, and also possibly in the early Aptian of Virginia (Figs. 4, 7). Putative lissamphibians of Late Triassic age have also been reported from two formations in the eastern USA: the first in the middle Carnian of Virginia and the second in the early Norian of North Carolina (Fig. 3).

Of the 61 formations included in our review, about one-third contains just one known or purported lissamphibian-bearing locality. Depending on how many localities are known for each formation and how broadly spaced they are geographically or stratigraphically, we may deal with those as a series of isolated localities, as groups of localities or as some combination of these two approaches. Typically, geographically dispersed localities within the same formation are grouped first by geographical area (e.g. basin or valley) and then by state or province. From a stratigraphic perspective, we are generally interested in occurrences only at the formational level. In some cases, however, it is appropriate or informative to consider the stratigraphic positions of localities within formations. Examples of such situations include: (1) formations that are

Fig. 1 Representative specimens and taxa of Gymnophiona from the Early Jurassic and Caudata from the Late Jurassic to Palaeocene of western North America. Specimens are generally arranged from oldest to youngest, are depicted at different magnifications (unless indicated otherwise, corresponding *scale bars* are 1 mm), and except where noted are referred specimens. **a** Gymnophiona. *Eocaecilia micropodia* Jenkins and Walsh, 1993 (Gymnophiona); nearly complete atlas (MCZ 9231) in oblique left lateral, anterior, and dorsal view; from Gold Spring Quarry 1, Coconino County, northeastern Arizona, USA; "silty facies" of the Kayenta Formation; Sinemurian–Pliensbachian. **b**–**y** Caudata. **b** Urodela gen. et sp. indet (family incertae sedis); incomplete trunk vertebra (OMNH 67097) in oblique right lateral, anterior and dorsal view; from OMNH loc. V1243, Fall River County, southwestern South Dakota, USA; Chilson Member, lower part of Lakota Formation; late Berriasian–Valanginian. **c** Caudata gen. et sp. nov. (family incertae sedis); undescribed incomplete skeletons, detail of part of composite block (DINO 14711C, 14713, 14714, and 14715) showing partially associated skulls (arrows), articulated strings of vertebrae, and disassociated bones belonging to several individuals; from Rainbow Park, Dinosaur National Monument, Uintah County, northeastern Utah, USA; Morrison Formation; Kimmeridgian–earliest Tithonian. **d** Caudata gen. et sp. indet. (family incertae sedis); three incomplete atlantal centra (bulk catalogued as OMNH 23259) in ventral (*left*) and dorsal (*centre and right*) views, and all with anterior towards *top* of page; from OMNH loc. V62, Horn County, north-central Wyoming; Unit V of Ostrom (1970), Cloverly Formation; Aptian–Albian. **e** *Prosiren elinorae* Goin and Auffenberg, 1958 (Prosirenidae); incomplete holotype trunk vertebra (FMNH PR391) in left lateral view; from Greenwood Canyon, Montague County, north-central Texas, USA; Antlers Formation; early–middle Albian. **f**, Urodela gen. et sp. nov. (family incertae sedis); nearly complete trunk vertebra (UMNH 13431) in oblique left lateral and dorsal view; from UMNH loc. VP 129 (= MNA 995), Kaiparowits Plateau, south-central, Utah, USA; Smoky Hollow Member, Straight Cliffs Formation; late Turonian. **g** *Habrosaurus* sp. (Sirenidae); nearly complete trunk vertebra (UW 39442) in dorsal view and with anterior towards *right*; from UW loc. V-81006, Natrona County, central Wyoming, USA; Mesaverde Formation; middle Campanian (Judithian NALMA). **h** *Habrosaurus dilatus* Gilmore, 1928b (Sirenidae); incomplete right dentary (UWBM 94118) in lingual view; from UWBM loc. C1103, Garfield County, northeastern Montana, USA; Hell Creek Formation; late Maastrichtian (Lancian NALMA). **i** *Proamphiuma cretacea* Estes, 1969c (Amphiumidae); nearly complete trunk vertebra (PTRM 16473) in oblique left lateral and dorsal view; from PTRM loc. V86002, Slope County, southwestern North Dakota, USA; Hell Creek Formation; late Maastrichtian (Lancian NALMA). **j** *Paranecturus garbanii* DeMar, 2013 (Proteidae); holotype atlas lacking dorsal part of neural arch (UWBM 93370) in anterior view; from UWBM loc. C1153, Garfield County, northeastern Montana, USA; Hell Creek Formation; late Maastrichtian (Lancian NALMA). **k** *Paranecturus garbanii* DeMar, 2013 (Proteidae); nearly complete trunk vertebra (UWBM 94999) in oblique right lateral and anterior view; from UWBM loc. C1153, Garfield County, northeastern Montana, USA; Hell Creek Formation; late Maastrichtian (Lancian NALMA). **l** *Scapherpeton tectum* Cope, 1876 (Scapherpetontidae); nearly complete atlas (UALVP 40104) in anterior view; from Bug Creek Anthills, McCone County, northeastern Montana, USA; Hell Creek Formation; latest Cretaceous (Lancian NALMA) or earliest Palaeocene (Puercan NALMA). **m** *Scapherpeton tectum* Cope, 1876

(Scapherpetontidae); nearly complete trunk vertebra (UALVP 40108) in left lateral view; from Bushy Tailed Blowout (= UCMP loc. V5711), Niobrara County, east-central Wyoming, USA; Lance Formation; late Maastrichtian (Lancian NALMA). **n** *Lisserpeton bairdi* Estes, 1965 (Scapherpetontidae); nearly complete atlas (UALVP 40134) in anterior view; from Bug Creek Anthills, McCone County, northeastern Montana, USA; Hell Creek Formation; latest Cretaceous (Lancian NALMA) or earliest Palaeocene (Puercan NALMA). **o** *Lisserpeton bairdi* Estes, 1965 (Scapherpetontidae); nearly complete trunk vertebra (UALVP 14893) in left lateral view; from Bug Creek Anthills, McCone County, northeastern Montana, USA; Hell Creek Formation; latest Cretaceous (Lancian NALMA) or earliest Palaeocene (Puercan NALMA). **p** *Opisthotriton kayi* Auffenberg, 1961 (Batrachosauroididae); nearly complete atlas (UALVP 40061) in anterior view; from Bug Creek Anthills, McCone County, northeastern Montana, USA; Hell Creek Formation; latest Cretaceous (Lancian NALMA) or earliest Palaeocene (Puercan NALMA). **q** *Opisthotriton kayi* Auffenberg, 1961 (Batrachosauroididae); nearly complete trunk vertebra (UALVP 40071) in right lateral view; from Bushy Tailed Blowout (= UCMP loc. V5711), Niobrara County, east-central Wyoming, USA; Lance Formation; late Maastrichtian (Lancian NALMA). **r** *Prodesmodon copei* Estes, 1964 (Batrachosauroididae); nearly complete atlas (UALVP 40075) in anterior view; from Bushy Tailed Blowout (= UCMP loc. V5711), Niobrara County, east-central Wyoming, USA; Lance Formation; late Maastrichtian (Lancian NALMA). **s** *Prodesmodon copei* Estes, 1964 (Batrachosauroididae); nearly complete trunk vertebra (UCM 43328) in right lateral view; from Bug Creek Anthills, McCone County, northeastern Montana, USA; Hell Creek Formation; latest Cretaceous (Lancian NALMA) or earliest Palaeocene (Puercan NALMA). **t** *Opisthotriton kayi* Auffenberg, 1961 (Batrachosauroididae); undescribed nearly complete skeleton (UALVP 16274) in dorsal view and with anterior towards *upper left*; from UALVP Genesee #2 locality, central Alberta, Canada; upper part of Scollard Formation; early Palaeocene (Puercan NALMA). **u** *Proamphiuma cretacea* Estes, 1969c (Amphiumidae); trunk vertebra missing anterior portion of neural arch roof and prezygapophyses (UCMP 192523) in left lateral view; from UCMP loc. V74122, Garfield County, northeastern Montana, USA; Tullock Formation; early Palaeocene (Puercan NALMA). **v** *Piceoerpeton willwoodense* (Meszoely, 1967) (Scapherpetontidae); trunk vertebra (SMM P76.28.238) in oblique right lateral and anterior view; from Wannagan Creek Quarry, Billings County, southwestern North Dakota, USA; Tongue River (= Bullion Creek) Formation; late Palaeocene (Tiffanian NALMA). **w** *Necturus krausei* Naylor, 1978b (Proteidae); holotype trunk vertebra missing anterior portion of neural arch roof and prezygapophyses (UALVP 14310) in oblique right lateral and dorsal view; from UALVP Roche Percée loc. UAR 2 g, southeastern Saskatchewan, Canada; upper part of Ravenscrag Formation; late Palaeocene (Tiffanian NALMA). **x** *Cryptobranchus saskatchewanensis* Naylor, 1981b (Cryptobranchidae); holotype, symphyseal end of left dentary (UALVP 14858) in lingual view; from UALVP Roche Percée loc. UAR 2, southeastern Saskatchewan, Canada; upper part of Ravenscrag Formation; late Palaeocene (Tiffanian NALMA). **y** *Dicamptodon antiquus* Naylor and Fox, 1993 (Dicamptodontidae); holotype incomplete skeleton (UALVP 32387) in ventral view and with anterior towards *top* of page; from UALVP Smoky Tower #1 locality, west-central Alberta, Canada; Paskapoo Formation; late Palaeocene (Tiffanian NALMA)

traversed by major temporal boundaries (e.g. the latest Cretaceous and early Palaeocene age Scollard Formation, Alberta); (2) thick formations that are subdivided into smaller, more age-constrained members or other units (e.g. the Coniacian–Santonian age Straight Cliffs Formation, Utah);

(3) localities whose relative stratigraphic positions and ages have been reliably established biostratigraphically, radiometrically or through other means. In contrast to the final example, it is worth noting that the stratigraphic positions and ages of some localities and formations are poorly constrained.
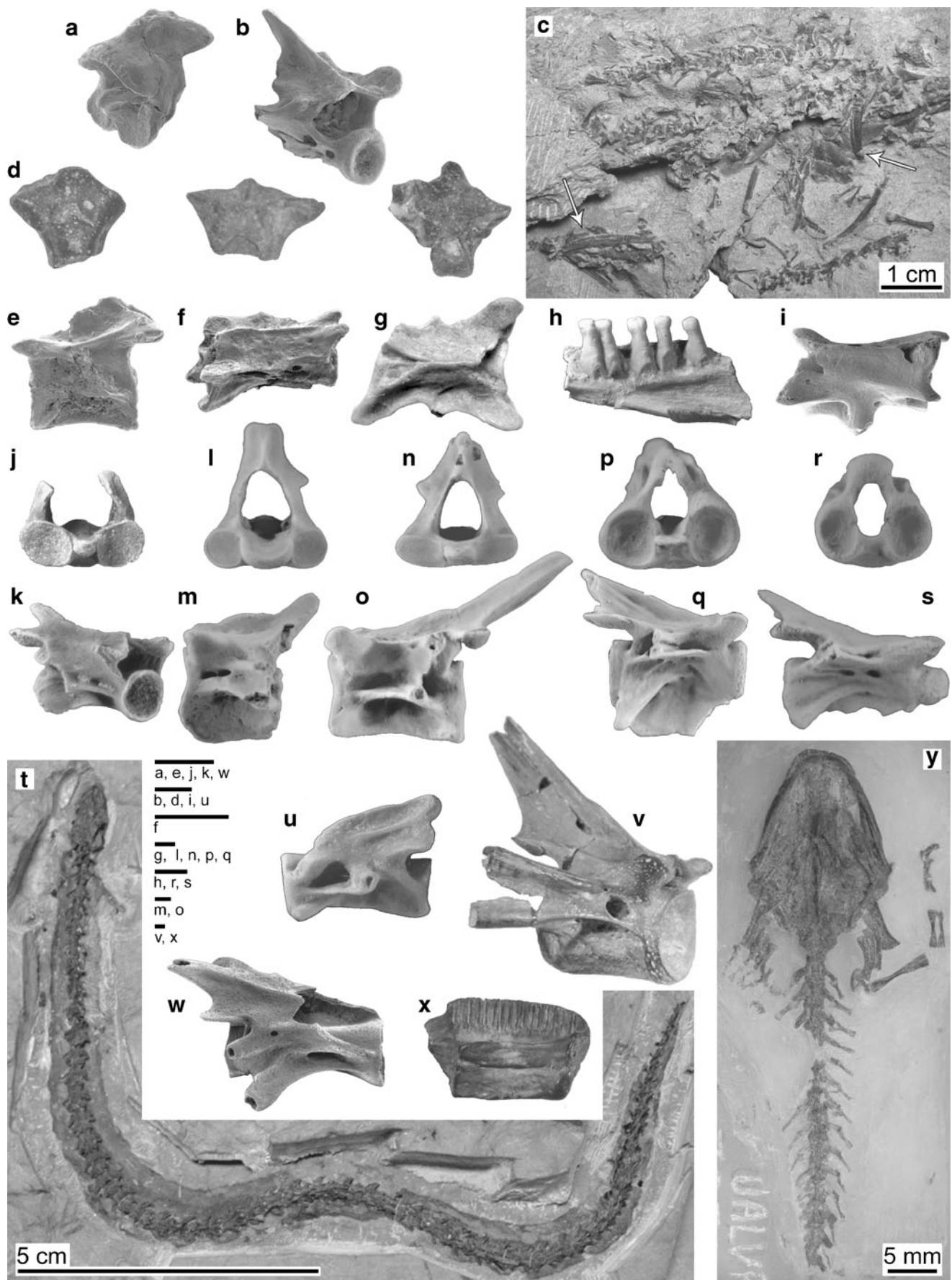
Fig. 2 Representative specimens and taxa of Allocaudata and Anura from the Cretaceous and Palaeocene of western North America. Specimens are arranged from oldest to youngest, are depicted at different magnifications (unless indicated otherwise, corresponding *scale bars* are 1 mm), and except where noted are referred specimens. **a**–**g** Allocaudata. **a** Albanerpetontidae gen. et. sp. indet.; atlantal centrum (UMNH VP 12935) in dorsal view and with anterior towards *top* of page; from UMNH loc. VP 162, Markagunt Plateau, southeastern Utah, USA; unnamed middle member, Dakota Formation; middle? Cenomanian. **b** cf. *Albanerpeton nexuosum* (Albanerpetontidae); fused premaxillae (UMNH VP 14459) in labial (*left*) and lingual (*right*) views; from UMNH loc. VP 424, Paunsaugunt Plateau, southeastern Utah, USA; upper part of John Henry Member, Straight Cliffs Formation; late Santonian (Aquilan NALMA). **c** *Albanerpeton nexuosum* (Estes, 1981) (Albanerpetontidae); fused premaxillae (UALVP 16206) in labial (*left*) and lingual (*right*) views; from UALVP loc. MR-20, Verdigris Coulee, south-central Alberta, Canada; Deadhorse Coulee Member, Milk River Formation; late Santonian (Aquilan NALMA). **d** *Albanerpeton galaktion* Fox and Naylor, 1982 (Albanerpetontidae); holotype, nearly complete left premaxilla (UALVP 16203) in labial (*left*) and lingual (*right*) views; from UALVP loc. MR-6, Verdigris Coulee, south-central Alberta, Canada; Deadhorse Coulee Member, Milk River Formation; late Santonian (Aquilan NALMA). **e** *Albanerpeton gracile* (Gardner, 2000a) (Albanerpetontidae); nearly complete left maxilla (TMP 95.157.73) in lingual view; from TMP loc. L1108, Dinosaur Provincial Park, southeastern Alberta, Canada; Dinosaur Park Formation; middle Campanian (Judithian NALMA). **f** *Albanerpeton gracile* (Gardner, 2000a) (Albanerpetontidae); anterior part of left dentary (TMP 96.78.103) in lingual view; from TMP loc. L1127, Milk River Valley, southeastern Alberta, Canada; Oldman Formation; middle Campanian (Judithian NALMA). **g** *Albanerpeton gracile* (Gardner, 2000a) (Albanerpetontidae); fused and nearly complete frontals (TMP 86.194.8) in dorsal (*left*) and ventral (*right*) views, both with anterior towards *top* of page; from TMP loc. L0410, Dinosaur Provincial Park, southeastern Alberta, Canada; Dinosaur Park Formation; middle Campanian (Judithian NALMA). **h**–**v** Anura. **h** Anura gen. et. sp. indet. (family incertae sedis); incomplete left maxilla (OMNH 32336) in labial (*upper*) and lingual (*lower*) views; from McLeod Honor Farm (= OMNH loc. V706), Atoka County, southeastern Oklahoma, USA; Antlers Formation; late Aptian–early Albian. **i** Anura gen. et sp. indet (family incertae sedis); nearly complete right maxilla (OMNH 27374) in labial (*upper*) and lingual (*lower*) views; from OMNH loc. V695, Emery County, central Utah, USA; Mussentuchit Member, Cedar Mountain Formation; latest Albian–earliest Cenomanian. **j**, Anura gen. et sp. indet (family incertae sedis); incomplete right maxilla (OMNH 28434) in labial (upper) and lingual (lower) views; from OMNH loc. V695, Emery County, central Utah, USA; Mussentuchit Member, Cedar Mountain Formation; latest Albian–earliest Cenomanian. **k** Anura gen. et sp. nov. 2 (family incertae sedis); nearly complete right maxilla (UALVP 40167) in labial (upper) and lingual (lower) views; from UALVP Irvine vertebrate microfossil locality, southeastern Alberta, Canada; upper part of Dinosaur Park Formation; late Campanian (Judithian NALMA). **l** Anura gen. et sp. nov. 3 (family incertae sedis); incomplete right maxilla (TMP 1985.66.35) in labial (*upper*) and lingual (*lower*) views; from TMP loc. BB 98, Dinosaur Provincial Park, southeastern Alberta, Canada; Dinosaur Park Formation; late Campanian (Judithian NALMA). **m** Anura gen. et. sp. indet. (family incertae sedis); incomplete left maxilla (UALVP 40192) in labial (*upper*) and lingual (*lower*) views; from UALVP Irvine vertebrate microfossil locality, southeastern Alberta, Canada; upper part of Dinosaur Park Formation; late Campanian (Judithian NALMA). **n** Anura gen. et sp. indet. (family incertae sedis); incomplete right maxilla (OMNH 67095) in labial (*upper*) and lingual (*lower*) views; from OMNH loc. V6, Kaiparowits Plateau, south-central Utah, USA; Kaiparowits Formation; late Campanian (Judithian NALMA). **o** *Scotiophryne pustulosa* Estes, 1969b (family incertae sedis); incomplete right maxilla (OMNH 67093) in labial (*upper*) and lingual (*lower*) views; from OMNH loc. V9, Kaiparowits Plateau, south-central Utah, USA; Kaiparowits Formation; late Campanian (Judithian NALMA). **p** cf. *Eopelobates* sp. (family incertae sedis); incomplete right maxilla (OMNH 23837) in labial (*upper*) and lingual (*lower*) views; from OMNH loc. V5, Kaiparowits Plateau, south-central Utah, USA; Kaiparowits Formation; late Campanian (Judithian NALMA). **q** Anura gen. et sp. nov. 1 (family incertae sedis); undescribed skeleton (MOR 938) in dorsal view and with anterior towards *top* of page; from MOR loc. TM-088, Glacier County, north-central Montana, USA; Two Medicine Formation; late Campanian (Judithian NALMA). **r** *Theatonius* sp. nov. (family incertae sedis); nearly complete left maxilla (OMNH 67082) in labial (*upper*) and lingual (*lower*) views; from OMNH loc. V6, Kaiparowits Plateau, south-central Utah, USA; Kaiparowits Formation; late Campanian (Judithian NALMA). **s** *Palaeobatrachus? occidentalis* (Estes and Sanchíz, 1982) (Palaeobatrachidae); right ilium (UCMP 55705) in lateral view; from Bushy Tailed Blowout (= UCMP loc. V5711), Niobrara County, east-central Wyoming, USA; Lance Formation; late Maastrichtian (Lancian NALMA). **t** *Paradiscoglossus americanus* Estes and Sanchíz, 1982 (family incertae sedis); holotype left ilium (UCMP 125827) in lateral view; from Bushy Tailed Blowout (= UCMP loc. V5711), Niobrara County, east-central Wyoming, USA; Lance Formation; late Maastrichtian (Lancian NALMA). **u** Anura gen. et sp. indet. (family incertae sedis); sacrum (UCMP 557556) in anterior (*upper left*), posterior (*upper right*), and ventral (*lower centre*) views; from UCMP loc. V74122, Garfield County, northeastern Montana, USA; Tullock Formation; early Palaeocene (Puercan NALMA). **v** Anura gen. et sp. indet. (family incertae sedis); left ilium (UALVP 40219) in lateral view; from UALVP Roche Percée loc. UAR 2 g , southeastern Saskatchewan, Canada; upper part of Ravenscrag Formation; late Palaeocene (Tiffanian NALMA)

For example, the age of the Cloverly Formation of Montana and Wyoming can be resolved only to Aptian–Albian, which is a substantial interval of about 25 million years in duration.

Nature of the fossil record

In addition to being geographically and temporally discontinuous, the North America Mesozoic and Palaeocene lissamphibian record is heavily biased in terms of the kinds of fossils that are available, as well as the taxa and palaeoenvironments represented by those fossils. Most of the available specimens are isolated, three-dimensionally preserved bones.

About 95% of the occurrences documented here consist exclusively of isolated bones and about four-fifths (25 of 31) of the formally named, body fossil-based species recognised in our review have an isolated bone as their holotype.

The primary source for isolated lissamphibian bones is vertebrate microfossil localities, which are accumulations of small-sized (i.e. ≤50 mm) bones, teeth and scales (sensu Eberth 1990; Rogers and Brady 2010) that typically occur in terrigenous sediments deposited in fluvial and associated (e.g. overbank, crevasse splay, floodplain, swamp and oxbow lake) lowland palaeoenvironments. Vertebrate microfossil localities may have complex taphonomic histories involving
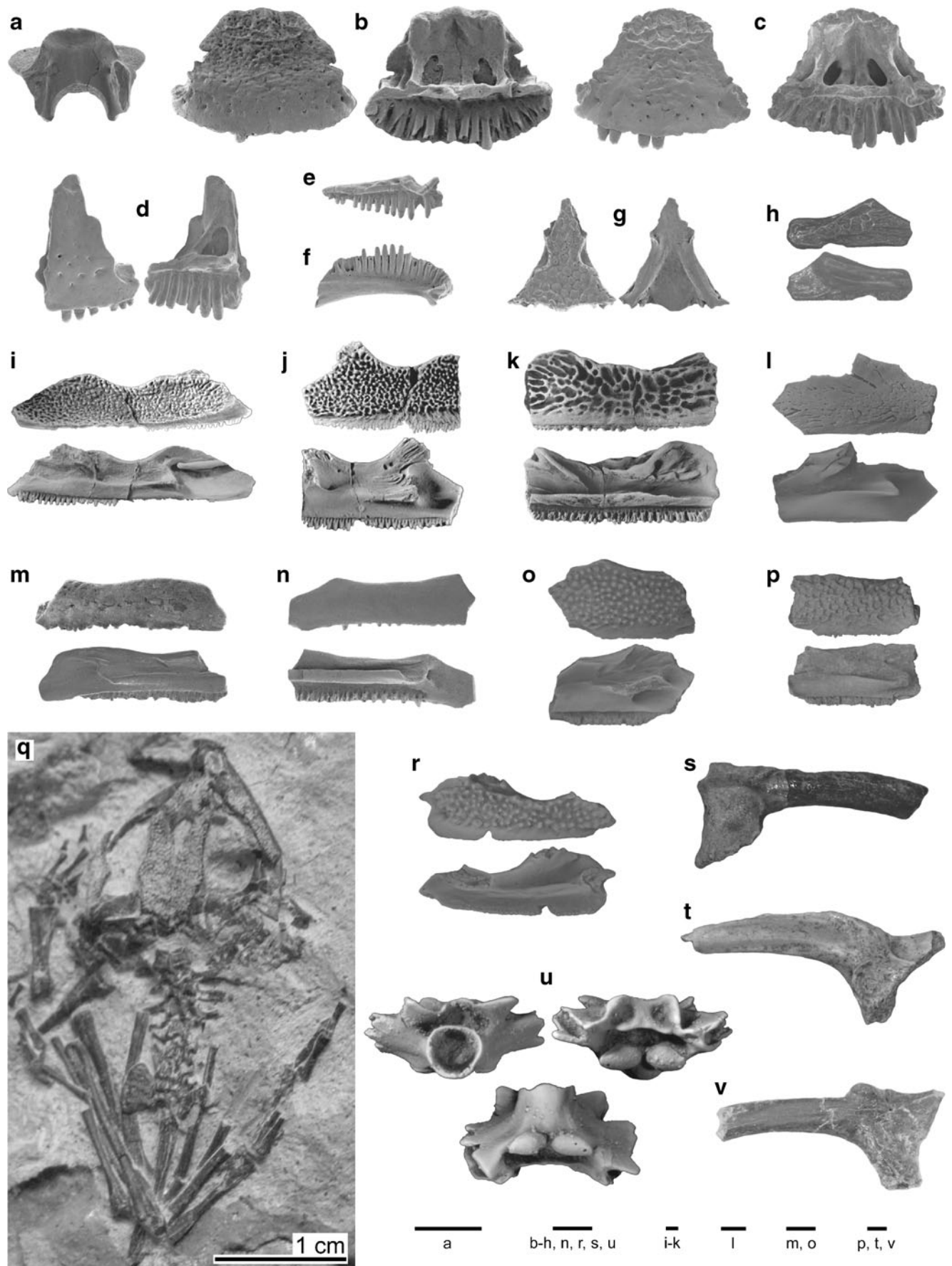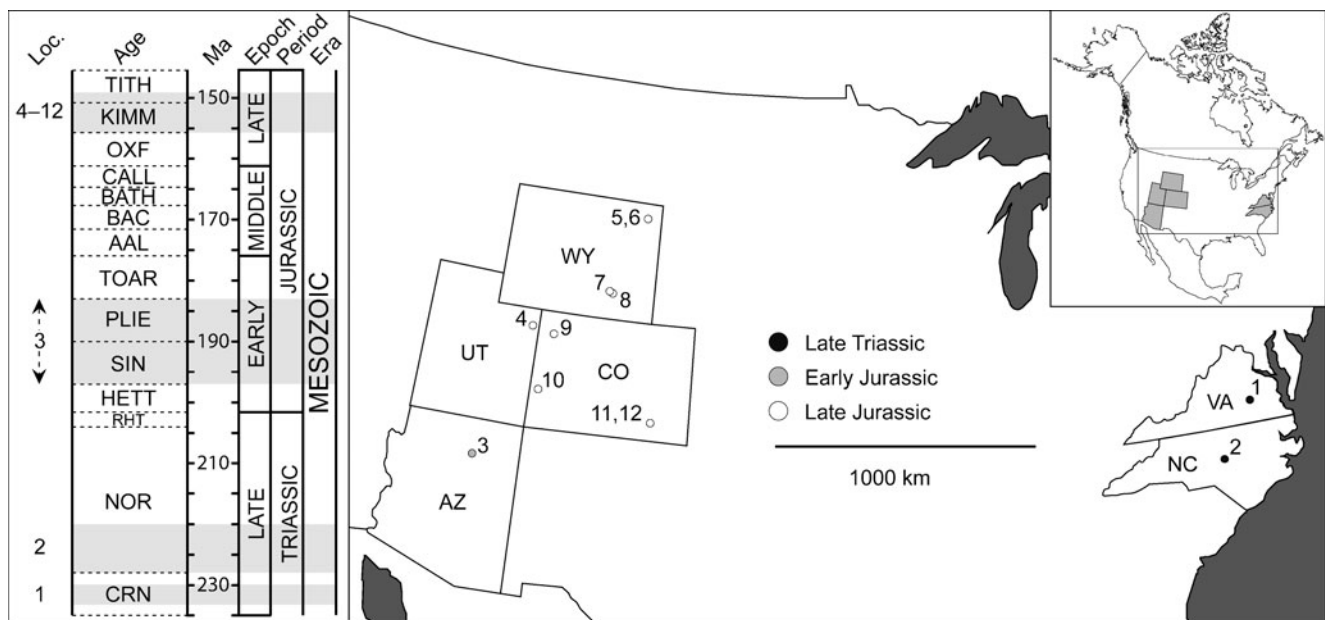
Fig. 3 Temporal and geographical distributions of Triassic and Jurassic lissamphibian localities in North America. Localities are denoted by the same *numbers* used in the corresponding faunal list (Table 1) and ESM Appendix 1, and are listed in approximate chronological sequence and, where appropriate, grouped by state. Time scale (*left side*): fossiliferous intervals depicted in this figure are *shaded*; localities are placed in their approximate temporal positions; *dashed arrows* indicate poorly constrained age range for locality 3; absolute ages and boundaries follow Walker and Geissman (2009). Positions of localities on the main map are approximate. *Inset map* (*upper right*) shows portion of North American continent depicted in the main map. See text for abbreviations used in figure. *Numbers 1–12* designate localities. *1* Tomahawk locality, Richmond Basin, Chesterfield County, east-central Virginia, USA; Vinita Formation (formerly Turkey Branch Formation), Newark Supergroup; middle Carnian. *2* Moncure locality, Deep River Basin (Sanford sub-basin), Chatham County, central North Carolina, USA; Cumnock Formation, Newark Supergroup; early Norian. *3* Gold Spring Quarry 1, Coconino County, northeastern Arizona, USA; "silty facies" of the Kayenta Formation; Sinemurian–Pliensbachian. *4* Rainbow Park, Dinosaur National Monument, Uintah County, northeastern Utah, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian. *5* Little Houston Quarry, Crook County, northeastern Wyoming, USA; lower middle part of Morrison Formation; Kimmeridgian–earliest Tithonian. *6* Mile 175, Crook County, northeastern Wyoming, USA; uncertain member within Morrison Formation; Kimmeridgian–earliest Tithonian. *7* Ninemile Hill, Carbon County, east-central Wyoming, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian. *8* Quarry 9, Como Bluff, Albany County, southeastern Wyoming, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian. *9* Wolf Creek Quarry, Moffat County, northwestern Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian. *10* Fruita Paleontological area, Mesa County, west-central Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian. *11* Garden Park, El Paso County, southeastern Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian. *12* Small Quarry, El Paso County, southeastern Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian

some combination of transport, sorting, re-working, time-averaging and pre- and post-depositional damage to specimens (e.g. Eberth 1990; Rogers and Brady 2010). Fossils are recovered from these localities by surface collecting, screen-washing or both. The process of recovering fossils by bulk sampling fossiliferous rock and then screenwashing (for details about those techniques, see Cifelli et al. 1996; Eaton 2004; McKenna 1962) may result in additional damage to specimens. Even so, vertebrate microfossil localities can be richly fossiliferous, with the best ones yielding a diversity of taxa and anatomically well-preserved elements. Identifying and trying to associate elements from different parts of a skeleton (e.g. tooth-bearing bones, skull roof bones, vertebrae and girdle and limb bones) can be a challenging task, especially when dealing with samples that may contain several osteologically similar taxa and, as is the case for many small-bodied taxa, without the benefit of having articulated material to show the correct associations of elements. Intraspecific variation (e.g. ontogenetic, individual and sexual), as well as temporal and geographic variation, can further complicate matters. Given these kinds of potential problems, there is a real danger of creating an artificial chimera by incorrectly associating bones from different taxa. Various lines of evidence can be used to associate isolated elements; for example, elements share complementary structures (e.g. similar teeth), are from comparably sized individuals, occur in similar relative abundances, consistently co-occur in multiple localities or have similar stratigraphic distributions. The ultimate test for evaluating hypothesised associations of isolated elements is to find an associated or articulated skeleton.

A lesser number of isolated bones, along with some associated bones and skeletons, have been recovered by
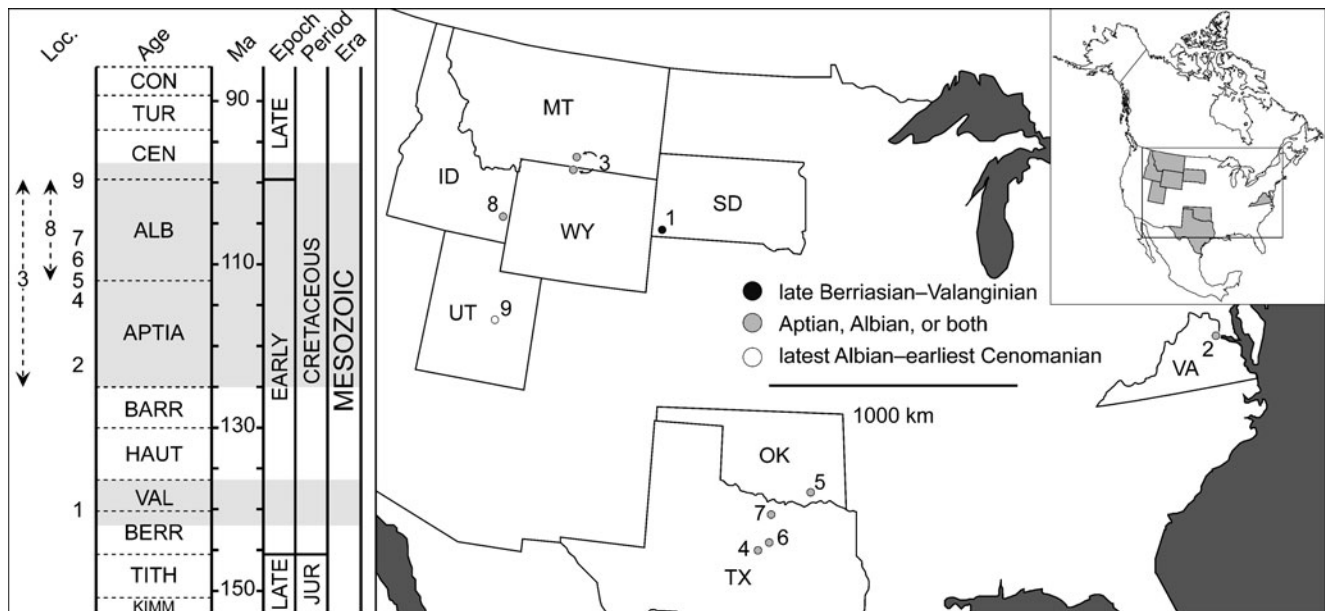
Fig. 4 Temporal and geographical distributions of Early Cretaceous lissamphibian localities in North America. Localities are denoted by the same *numbers* used in the corresponding faunal list (Table 2) and ESM Appendix 2, and are listed in approximate chronological sequence. Time scale (*left side*): fossiliferous intervals depicted in this figure are *shaded*; localities are placed in their approximate temporal positions; *dashed arrows* indicate poorly constrained age ranges for localities; absolute ages and boundaries follow Walker and Geissman (2009). Positions of localities on the main map are approximate. *Inset map* (*upper right*) shows portion of North American continent depicted in the main map. See text for abbreviations used in figure. *Numbers 1–9* designate localities. *1* OMNH loc. V1243, Fall River County, southwestern South Dakota, USA; Chilson Member, lower part of Lakota Formation; late Berriasian–Valanginian. *2* Bachman locality, Stafford County, northeastern Virginia, USA; Patuxent facies, Potomac Formation; early Aptian. *3* Bighorn Basin localities in north-central Wyoming (OMNH loc. V62; USNM locs. 42138, 42146, 42175, 42222, 43420; and YPM loc. 63–19) and in south-central Montana (OMNH loc. V184), both USA; middle and upper parts (= Units V–VII of Ostrom 1970), Cloverly Formation; Aptian–Albian. *4* Paluxy Church, Hood County, central Texas, USA; upper part of Twin Mountains Formation; late Aptian. *5* McLeod Honor Farm (= OMNH loc. V706), Atoka County, southeastern Oklahoma, USA; middle part of Antlers Formation; late Aptian–early Albian. *6* Pecan Valley Estates and Huggins #1 and #2, all in Erath County, central Texas, USA; base of Paluxy Formation; early Albian. *7* Greenwood Canyon, Montague County, and Butler Farm, Wise County, both in north-central Texas, USA; upper part of Antlers Formation; early–middle Albian. *8* Tincup Creek, Caribou County, southeastern Idaho, USA; Wayan Formation; Albian. *9* Mussentuchit local fauna (e.g. OMNH locs. V235, V237, V239, V240, V695, and V801), Emery County, central Utah, USA; Mussentuchit Member, Cedar Mountain Formation; latest Albian–earliest Cenomanian

surface collecting and hand quarrying of generally finer-grained overbank, swamp, oxbow lake or lacustrine sediments. Articulated or associated skeletons from these kinds of localities in the Mesozoic and Palaeocene of North America are limited to the following: (1) an anuran and gymnophionan from Gold Spring Quarry 1 in the Lower Jurassic Kayenta Formation, Arizona; (2) anurans and caudates from Quarry 9 (Wyoming) and Rainbow Park (Utah) in the Upper Jurassic Morrison Formation; (3) an unnamed anuran from several localities that straddle the Early–Late Cretaceous boundary in the upper part of the Cedar Mountain Formation, Utah; (4) an unnamed anuran from an Upper Cretaceous (Campanian) locality in the Two Medicine Formation, Montana; (5) an indeterminate anuran from an Upper Cretaceous (Maastrichtian) locality in the North Horn Formation, Utah; (6) anurans from the Palaeocene and, perhaps, latest Maastrichtian and earliest Eocene portions of the Sheep Pass Formation, Nevada; (7) multiple urodele taxa from Palaeocene localities in the Coalspur, Paskapoo, and Scollard formations of Alberta, in the Fort Union and Lebo formations of Montana, in the Sentinel Butte and Tongue River formations of North Dakota and in the Fort Union Formation of Wyoming. Six of the 31 formally named, body fossil-based species documented here have an articulated or associated skeleton as their holotype. Although skeletal specimens of fossil gymnophionans, caudates and anurans are known from North America, the continent's albanerpetontid record remains limited to isolated bones.

Other kinds of body fossils and depositional systems that elsewhere have provided important information about lissamphibians are as yet unknown for the Mesozoic and Palaeocene of North America. For example, there are no examples of the following: (1) fissure fill deposits containing abundant isolated and articulated elements, like those that have produced lissamphibian bones in the Triassic of Poland (e.g. Borsuk-Białynicka et al. 1999) and the Neogene of France and Hungary (e.g. Estes and Hoffstetter 1976; Venczel and Gardner 2005); (2) exquisite preservation of soft tissues,
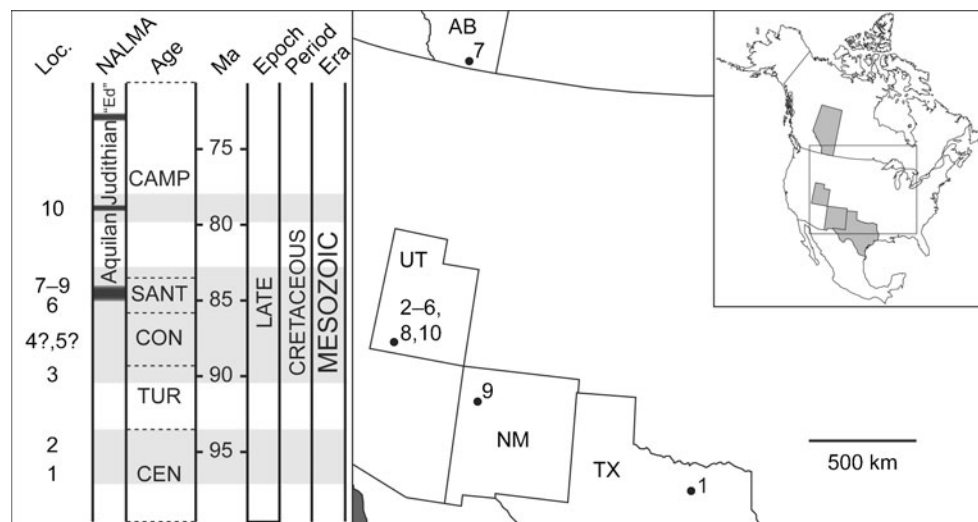
Fig. 5 Temporal and geographical distributions of Late Cretaceous (middle Cenomanian to early–middle Campanian) lissamphibian localities in North America. Localities are denoted by the same *numbers* used in the corresponding faunal list (Table 3) and ESM Appendix 3, and are listed in approximate chronological sequence. *Time scale (left side)*: fossiliferous intervals depicted in this figure are *shaded*; localities are placed in their approximate temporal positions (for a more detailed correlation of the Utah localities, see Roček et al. 2010, fig. 2); *question mark* following locality number indicates uncertain age; absolute ages and boundaries follow Walker and Geissman (2009); *thicker black horizontal lines in NALMA column* indicate uncertainties about placement of boundaries between NALMAs. Positions of localities on the main map are approximate. *Inset map (upper right)* shows portion of North American continent depicted in the main map. See text for abbreviations used in figure. *Numbers 1–10* designate localities. *1* Arlington Archosaur Site and unspecified localities, between Fort Worth and Dallas, north-central Texas; Woodbine Formation; middle Cenomanian. *2* Localities on Markagunt, Paunsaugunt, and Kaiparowits plateaus, southwestern and south-central Utah, USA; unnamed middle member, Dakota Formation; middle? and late Cenomanian. *3* Localities

on Kaiparowits Plateau, south-central, Utah, USA; Smoky Hollow Member, Straight Cliffs Formation; late Turonian. *4* MNA loc. 1260, Markagunt Plateau, southwestern Utah, USA; undifferentiated Straight Cliffs Formation; ?Coniacian. *5* Localities on Paunsaugunt and Kaiparowits plateaus, south-central, Utah, USA; basal part of John Henry Member, Straight Cliffs Formation; ?Coniacian. *6* Localities on Paunsaugunt and Kaiparowits plateaus, south-central, Utah, USA; middle and upper parts of John Henry Member, Straight Cliffs Formation; early– late Santonian (Aquilan). *7* Multiple localities in Verdigris Coulee, south-central Alberta, Canada; Deadhorse Coulee Member, Milk River Formation; late Santonian (Aquilan). *8* MNA loc. 1230 (= UMNH VP 12) in Iron Springs Formation and UMNH loc. VP 10 in uncertain formation; both on Markagunt Plateau, southwestern Utah, USA, and ages uncertain, likely late Santonian or early Campanian. *9* NMMNH loc. L-5636, northwestern New Mexico, USA; Allison Member, Menefee Formation; late Santonian–early Campanian. *10* Localities on Paunsaugunt and Kaiparowits plateaus, south-central, Utah, USA; Wahweap Formation; early–middle Campanian (?intermediate between Aquilan and Judithian)

such as gill rakers and internal organs seen in some urodele body fossils preserved in volcanic ash rich lake deposits from the Late Jurassic–Early Cretaceous of China (e.g. Gao et al. 2013), and of delicate hard parts, such as tiny osteoderms in the skin of an albanerpetontid body fossil preserved in a lake deposit from the Early Cretaceous of Spain (McGowan and Evans 1995); (3) body fossils of larvae, like those known for urodeles from the Late Jurassic–Early Cretaceous of China (e.g. Gao et al. 2013) and for anurans from the Early Cretaceous of Israel (Estes et al. 1978) and the Oligo-Miocene of the Czech Republic (e.g. Špinar 1972).

The North American Mesozoic and Palaeocene record also includes a small number of putative lissamphibian tracks from the Aptian–Albian of Virginia, the Campanian of Utah, the latest Campanian of Alberta and the Palaeocene of Wyoming and Montana. One such specimen, a trackway from the Palaeocene of Montana, is the holotype for the urodele ichnotaxon *Ambystomichnus montanensis* (Gilmore 1928a). To our knowledge, there are no reports of other kinds of trace fossils, such as so-called "tadpole nests" (i.e.

shallow depression created by tadpoles while feeding in fine-grained sediments at the bottom of ponds or lakes; see review by Cameron and Estes 1971), in the North American Mesozoic or Palaeocene fossil record that can be attributed to lissamphibians.

Taxonomic identifications

We firmly believe that reliable taxonomic identifications are the foundation for virtually all areas of palaeontological study, yet in publications it is not uncommon for little or no information to be provided about what diagnostic features or what kinds of specimens were used to make taxonomic identifications. We recognise there may be reasons why unsupported identifications have and continue to be commonplace in the literature (e.g. limited page space in journals; time and effort required to adequately document specimens; detailed information on taxonomic identifications not considered important to a study's objectives), but that does not negate the point that without such supporting information
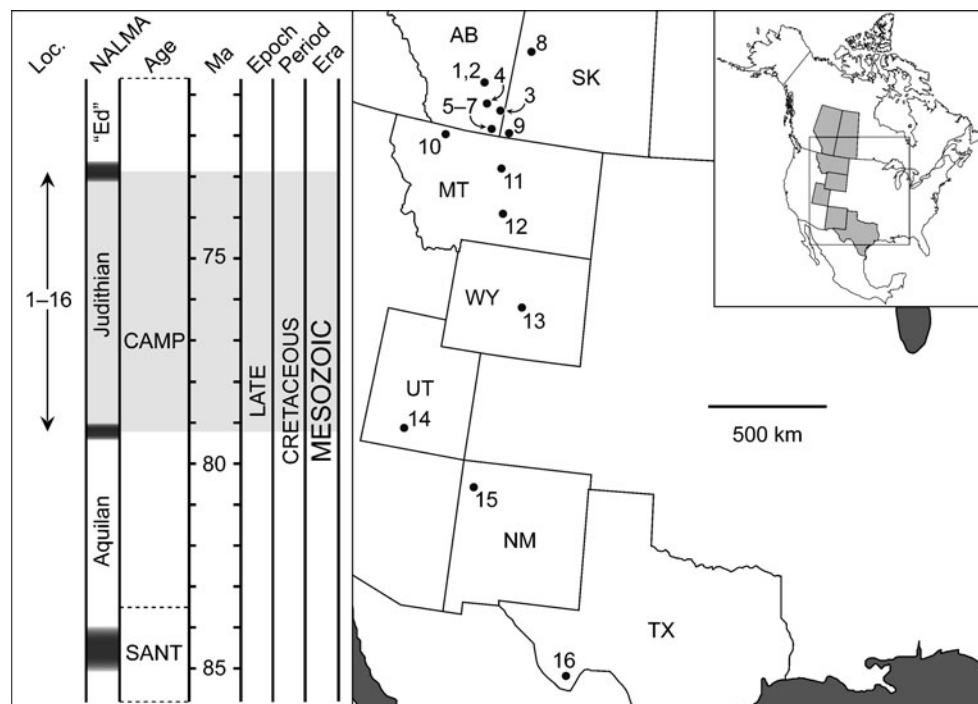
Fig. 6 Temporal and geographical distributions of Late Cretaceous (middle–late Campanian; Judithian NALMA) lissamphibian localities in North America. Localities are denoted by the same *numbers* used in the corresponding faunal list (Table 4) and ESM Appendix 4, and are plotted north to south within each province and state. Time scale (*left side*): fossiliferous interval depicted in this figure is *shaded*; for simplicity and because reliable, regional correlations are not available, localities are shown grouped together within the Judithian (for a regional correlation chart, see Roberts et al. 2005, figs. 6, 8; for more detailed correlations in more limited areas, see Eberth 1990, fig. 5 and Brinkman et al. 2004, fig. 2 for southeastern Alberta, Rogers and Brady, fig. 11 for north-central Montana and Roček et al. 2010, fig. 2 for southern Utah); *thicker*, *fuzzy horizontal lines in NALMA column* indicate uncertainties about placement of boundaries between NALMAs; other boundaries and absolute ages follow Walker and Geissman (2009). Positions of localities on the main map are approximate. *Inset map* (*upper right*) shows portion of North American continent depicted in the main map. See text for abbreviations used in figure. *Numbers 1–16* designate localities. *1* Localities in Dinosaur Provincial Park and area, southeastern Alberta, Canada; Dinosaur Park Formation. *2* Localities in Dinosaur Provincial Park and area, southeastern Alberta, Canada; upper part of Oldman Formation. *3* UALVP Irvine vertebrate microfossil locality, southeast Alberta, Canada; upper part of Dinosaur Park Formation. *4* SPS locality along Oldman River, southeastern Alberta, Canada; upper part of Foremost Formation. *5*, Localities along eastern portion of Milk River Valley, southeastern Alberta, Canada; Oldman Formation. *6* Pinhorn Ranch localities (PHRN, PHR-1, and PHR-2) along eastern portion of Milk River Valley, southeastern Alberta, Canada; upper part of Foremost Formation. *7* Localities near Onefour, southeastern Alberta, Canada; upper part of Dinosaur Park Formation. *8*, Muddy Lake bonebed (= RSMNH loc. 73C06-0001), near Unity, west-central Saskatchewan, Canada; Dinosaur Park Formation. *9* Woodpile Creek, southwestern Saskatchewan, Canada; Dinosaur Park or Oldman Formation. *10* MOR loc. TM-088, Glacier County, north-central Montana, USA; Two Medicine Formation. *11* J. B. Hatcher's localities, Clam Bank Hollow, and multiple UC vertebrate microfossil localities, Missouri River Valley, north-central Montana, USA; type area of Judith River Formation. *12* Top Cat Quarry, Golden Valley County, central Montana, USA; Judith River Formation. *13* Barwin Quarry (unnumbered AMNH locality) and Fales Rocks (= Fales Rocks 1 of the UCMP; UCMP V81101=UW V-81006) localities, Natrona County, Wyoming, USA; Mesaverde Formation. *14* Localities on Kaiparowits Plateau, south-central, Utah, USA; Kaiparowits Formation. *15* Localities in San Juan Basin, northwestern New Mexico, USA; Fruitland Formation. *16* Localities in Big Bend National Park, southwestern Texas, USA; Aguja Formation

those identifications cannot be easily substantiated. Unquestionably accepting such identifications and, perhaps, using them as data in larger scale analyses (e.g. rates of survivorship and extinction, patterns of palaeobiodiversity, or palaeobiogeographic histories) is at best naïve or at worst irresponsible. Thanks to our familiarity with the relevant taxa and fossil record, we are in a position to provide our opinions on the relative reliability of taxonomic identifications presented in this paper. We recognise three categories of taxonomic identifications, which can be ranked from most to least reliable, as considered below:

1) Published identifications in which specimens are described, figured or both in sufficient detail that the relevant diagnostic features are evident and their taxonomic identification can be verified from the publication, without necessarily having to examine the relevant specimen(s) firsthand. Also, specimens, whether previously published or not, that at least one of us has personally examined and identified; where relevant, such unpublished specimens are documented in our appendices.

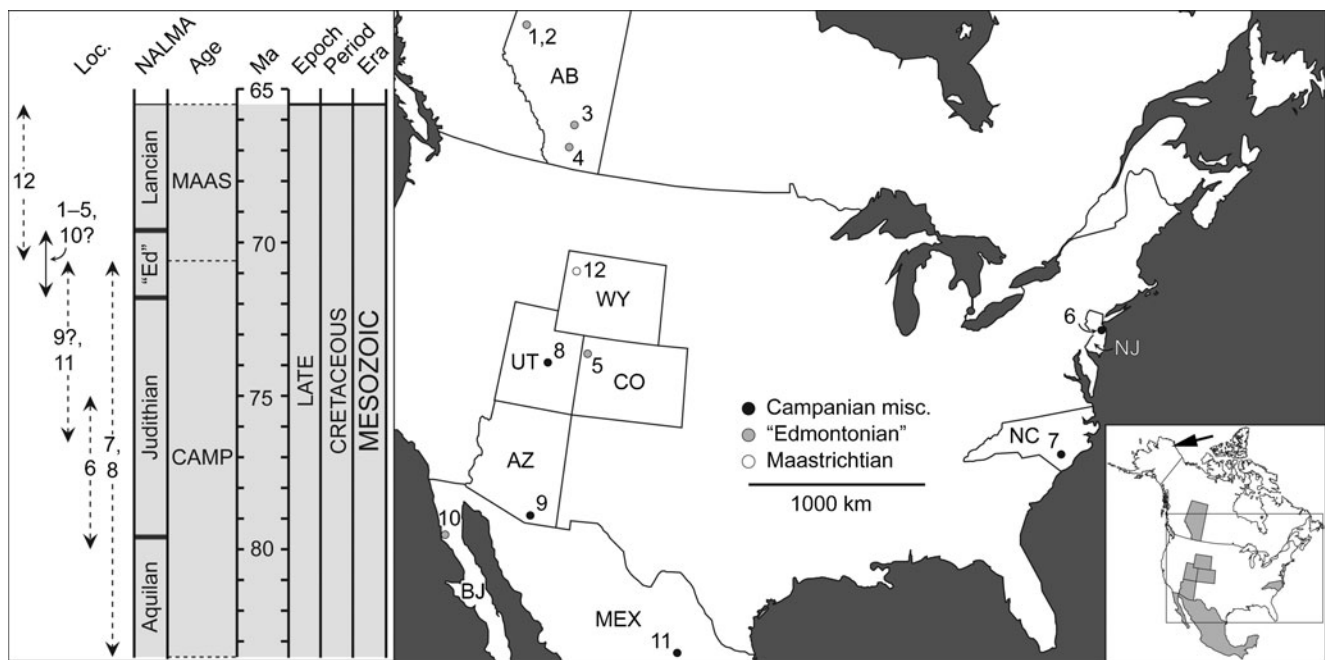2) Published specimens that may have been properly identified, but this cannot be directly verified solely from

Fig. 7 Temporal and geographical distributions of Late Cretaceous (late Campanian–early Maastrichtian ["Edmontonian" NALMA] and Campanian and Maastrichtian not assignable to NALMA) lissamphibian localities in North America. Localities are denoted by the same *numbers* used in the corresponding faunal list (Table 5) and ESM Appendix 5. "Edmontonian" localities (*1–5*) are listed first; other localities are listed approximately east to west and north to south. Time scale (*left side*): fossiliferous interval depicted in this figure is *shaded*; localities are placed in their approximate temporal positions; *dashed arrows* indicate poorly constrained age ranges for localities; *question mark* following locality number indicates uncertain age; *thicker, fuzzy horizontal lines in NALMA column* indicate uncertainties about placement of boundaries between NALMAs; other boundaries and absolute ages follow Walker and Geissman (2009). Positions of localities on the main map are approximate. *Inset map* (*lower right*) shows portion of North American continent depicted in the main map and arrow points to North Slope of Alaska, USA, where a latest Cretaceous assemblage of vertebrates that does not include lissamphibians or non-dinosaurian reptiles has been reported. See text for abbreviations used in figure. *Numbers 1–12* designate localities. *1* Kleskun Hill Park, west-central Alberta, Canada; middle part of Wapiti Formation; late Campanian ("Edmontonian" NALMA). *2* Red Willow Falls, west-central Alberta, Canada; middle part of Wapiti Formation; late Campanian ("Edmontonian" NALMA). *3* Multiple localities, Red Deer River Valley, south-central Alberta, Canada; upper part of Horseshoe Canyon Formation; early Maastrichtian ("Edmontonian" NALMA). *4* Scabby Butte, southern Alberta, Canada; St. Mary River Formation; late Campanian–early Maastrichtian ("Edmontonian" NALMA). *5* Unspecified locality(ies), Rio Blanco County, northwestern Colorado, USA; Williams Fork Formation; late Campanian–early Maastrichtian ("Edmontonian" NALMA). *6* Ellisdale, Monmouth County, New Jersey, USA; Marshalltown Formation; middle Campanian and possibly equivalent to Aquilan and Judithian NALMAs. *7* Bladen County Landfill Annex, Bladen County, North Carolina, USA; Bladen Formation; Campanian. *8*, Meetinghouse Canyon, east-central Utah, USA; Blackhawk Formation; Campanian. *9* Unspecified locality(ies) in Adobe Canyon area, southeastern Arizona, USA; Fort Crittenden Formation, late? Campanian and possibly equivalent to Judithian NALMA. *10* Unspecified locality(ies), western Baja California, Mexico; "El Gallo Formation", Campanian and possibly equivalent to "Edmontonian" NALMA. *11* La Parrita, Coahuila, northeastern Mexico; Cerro del Pueblo Formation; late Campanian. *12* Harebell vertebrate locality, Teton County, northwestern Wyoming; Bobcat Member, Harebell Formation; Maastrichtian

the published work because the relevant specimens were not adequately described or figured. This situation is most common in larger, faunal review-style papers in which short taxonomic accounts are presented. It also has been our experience that most taxonomic identifications recorded in institutional collections databases also fall within this category. Such database records usually are not accompanied by informative images, lack any justification for the recorded identification and do not identify the authority who made the identification.

3) Published identifications for which no specimens were described or figured, no diagnostic features were mentioned and typically no voucher specimens were listed.

These kinds of identifications often appear in faunal lists, distribution tables, specimen counts, conference abstracts or within the body of larger papers or books. Also problematic are user-contributed, on-line compilations of occurrence data (e.g. Paleobiology Database), which are becoming a popular and, admittedly, convenient way to assemble and access large amounts of information. In our experience, such repositories typically are uncritical compilations of data that have not been gathered in any systematic manner or checked for accuracy before being posted. Any information accessed from such repositories needs to be checked by consulting the original sources (e.g. records, specimens or publications), assuming that
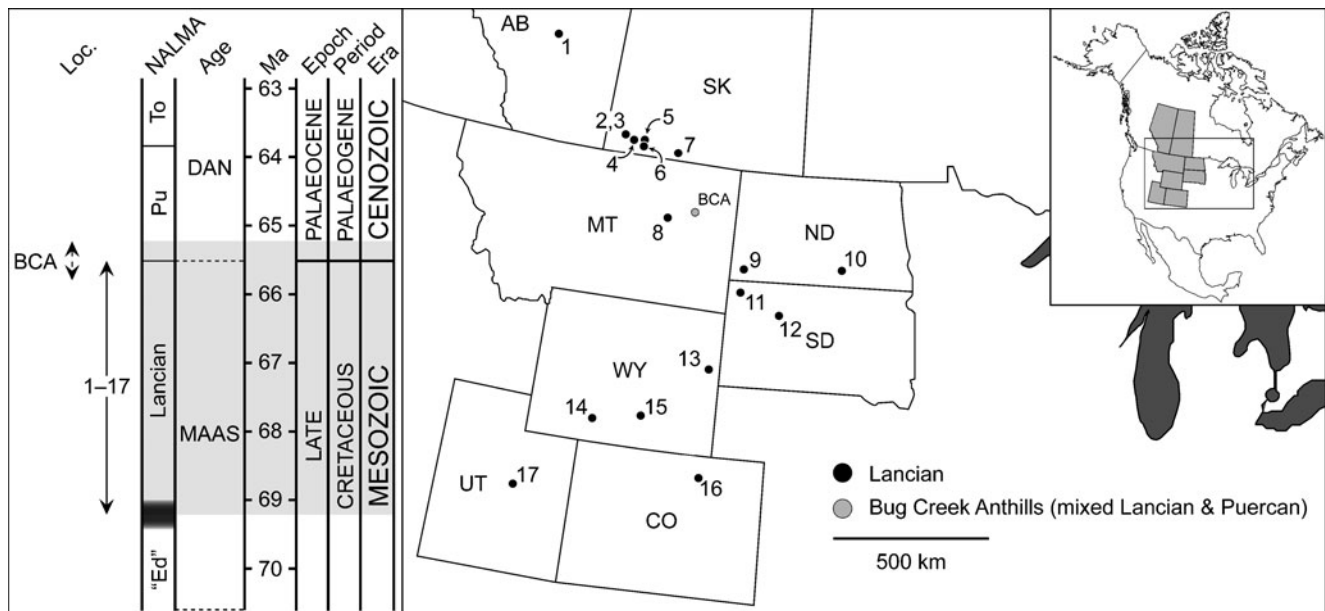
Fig. 8 Temporal and geographical distributions of latest Cretaceous (late Maastrichtian; Lancian NALMA) lissamphibian localities and the Bug Creek Anthills locality in North America. Lancian localities are denoted by the same *numbers* used in the corresponding faunal list (Table 6) and in ESM Appendix 6, and are plotted north to south within each province and state. The temporally mixed (Lancian–Puercan NALMAs) Bug Creek Anthills (*BCA*) locality in McCone County, northeastern Montana, USA, is included in this figure (see Table 7 and ESM Appendix 7 for the faunal list and sources of taxonomic identifications, respectively, for BCA). *Time scale* (*left side*): fossiliferous interval depicted in this figure is *shaded*; for simplicity Lancian localities are shown grouped together, even though many of those occur in the latter two-thirds of the Lancian (see correlation chart in Wilson et al. 2010, fig. 1); *dotted arrows* denote the inferred age range for BCA; the *thicker*, *fuzzy horizontal line in NALMA column* indicates uncertain placement of the boundary between the Lancian and "Edmontonian"; other boundaries and absolute ages follow Walker and Geissman (2009). Positions of localities on the main map are approximate. *Inset map* (*upper right*) shows portion of North American continent depicted in the main map. See text for abbreviations used in figure. *Numbers 1–17* designate localities. *1* KUA-1 and unspecified localities, Red Deer River Valley, south-central Alberta, Canada; lower part of Scollard Formation. *2* Long Fall horizon in Medicine Hat Brick and Tile Quarry, Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; Frenchman Formation. *3* FR-1, Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; Frenchman Formation. *4* "Scotty" Quarry (= RSMNH loc. 72 F07-0022), Frenchmen River Valley, south of Shaunavon, southwestern Saskatchewan, Canada; Frenchmen Formation. *5* Wounded Knee, Frenchmen River Valley, south of Shaunavon, southwestern Saskatchewan, Canada; Frenchman Formation. *6* Gryde (= RSMNH loc. 72 F08-0012), Frenchmen River Valley, south of Shaunavon, southwestern Saskatchewan, Canada; Frenchman Formation. *7* Morgan Creek Badlands (= Killdeer Badlands), south-central Saskatchewan, Canada; Frenchman Formation. *8* Localities in Garfield County, northeastern Montana, USA; Hell Creek Formation. *9* Localities in Slope and Bowman counties, southwestern North Dakota, USA; Hell Creek Formation. *10* NDSFC loc. L064, Logan County, south-central North Dakota, USA; Iron Lightning Member, Fox Hills Formation. *11* SDSMT localities, Harding County, northwestern South Dakota, USA; Hell Creek Formation. *12* "Sue" Quarry, Cheyenne River Indian Reservation, northwestern South Dakota, USA; Hell Creek Formation. *13* Type Lance localities and Greasewood Creek, all Niobrara County, east-central Wyoming, USA; Lance Formation. *14* Robber's Roost (= UW loc. V-79032), Sweetwater County, south-central Wyoming, USA; Lance Formation. *15* Localities in the Hanna Basin, southeastern Wyoming, USA; lower part of Ferris Formation. *16* Localities in the Cheyenne Basin, northeastern Colorado, USA; Laramie Formation and D1 Sequence of Denver Formation. *17* OMNH loc. V812, central Utah, USA; lower part of North Horn Formation

information was even provided. As with the previous category, there is no way to directly verify these kinds of identifications based solely on information contained in the publication or data repository in which those identifications appear.

Of the approximately 425 occurrences tabulated in our summary, nearly three-quarters fall into the first category; this leaves about one-quarter of the occurrences—all of which have been reported previously in the literature—as unverified, although some undoubtedly are correct. Our use of the term "unverified" means that we have not been able to confirm a published identification based either on information contained in the published account or, in a minority of instances, by firsthand examination of the relevant specimen(s). For identifications that fall into the second or third category, it may be possible to locate the relevant specimen(s) in an institutional collection and verify their identifications firsthand. In our experience, however, if the institutional catalogue number is not listed in the publication of interest, then the probability of locating the relevant specimen is remote. For that reason, we feel it is important to include institutional catalogue numbers for voucher specimens or, if a number is not currently
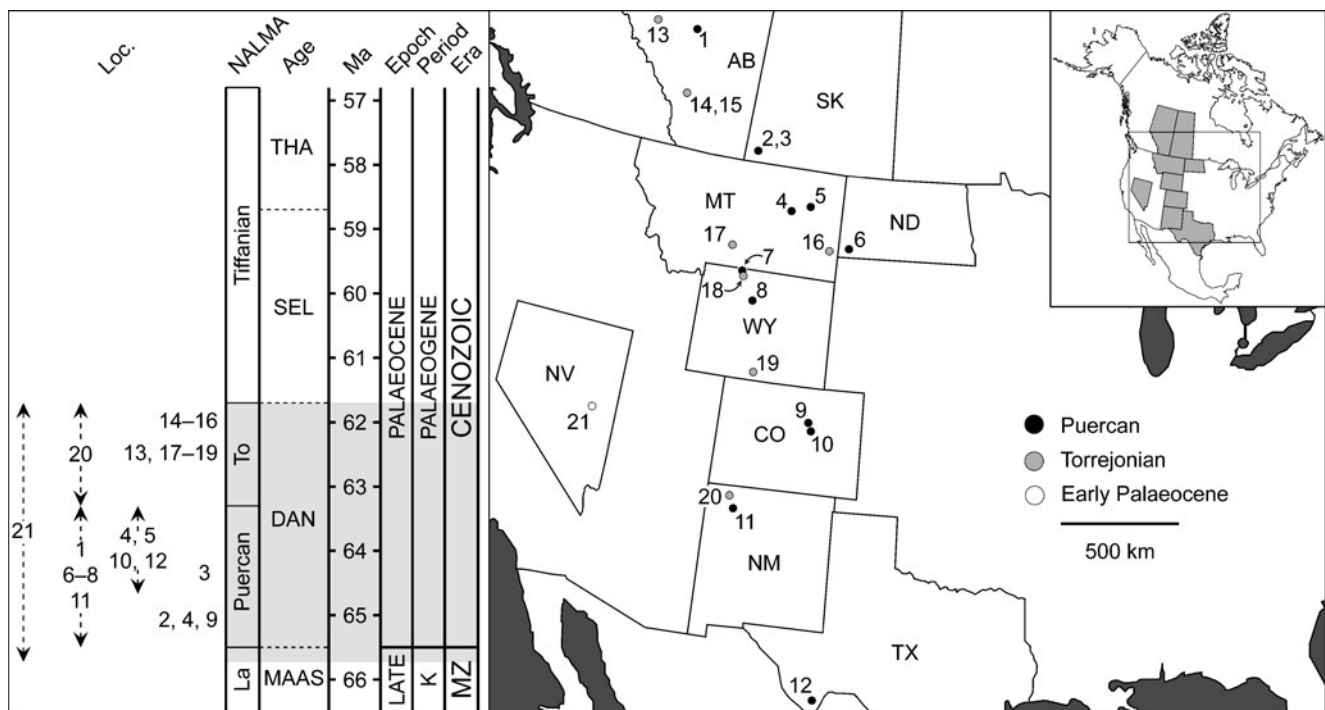
Fig. 9 Temporal and geographical distributions of early Palaeocene (Puercan and Torrejonian NALMAs) lissamphibian localities in North America. Localities are denoted by the same *numbers* used in the corresponding faunal list (Table 8) and ESM Appendix 8, and are grouped by NALMA (Puercan: *1–12*; Torrejonian: *13–20*; Puercan or Torrejonian: *21*). *Time scale* (*left side*): fossiliferous interval depicted in this figure is *shaded*; localities are placed in their approximate temporal positions; *dashed arrows* indicate poorly constrained ages for localities; the duplicate appearance of *4* (Garfield County localities) is because this grouping includes one locality (UCMP V74111) that clearly is Pu1 in age, but the rest occur stratigraphically higher and are of undifferentiated Pu2/3 age; boundaries for NALMAs follow Lofgren et al. (2004); other boundaries and absolute ages follow Walker and Geissman (2009). Positions of localities on the main map are approximate and, within each NALMA grouping, localities are plotted north to south in each province and state. *Inset map* (*upper right*) shows portion of North American continent depicted in the main map. See text for abbreviations used in figure. *Numbers 1–21* designate localities. *1* UALVP Genesee #2, central Alberta, Canada; upper part of Scollard Formation. *2* Rav W-1 horizon in Medicine Hat Brick and Tile Quarry, Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; lower part of Ravenscrag Formation. *3* Croc Pot, Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; lower part of Ravenscrag Formation. *4* Localities in Garfield County, northeastern Montana, USA; Tullock Formation. *5* Purgatory Hill, McCone County,

northeastern Montana, USA; Tullock Formation. *6* PTRM localities, Slope and Bowman counties, southwestern North Dakota; Fort Union Formation. *7* Unnamed locality, Bighorn Basin, Park County, north-central Wyoming, USA; "Hunt Creek member", Fort Union Formation. *8* Bugger-to-get-to (UW loc. V-82010), Washakie County, north-central Wyoming, USA; Polecat Bench Formation. *9* Alexander (= UCM loc. 77267), Arapahoe County, north-central Colorado, USA; Denver Formation. *10* West Bijou Creek (= UCM loc. 78191), Denver Basin, Elbert County, north-central Colorado, USA; Denver Formation. *11* Kimbetoh E (UCMP loc. V1312), San Juan County, northwestern New Mexico, USA; Nacimiento Formation. *12* Localities in Big Bend National Park, Brewster County, southwestern Texas, USA; upper part of Javelina Member, Tornillo Formation. *13* Diss, west-central Alberta, Canada; Coalspur Formation. *14* ?Who Nose, Calgary, southern Alberta, Canada; Paskapoo Formation. *15* Locality 2E (sensu Russell 1929), Elbow River, Calgary, southern Alberta, Canada; Paskapoo (= Porcupine Hills) Formation. *16* Medicine Rocks I localities, Carter County, southeastern Montana, USA; Fort Union Formation (= Tongue River Formation). *17* Gidley Quarry, Sweetgrass County, south-central Montana, USA; Lebo Formation. *18* Rock Bench Quarry, Park County, northwestern Wyoming, USA; Fort Union Formation. *19* Swain Quarry, Carbon County, south-central Wyoming, USA; Fort Union Formation. *20* Kutz Canyon, San Juan County, northwestern New Mexico, USA; Nacimiento Formation. *21* Sheep Pass Canyon, southern Egan Range, east-central Nevada, USA; Member B, Sheep Pass Formation

available, to at least identify the relevant institutional collection.

Analysis of North American Mesozoic and Palaeocene lissamphibian temporal richness

The raw taxonomic and occurrence data compiled for our review were analysed to assess long-term trends in taxonomic richness of North American lissamphibians from the Early

Jurassic–Palaeocene (approx. 190–55.8 Ma). We calculated richness at the species level. We included all formally named and accepted taxa, plus unnamed and potentially diagnosable taxa that are recognised by us as distinct taxonomic entities, based either on specimens and taxa adequately documented in publications or on specimens personally examined by us (i.e. category 1 in preceding section). See notations in Tables 1, 2, 3, 4, 5, 6, 7, 8, and 9 and comments in the accompanying appendices (ESM Appendices 1–9) for our taxonomic
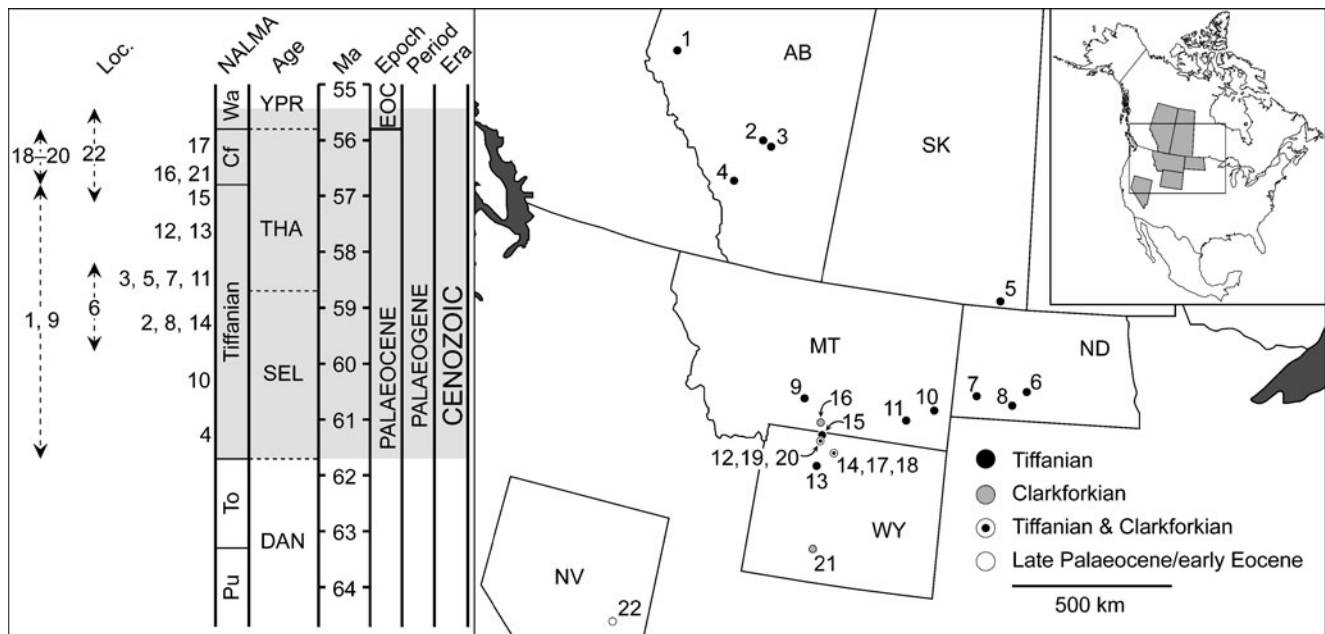
Fig. 10 Temporal and geographical distributions of late Palaeocene (Tiffanian–Clarkforkian NALMAs) lissamphibian localities in North America. Localities are denoted by the same *numbers* used in the corresponding faunal list (Table 9) and ESM Appendix 9, and are grouped by NALMA (Tiffanian: *1–15*; Clarkforkian: *16–21*; late Palaeocene or early Eocene: *22*). *Time scale* (*left side*): fossiliferous interval depicted in this figure is *shaded*; localities are placed in their approximate temporal positions; *dashed arrows* indicate poorly constrained age ranges for localities; boundaries for NALMAs follow Lofgren et al. (2004); other boundaries and absolute ages follow Walker and Geissman (2009). Positions of localities on the main map are approximate and, within each NALMA grouping, localities are plotted north to south in each province and state. *Inset map* (*upper right*) shows portion of North American continent depicted in the main map. See text for abbreviations used in figure. *Numbers 1–22* designate localities. *1* UALVP Smoky Tower #1, west-central Alberta, Canada; Paskapoo Formation. *2* UALVP DW localities along Blindman River, central Alberta, Canada; Paskapoo Formation. *3* Canyon Ski Quarry along Red Deer River, central Alberta, Canada; Paskapoo Formation. *4*, Cochrane 2, south-central Alberta, Canada; Paskapoo (= Porcupine Hills) Formation. *5* Roche Percée localities, southeastern Saskatchewan, Canada; upper part of Ravenscrag Formation. *6* Almont, Morton County, central North Dakota, USA; Sentinel Butte Formation. *7* Wannagan Creek Quarry, Billings County, southwestern North Dakota, USA; Tongue River (= Bullion Creek) Formation. *8* Brisbane, Grant County, southwestern North Dakota, USA; Tongue River Formation. *9* Unspecified locality, Bear Butte, Sweetgrass County, south-central Montana, USA; Fort Union Formation. *10* Highway Blowout, Carter County, southeastern Montana, USA; Tongue River Formation. *11* Olive, southeastern Montana, USA; Tongue River Formation. *12* UM loc. SC-198 (Fossil Hollow) and UM loc. SC-273, both Park County, northwestern Wyoming, USA; Polecat Bench Formation. *13* Princeton Quarry local fauna (Princeton [= Silver Coulee], Fritz, and Schaff quarries), Park County, northwestern Wyoming, USA; Fort Union (= Polecat Bench) Formation. *14* Cedar Point Quarry, Bighorn County, northwestern Wyoming, USA; Fort Union (= Polecat Bench) Formation. *15* UM loc. SC-270, Park County, northwestern Wyoming, USA; Fort Union Formation. *16* Bear Creek local fauna, Carbon County, south-central Montana, USA; Willwood Formation. *17* UM loc. FG-6, Foster Gulch, Bighorn County, northwestern Wyoming, USA; ?Polecat Bench Formation. *18* UM loc. SC-171 and unnamed locality (= type locality for *Piceoerpeton willwoodense*), Park County, northwestern Wyoming, USA; Willwood Formation. *19* UM loc. SC-227, Park County, northwestern Wyoming, USA; Willwood Formation. *20* SC-29 Discovery Site (carbonate lens J), Park County, northwestern Wyoming, USA; Willwood Formation. *21* Big Multi Quarry, Sweetwater County, southwestern Wyoming, USA; Fort Union Formation. *22* Sheep Pass Canyon, southern Egan Range, east-central Nevada, USA; Member C, Sheep Pass Formation; note this member straddles the Palaeocene/Eocene boundary, but the occurrence is included here for completeness

decisions. The occurrences of several indeterminate taxa at the family, genus and species levels, here referred to as 'specifically indeterminate occurrences' (sensu Fara 2004), also are included in our analyses where they are informative for calculating minimal lineage level richness estimates (see below). We intentionally excluded from our analyses the following occurrences: (1) questionable lissamphibian material from the Upper Triassic Vinita and Cumnock formations of the eastern USA (Sues and Olsen 1990 and Heckert et al. 2012, respectively); (2) questionable anuran material from the Albian age Wayan Formation, Idaho, USA (Dorr 1985); (3) all lissamphibian taxa from the temporally mixed late

Maastrichtian and earliest Palaeocene (Lancian and Puercan NALMAs) Bug Creek Anthills locality, Hell Creek Formation, Montana, USA. Except for the possible cryptobranchid (Table 7), all other lissamphibian taxa recognised at Bug Creek Anthills are known to have unequivocal Lancian or both Lancian and Puercan occurrences (Tables 6 and 8, respectively); thus, our results were not adversely affected by excluding the single cryptobranchid occurrence at Bug Creek Anthills.

We estimated lissamphibian species richness by applying taxic and minimal lineage level approaches to our taxonomic and occurrence data. Richness estimates were further calculated

Table 1 Triassic and Jurassic lissamphibian occurrences[a] in North America

Late Triassic (middle Carnian and early Norian):

?Lissamphibia incertae sedis [1, 2]

Early Jurassic (Sinemurian–Pliensbachian):

Gymnophiona

   Eocaecilia micropodia Jenkins and Walsh, 1993 [3]

Anura

   Prosalirus bitis Shubin and Jenkins, 1995 [3]

Late Jurassic (all Kimmeridgian–earliest Tithonian)

Caudata

   Comonecturoides marshi nomen dubium (Hecht and Estes, 1960) [8]

   Gen. et sp. nov. [4]

   Gen. et sp. indet. [5, 6, 7, 8, 9, 12]

     Urodela

       Iridotriton hechti Evans et al., 2005 [4]

Anura

   Eobatrachus agilis nomen dubium (Marsh, 1887) [8]

   Comobatrachus aenigmatis nomen dubium (Hecht and Estes, 1960) [8]

     Discoglossidae sensu lato

       Enneabatrachus hechti Evans and Milner, 1993 [8]

       cf. *Enneabatrachus hechti* [4]

       Gen. et sp. indet. [4]

     Pelobatidae sensu lato

       Gen. et sp. indet. [8]

     ?Rhinophrynidae

       Rhadinosteus parvus Henrici, 1998b [4]

     Family incertae sedis

       Gen. et sp. indet. A sensu Henrici (1998a) [4]

       Gen. et sp. indet. B sensu Henrici (1998a) [4]

       Gen. et sp. indet. (?multiple taxa) [5, 8, 9, 10, 11]

[a] Localities are denoted by the same *numbers* (*1–12*) used in the corresponding locality map (Fig. 3) and ESM Appendix 1. Localities are listed in approximate chronological sequence and, where appropriate, are grouped by state. Numbers in square brackets denote localities: bold numbers denote holotype localities; underlined numbers denote occurrences which need verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* Tomahawk locality, Richmond Basin, Chesterfield County, east-central Virginia, USA; Vinita Formation (formerly Turkey Branch Formation), Newark Supergroup; middle Carnian (Milner 1994; Sues and Olsen 1990). *2* Moncure locality, Deep River Basin (Sanford sub-basin), Chatham County, central North Carolina, USA; Cumnock Formation, Newark Supergroup; early Norian (Heckert et al. 2012). *3* Gold Spring Quarry 1, Coconino County, northeastern Arizona, USA; "silty facies" of the Kayenta Formation; Sinemurian–Pliensbachian (Curtis and Padian 1999; Jenkins and Shubin 1998; Jenkins and Walsh 1993; Jenkins et al. 2007; Shubin and Jenkins 1995; Sues, Clark et al. 1994). *4* Rainbow Park, Dinosaur National Monument, Uintah County, northeastern Utah, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian (Chure et al. 2006; Evans et al. 2005; Gardner and Chure unpublished observation; Henrici 1998a, b; Nessov 1992). *5* Little Houston Quarry, Crook County, northeastern Wyoming, USA; lower middle part of Morrison Formation; Kimmeridgian–earliest Tithonian

(Foster 2001, 2007). *6* Mile 175, Crook County, northeastern Wyoming, USA; uncertain member within Morrison Formation; Kimmeridgian–earliest Tithonian (Foster and Heckert 2011). *7* Ninemile Hill, Carbon County, east-central Wyoming, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian (Foster 2007). *8* Quarry 9, Como Bluff, Albany County, southeastern Wyoming, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian (Carrano and Valez-Juarbe 2006; Estes 1981; Evans and Milner 1993; Hecht and Estes 1960; Marsh 1887; Moodie 1912, 1914). *9* Wolf Creek Quarry, Moffat County, northwestern Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian (Foster 2007). *10* Fruita Paleontological area, Mesa County, west-central Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian (Callison 1987). *11* Garden Park, El Paso County, southeastern Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian (Foster 2007). *12* Small Quarry, El Paso County, southeastern Colorado, USA; Brushy Basin Member, Morrison Formation; Kimmeridgian–earliest Tithonian (Foster 2007). Taxonomic authorships are provided only for species named on material from the indicated time interval. See text and ESM Appendix 1 for further information about the taxonomic identifications presented in this faunal list

using the sampled-in-bin method versus only including taxa that occur in multiple time bins ('boundary-crossers'; see Fara 2004 and references therein) because the latter approach would exclude multiple singleton occurrences in our dataset (e.g. the earliest crown frog and the stem caecilian). The taxic approach, which is a simple compilation of observed first and last occurrences of taxa partitioned into discrete temporal intervals or bins (Levinton 1988), was applied to the raw taxonomic and occurrence data per 5-Myr time bin. Bin duration was chosen to accommodate the poor age control for several taxa (e.g. Cloverly Formation taxa of Wyoming and Montana, USA) and also because the number of taxonomic occurrences are too few at finer temporal durations for certain time intervals (e.g. most pre-Late Cretaceous taxa). Raw taxic richness was corrected for by including species range-through occurrences (i.e. a species was inferred to occur in an intervening time bin if it occurs in both an earlier and later bin, but not in the intervening bin). This approach was used only across time bin 33 (75.5–70.5 Ma), or approximately the "Edmontonian" NALMA, for which eight species are known from the surrounding time bins, but not from bin 33 (see Tables 4 and 6). The minimal lineage level approach, which was first introduced by Alroy (1996) and later refined by Fara (2004) for his case study of the global diversity of fossil lissamphibians, is based on the principle of evolutionary continuity and allows for specifically inde-terminate occurrences to be incorporated into the richness estimate (e.g. Fara 2004, fig. 2B vs. 2C). This method is intermediate between the taxic and phylogenetic approaches and is used to calculate "… the *minimal* number of lineages present in a time interval given the observed occurrences" by

Table 2 Early Cretaceous lissamphibian occurrences[a] in North America

late Berriasian–Valanginian

Albanerpetontidae

Gen. et sp. indet. [1]

Urodela

Family incertae sedis

Gen. et sp. indet. [1]

Aptian–Albian

Albanerpetontidae

Albanerpeton arthridion Fox and Naylor, 1982 [5, **7**]

Albanerpeton sp. [3]

Gen. et sp. indet. [3]

Caudata

Family incertae sedis

Gen. et sp. indet. [3]

Urodela

Batrachosauroididae

Gen. et sp. indet. [3]

Scapherpetontidae

Gen. et sp. indet. [3]

Prosirenidae

Prosiren elinorae Goin and Auffenberg, 1958 [4, 6, **7**]

Anura

Family incertae sedis

cf. *Scotiophryne* sp. [3]

Gen. et sp. indet. (multiple taxa) [2, 3, 4, 5, 6, 7, 8]

latest Albian–earliest Cenomanian

Albanerpetontidae

cf. *Albanerpeton nexuosum* [9]

Gen. et sp. indet. [9]

Urodela

Scapherpetontidae

Gen. et sp. indet. [9]

Anura

Family incertae sedis

Gen. et sp. indet. (multiple taxa) [9]

[a] Localities are denoted by the same *numbers* (*1–9*) used in the corresponding locality map (Fig. 4) and ESM Appendix 2. Localities are listed in approximate chronological sequence and, where appropriate, grouped by state. Numbers in square brackets denote localities: bold numbers denote holotype localities; underlined numbers denote occurrences needing verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* OMNH loc. V1243, Fall River County, southwestern South Dakota, USA; Chilson Member, lower part of Lakota Formation; late Berriasian–Valanginian (Cifelli et al. in press; Gardner and Böhme 2008; Gardner and Cifelli unpublished observation). *2* Bachman locality, Stafford County, northeastern Virginia, USA; Patuxent facies, Potomac Formation; early Aptian (Kranz 1998; Weems and Bachman 1997). *3* Bighorn Basin localities in north-central Wyoming (OMNH loc. V62; USNM locs. 42138, 42146, 42175, 42222, 43420; and YPM loc. 63-19) and in south-central Montana (OMNH loc. V184), both USA; middle and upper parts (= Units V–VII of Ostrom 1970), Cloverly Formation;

Aptian–Albian (Gardner 1999a; Gardner and Cifelli, unpublished observation; Oreska et al. 2013). *4* Paluxy Church, Hood County, central Texas, USA upper part of Twin Mountains Formation; late Aptian (Winkler et al. 1990). *5* McLeod Honor Farm (OMNH V706), Atoka County, southeastern Oklahoma, USA; middle part of Antlers Formation; late Aptian–early Albian (Cifelli et al. 1997a; Gardner 1999a). *6* Pecan Valley Estates and Huggins #1 and #2, all in Erath County, central Texas, USA; base of Paluxy Formation; early Albian (Winkler et al. 1990). *7* Greenwood Canyon, Montague County, and Butler Farm, Wise County, both in north-central Texas, USA; upper part of Antlers Formation; early–middle Albian (Estes 1969a; Fox and Naylor 1982; Gardner 1995, 1999a; Goin and Auffenberg 1958; Hecht 1963; Zangerl and Denison 1950). *8* Tincup Creek, Caribou County, southeastern Idaho, USA; Wayan Formation; Albian (Dorr 1985). *9* Mussentuchit local fauna (e.g., OMNH locs. V235, V237, V239, V240, V695 and V801), Emery County, central Utah, USA; Mussentuchit Member, Cedar Mountain Formation; latest Albian–earliest Cenomanian (Cifelli et al. 1999c; Gardner 1994, 1999b). Taxonomic authorships provided only for species named on material from the indicated time interval. See text and ESM Appendix 2 for further information about taxonomic identifications presented in this faunal list

connecting stratigraphic ranges of related taxa (Fara 2004, p. 63). For example, the occurrence of an indeterminate albanerpetontid during the late Berriasian–Valanginian (Table 2) implies that at least one lineage (or species) of that family can be counted in all subsequent time intervals between it and the next occurrence of an albanerpetontid (Aptian–Albian; Table 2) regardless of the latter's taxonomic assignment (e.g. Albanerpetontidae indet., *Albanerpeton* sp. or *Albanerpeton arthriodon*; see Fig. 11, taxic vs. lineage richness curves). The assumption of evolutionary continuity begins to weaken for this method when the intervening time interval between occurrences of closely related taxa increases or extends beyond the given interval (e.g. towards the Recent) and the geographic area under study decreases (e.g. global to regional), because of confounding factors such as migrations, range contractions and extirpations (Fara 2004). Given these kinds of problems, we could not directly apply the lineage level method to Gymnophiona because there are no known North American fossil records for caecilians between the single Early Jurassic (approx. 190 Ma) occurrence of *Eocaecilia* in Arizona (e.g. Jenkins and Walsh 1993) and the much younger Quaternary (Wake et al. 1999) and present-day occurrences (e.g. Frost 2013) of *Dermophis* in southernmost Mexico. All other taxa in our dataset have lineages that are confined to the study interval, range to the last time bin or have a North American fossil record that post dates the Palaeocene. Unlike the phylogenetic method, a fully resolved species level phylogeny is not required to estimate minimal lineage level richness, which is fortuitous because few cladistic studies exist for the Mesozoic and Palaeocene North American lissamphibians sampled here (e.g. DeMar 2013; Denton and O'Neill 1998; Gardner 2002). See the ESM for the raw taxic and minimal lineage level richness values (ESM Appendix 10)

Table 3 Late Cretaceous (middle Cenomanian to early–middle Campanian) lissamphibian occurrences[a] in North America

Albanerpetontidae

    Albanerpeton cifellii Gardner, 1999b [**3**]

    Albanerpeton galaktion Fox and Naylor, 1982 [**7**]

    Albanerpeton nexuosum [7]

    cf. *Albanerpeton nexuosum* [2, 6]

    Albanerpeton sp. [9]

    Gen. et sp. indet. (?multiple taxa) [2, 3, 5, 6, 7, 8, 10]

Urodela

    Scapherpetontidae

        Scapherpeton tectum [5*, 6*, 7, 10*]

        Gen. et sp. indet. (multiple taxa) [2, 4, 5, 8]

    Batrachosauroididae

        Opisthotriton kayi [6*, 7, 10*]

        Gen. et sp. nov. 1 [2]

        Gen. et sp. nov. 2 [3]

        Gen. et sp. nov. 3 [7]

        Gen. et sp. indet. [6, 8]

    Sirenidae

        Habrosaurus sp. [6, 8]

    Family incertae sedis

        Nezpercius dodsoni [10]

        Gen. et sp. nov. [3, 6, 10]

        Gen. et sp. indet. (multiple taxa) [1, 2, 3, 4]

Anura

    Family incertae sedis

        Scotiophryne pustulosa [6, 10]

        Gen. et sp. indet. (multiple taxa) [1, 2, 3, 5, 6, 7, 8, 10]

[a] Localities are denoted by the same *numbers* (*1–10*) used in the corresponding locality map (Fig. 5) and ESM Appendix 3. Localities are listed in approximate chronological sequence. Numbers in square brackets denote localities: bold numbers denote holotype localities; numbers with an asterisk denote only genus reported; underlined numbers denote occurrences needing verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* Arlington Archosaur Site and unspecified localities, between Fort Worth and Dallas, north-central Texas; Woodbine Formation; middle Cenomanian (Bennett et al. 2011, 2012; Lee 1997; Winkler and Jacobs 2002). *2* Localities on Markagunt, Paunsaugunt, and Kaiparowits plateaus, southwestern and south-central Utah, USA; unnamed middle member, Dakota Formation; middle? and late Cenomanian (Eaton et al. 1997, 1999; Gardner et al. 2013; Gardner, Cifelli and Eaton, unpublished observation; Roček et al. 2010). *3* Localities on Kaiparowits Plateau, south-central, Utah, USA; Smoky Hollow Member, Straight Cliffs Formation; late Turonian (Eaton et al. 1997, 1999; Gardner 1999b; Gardner et al. 2013; Roček et al. 2010). *4* MNA loc. 1260, Markagunt Plateau, southwestern Utah, USA; undifferentiated Straight Cliffs Formation; ?Coniacian (Gardner et al. 2013). *5* Localities on Paunsaugunt and Kaiparowits plateaus, south-central, Utah, USA; basal part of John Henry Member, Straight Cliffs Formation; ?Coniacian (Gardner 1999b; Gardner et al. 2013; Roček et al. 2010). *6* Localities on Paunsaugunt and Kaiparowits plateaus, south-central, Utah, USA; middle and upper parts of John Henry Member, Straight Cliffs Formation; early–late Santonian (Aquilan) (Gardner and Eaton, unpublished observation; Gardner et al. 2013; Roček et al. 2010). *7* Multiple localities in Verdigris Coulee, south-central Alberta, Canada;

Deadhorse Coulee Member, Milk River Formation; late Santonian (Aquilan) (Fox 1972; Fox and Naylor 1982; Gardner 2000a, b, 2005, unpublished observation; Naylor 1983). *8* MNA loc. 1230 (= UMNH loc. VP 12) in Iron Springs Formation and UMNH loc. VP 10 in uncertain formation; both on Markagunt Plateau, southwestern Utah, USA, and ages uncertain, likely late Santonian or early Campanian (Gardner and Eaton, unpublished observation; Gardner et al. 2013; Roček et al. 2010). *9* NMMNH loc. L-5636, northwestern New Mexico, USA; Allison Member, Menefee Formation; late Santonian–early Campanian (Lewis et al. 2006, 2007, 2008). *10* Localities on Paunsaugunt and Kaiparowits plateaus, south-central, Utah, USA; Wahweap Formation; early–middle Campanian (?intermediate between Aquilan and Judithian) (Eaton et al. 1999; Gardner and Eaton unpublished observation; Gardner et al. 2013; Roček et al. 2010). Taxonomic authorships provided only for species named on material from the indicated time interval. See text and ESM Appendix 3 for further information about taxonomic identifications presented in this faunal list

and age calculations (ESM Appendix 11) used in creating our temporal richness curves (Fig. 11).

Limitations of the North American lissamphibian fossil record (e.g. temporal discontinuity, unequal study of localities or ages and ambiguous taxonomic identifications) hinder our ability to accurately estimate richness patterns over long durations of time. Under such limitations, we freely acknowledge that our estimates of richness are minimal and that any interpretations derived from them (e.g. percentage extinction across the Cretaceous-Palaeogene [K-Pg] boundary) should be treated with caution. Akin to Fara (2004), we did not attempt to standardise our occurrence data (e.g. control for variation through time in sampling intensity by using rarefaction; sensu Alroy 1996) because the number of lissamphibian occurrences is too few at present to be informative. To provide a crude approximation of one aspect of 'sampling intensity' through time, or in our case the approximated amount of research effort afforded per 5-Myr time bin, we counted the numbers of nonrepeating taxonomic records based on the published literature and our personal observations reported in this review (Tables 1, 2, 3, 4, 5 and 6 and 8 and 9 and ESM Appendices 1–6, 8–9). Each publication and personal observation was treated as an independent sample with the sum of records equal to the total estimated sampling or research effort per bin. A numerical summary of these records is provided in ESM Appendix 12. The resulting 'sampling' profile was compared to the Lissamphibia richness curves to determine to what extent research efforts might have influenced the richness estimates (see vertical solid grey line vs. solid and dotted black lines, respectively, in Fig. 11). Tallied published records for the temporally mixed Bug Creek Anthills locality were included in ESM Appendix 12 for completeness, although the values were not incorporated into the sampling estimate. This was done to avoid artificially inflating the number of latest Cretaceous records (bin 34; 70.5–65.5 Ma) because some of the fossil occurrences listed in those records (see Table 7 and ESM Appendix 7) likely belong to specimens that are earliest Palaeocene in age (bin 35; 65.5–60.5 Ma).

Table 4 Late Cretaceous (middle–late Campanian; Judithian NALMA) lissamphibian occurrences[a] in North America

Albanerpetontidae

    Albanerpeton galaktion [2, 5, 14]

    Albanerpeton gracile (Gardner, 2000a) [**1**, 2, 5, 14, 16]

    Albanerpeton nexuosum [2, 5, 14, 15, 16]

    cf. *Albanerpeton nexuosum* [11]

    Albanerpeton sp. [4, 11]

    Gen. et sp. indet. [1, 6, 9, 11, 15, 16]

Urodela

    Scapherpetontidae

        Scapherpeton tectum Cope, 1876 [1, 2, 3, 4, 5, 6, 7, 8, 9*, **11**, 12, 13, 14*, 16*]

        Lisserpeton bairdi [3, 11, 13, 14*]

        Gen. et sp. nov. 1 [3]

        Gen. et sp. indet. (?multiple taxa) [3, 16]

    Batrachosauroididae

        Opisthotriton kayi [1, 2, 3, 4, 5, 6, 7, 9*, 11, 12, 13, 14*, 15]

        Prodesmodon copei [11*, 13, 14*, 15]

    Sirenidae

        Habrosaurus prodilatus Gardner, 2003a [**3**]

        Habrosaurus sp. [11, 13, 14]

    Family incertae sedis

        Nezpercius dodsoni Blob et al., 2001 [**11**]

        Gen. et sp. indet. (?multiple taxa) [3, 16]

Anura

    Family incertae sedis

        Scotiophryne pustulosa [13*, 14, 15]

        cf. *Eopelobates* sp. [13, 15]

        Theatonius sp. nov. [14]

        Gen. et sp. nov. 1 [1, 3, 10]

        Gen. et sp. nov. 2 [1, 2, 3]

        Gen. et sp. nov. 3 [1]

        Gen. et sp. indet. (multiple taxa) [1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 14, 16]

[a] Localities are denoted by the same *numbers* (*1–16*) used in the corresponding locality map (Fig. 6) and ESM Appendix 4. Localities are listed north to south within each province and state. Numbers in square brackets denote localities: bold numbers denote holotype localities; numbers with an asterisk denote only genus reported; underlined numbers denote occurrences needing verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* Localities in Dinosaur Provincial Park and area, southeastern Alberta, Canada; Dinosaur Park Formation (Brinkman 1990; Dodson 1983; Fox 1976a; Gardner 2000a, b, 2005; Gardner and Brinkman in press, unpublished observation). *2* Localities in Dinosaur Provincial Park and area, southeastern Alberta, Canada; upper part of Oldman Formation (Brinkman 1990; Dodson 1983; Fox 1976a; Gardner 2000a, b, 2005; Gardner and Brinkman in press, unpublished observation). *3* UALVP Irvine vertebrate microfossil locality, southeastern Alberta, Canada; upper part of Dinosaur Park Formation (Fox 1976a; Gardner 2000b, 2003a, 2005; Gardner and Brinkman in press, unpublished observation). *4* SPS locality along Oldman River, southeastern Alberta, Canada; Foremost Formation (Brinkman et al. 2004; Peng et al. 2001). *5* Localities along eastern portion of Milk River Valley, southeastern Alberta, Canada; Oldman Formation (Brinkman et al. 2004; Gardner 2000a, b; Peng et al. 1995, 2001). *6* Pinhorn Ranch

localities (PHRN, PHR-1, and PHR-2) along eastern portion of Milk River Valley, southeastern Alberta, Canada; upper part of Foremost Formation (Brinkman et al. 2004; Frampton 2006; Gardner 2000a, b; Peng et al. 1995, 2001). *7* Localities near Onefour, southeastern Alberta, Canada; upper part of Dinosaur Park Formation (Eberth and Brinkman 1997). *8* Muddy Lake bonebed (= RSMNH loc. 73C06-0001), near Unity, west-central Saskatchewan, Canada; Dinosaur Park Formation (Eberth et al. 1990; Tokaryk 1988). *9* Woodpile Creek, southwestern Saskatchewan, Canada; Dinosaur Park or Oldman Formation (Gardner 2000a; Storer 1993). *10* MOR loc. TM-088, Glacier County, north-central Montana, USA; Two Medicine Formation (Gardner, Henrici and Varricchio, unpublished observation; Varricchio 2002). *11* J. B. Hatcher's localities, Clam Bank Hollow, and multiple UC vertebrate microfossil localities, Missouri River Valley, north-central Montana, USA; type area of Judith River Formation (Blob et al. 2001; Cope 1876; Gardner 2003a; Gardner et al. 2010; Rogers 1995; Rogers and Brady 2010; Sahni 1972). *12* Top Cat Quarry, Golden Valley County, central Montana, USA; Judith River Formation (Fiorillo 1989). *13* Barwin Quarry (unnumbered AMNH locality) and Fales Rocks (= Fales Rocks 1 of the UCMP; UCMP V81101 = UW V-81006) localities, Natrona County, Wyoming, USA; Mesaverde Formation (Breithaupt 1985; DeMar and Breithaupt 2006, 2008; Gardner 2000b). *14* Localities on Kaiparowits Plateau, south-central Utah, USA; Kaiparowits Formation (Eaton et al. 1999; Gardner 2000a; Gardner and Cifelli unpublished observation; Gardner et al. 2013; Roček et al. 2010). *15* Localities in San Juan Basin, northwestern New Mexico, USA; Fruitland Formation (Armstrong-Ziegler 1978, 1980; Gao and Fox 1996; Gardner 2000a; Hunt and Lucas 1993). *16* Localities in Big Bend National Park, southwestern Texas, USA; Aguja Formation (Gardner 2000a; Langston et al. 1989; Rowe et al. 1992; Sankey 1998, 2008; Standhardt 1986). Taxonomic authorships provided only for species named on material from the indicated time interval. See text and ESM Appendix 4 for further information about taxonomic identifications presented in this faunal list

As for our chronological review, boundary dates are based on the Geologic Time Scale assembled by Walker and Geissmann (2009), Late Cretaceous NALMAs are based on Cifelli et al. (2004) and Palaeocene NALMAs are based on Lofgren et al. (2004). Following the approach of Wilson et al. (2012), we placed the lower boundary of the first time bin at 185.5 Ma so that a subsequent bin boundary would coincide with the K-Pg boundary at 65.5 Ma (i.e. the age estimate used by Walker and Geissman 2009, rather than the 66 Ma estimate for the K-Pg boundary advocated more recently by Walker et al. 2013 and Renne et al. 2013). Having bins on either side of the K-Pg boundary allows us to comment on patterns of turnover associated with the K-Pg mass extinction event.

Abbreviations

Geologic time unit abbreviations

Era: CZ=Cenozoic; MZ=Mesozoic.
Period: JUR=Jurassic; K=Cretaceous; PG=Palaeogene.
Epoch: EOC=Eocene.
Age: AAL=Aalenian; ALB=Albian; APTIA=Aptian; BAC=Bajocian; BARR=Barremian; BATH=Bathonian; BERR=Berriasian; CALL=Callovian; CAMP=Campanian;

Table 5 Late Cretaceous (late Campanian–early Maastrichtian ["Edmontonian" NALMA] and Campanian and Maastrichtian not assignable to NALMA) lissamphibian occurrences[a] in North America

?Lissamphibia

    Order, family, genus and species indet. [2]

Albanerpetontidae

    Gen. et sp. indet. [4, 6, 7]

Urodela

    Scapherpetontidae

        Scapherpeton tectum [3 *]

        cf. *Scapherpeton* sp. [9]

        Lisserpeton bairdi [11*]

        Gen. et sp. indet. [3]

    Batrachosauroididae

        Opisthotriton kayi [3 *, 4]

        cf. *Opisthotriton* sp. [9]

        Prodesmodon sp. [12]

        Parrisia neocesariensis Denton and O'Neill, 1998 [6]

    ?Sirenidae

        cf. *Habrosaurus* sp. [6]

    ?Amphiumidae

        cf. *Proamphiuma* sp. [6]

    Family incertae sedis

        Gen. et sp. indet. [1, 5]

Anura

    Discoglossidae sensu lato

        Gen. et sp. indet. [6]

    Pelobatidae sensu lato

        Gen. et sp. indet. [6]

    Palaeobatrachidae

        (?)*Palaeobatrachus occidentalis* [3]

    Family incertae sedis

        cf. *Scotiophryne* sp. [6]

        cf. *Theatonius* sp. [6]

        Gen. et sp. indet. (multiple taxa) [3, 5, 6, 8, 10, 11]

Localities are denoted by the same *numbers* (*1–12*) used in the corresponding locality map (Fig. 7) and ESM Appendix 5. "Edmontonian" localities (*1–5*) are listed first; other localities are listed approximately east to west and north to south. Numbers in square brackets denote localities: bold numbers denote holotype localities; numbers with an asterisk denote only genus reported; underlined numbers denote occurrences needing verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* Kleskun Hill Park, west-central Alberta, Canada; middle part of Wapiti Formation; late Campanian ("Edmontonian" NALMA) (Fanti and Miyashita 2009; Nydam et al. 2010; Tanke 2004). *2* Red Willow Falls, west-central Alberta, Canada; middle part of Wapiti Formation; late Campanian ("Edmontonian" NALMA) (Fanti et al. 2013). *3* Multiple localities, Red Deer River Valley, south-central Alberta, Canada; upper part of Horseshoe Canyon Formation; early Maastrichtian ("Edmontonian" NALMA) (Eberth et al. 2001; Larson et al. 2010). *4* Scabby Butte, southern Alberta, Canada; St. Mary River Formation; late Campanian–early Maastrichtian ("Edmontonian" NALMA) (Gardner 2000a; Langston 1975, 1976). *5* Unspecified locality(ies), Rio Blanco County, northwestern Colorado, USA; Williams Fork Formation; late Campanian–early Maastrichtian ("Edmontonian"

NALMA) (Archibald 1987). *6* Ellisdale, Monmouth County, New Jersey, USA; Marshalltown Formation; middle Campanian and possibly equivalent to Aquilan and Judithian NALMAs (Denton and O'Neill 1998, 2012). *7* Bladen County Landfill Annex, Bladen County, North Carolina, USA; Bladen Formation; Campanian (Crane 2011, 2012). *8* Meetinghouse Canyon, east-central Utah, USA; Blackhawk Formation; Campanian (Robison 1991). *9* Unspecified locality(ies) in Adobe Canyon area, southeastern Arizona, USA; Fort Crittenden Formation, late? Campanian and possibly equivalent to Judithian NALMA (Heckert et al. 2003; Lucas and Heckert 2005; McCord et al. 2001; Ratkevich and Duffek 1996). *10* Unspecified locality(ies), western Baja California, Mexico; "El Gallo Formation", Campanian and possibly equivalent to "Edmontonian" NALMA (Lillegraven 1972, 1976). *11* La Parrita, Coahuila, northeastern Mexico; Cerro del Pueblo Formation; late Campanian (Aguillon Martinez 2010). *12* Harebell vertebrate locality, Teton County, northwestern Wyoming; Bobcat Member, Harebell Formation; Maastrichtian (Breithaupt 1985; Love 1973; McKenna 1980). Taxonomic authorships provided only for species named on material from the indicated time interval. See text and ESM Appendix 5 for further information about taxonomic identifications presented in this faunal list

CEN=Cenomanian; CON=Coniacian; CRN=Carnian; DAN=Danian; HAUT=Hauterivian; HETT=Hettangian; KIMM=Kimmeridgian; MAAS=Maastrichtian; NOR=Norian; OXF=Oxfordian; PLIE=Pliensbachian; RHT=Rhaetian; SANT=Santonian; SEL=Selandian; SIN=Sinemurian; THA=Thanetian; TITH=Tithonian; TOAR=Toarcian; TUR=Turonian; VAL=Valanginian; YPR=Ypresian.

North American Land Mammal Ages (NALMA): Cf=Clarkforkian; "Ed"="Edmontonian"; La=Lancian; Pu=Puercan; To=Torrejonian; Wa=Wasatchian.

North American political abbreviations

Canada: AB=Alberta; SK=Saskatchewan.
Mexico (MEX): BJ=Baja California.
United States of America (USA): AZ=Arizona; CO=Colorado; ID=Idaho; MT=Montana; NC=North Carolina; ND=North Dakota; NJ=New Jersey; NM=New Mexico; NV=Nevada; OK=Oklahoma; SD=South Dakota; TX=Texas; UT=Utah; VA=Virginia; WY=Wyoming.

Institutional abbreviations

AMNH=American Museum of Natural History, New York, New York, USA; ANSP=Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; CM=Carnegie Museum, Pittsburgh, Pennsylvania, USA; CMN=Canadian Museum of Nature (formerly National Museum of Canada), Ottawa, Ontario, Canada; DINO=US National Parks Service, Dinosaur National Monument, Utah, USA; DMNH=Denver Museum of Nature and Science (formerly the Denver Museum of Natural History), Denver, Colorado, USA; FMNH=Field Museum of Natural History, Chicago, Illinois, USA; KUVP=University of Kansas Vertebrate Paleontology collection, Lawrence, Kansas, USA; LACM=Natural

Table 6 Latest Cretaceous (late Maastrichtian; Lancian NALMA) lissamphibian occurrences[a] in North America

Albanerpetontidae

   Albanerpeton nexuosum (Estes, 1981) [8, **13**, 14, 16]

   Albanerpeton galaktion [8, 14]

   Gen. et sp. indet. [1, 5, 6, 8, 9, 12, 13, 14]

Urodela

   Scapherpetontidae

      Scapherpeton tectum [3 *, 5, 7, 8, 9, 11, 12*, 13, 14, 15, 16]

      cf. *Scapherpeton tectum* [1]

      Lisserpeton bairdi [8, 10, 13, 14, 16]

      Piceoerpeton naylori [8, 13]

      cf. *Piceoerpeton* sp. [8]

      Gen. et sp. nov. 1 [8, 9]

      Gen. et sp. nov. 2 [8, 9]

   Batrachosauroididae

      Opisthotriton kayi Auffenberg, 1961 [4*, 5, 8, 9, 10, 11, 12*, **13**, 14, 16]

      cf. *Opisthotriton kayi* [1]

      Prodesmodon copei Estes, 1964 [5, 8, 9, 12*, **13**, 14]

      Gen. et sp. nov. 4 [13]

      Gen. et sp. indet. [8]

   Sirenidae

      Habrosaurus dilatus Gilmore, 1928b [5, 8, 9, 11, **13**, 14, 15, 16]

      Habrosaurus prodilatus [8]

      Habrosaurus sp. [12]

   Amphiumidae

      Proamphiuma cretacea [9]

   Proteidae

      Paranecturus garbanii DeMar, 2013 [**8**]

   Family incertae sedis

      Gen. et sp. indet. [2, 5, 9, 15, 16]

Anura

   Palaeobatrachidae

      Palaeobatrachus? *occidentalis* (Estes and Sanchíz, 1982) [**13**]

   Family incertae sedis

      Scotiophryne pustulosa [5, 8, 13]

      Paradiscoglossus americanus Estes and Sanchíz, 1982 [**13**]

      Theatonius lancensis Fox, 1976b [8, **13**]

      cf. *Eopelobates* sp. [13, 14]

      Gen. et sp. indet. (multiple taxa) [1, 5, 8, 9, 11, 12, 13, 17]

[a] Localities are denoted by the same *numbers* (*1–17*) used in the corresponding locality map (Fig. 8) and ESM Appendix 6. Localities are listed north to south within each province and state. Numbers in square brackets denote localities: numbers in bold denote holotype localities; numbers with an asterisk denote only genus reported; underlined numbers denote occurrences needing verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* KUA-1 and unspecified localities, Red Deer River Valley, south-central Alberta, Canada; lower part of Scollard Formation (Eberth et al. 2001; Gardner 2000a; Gardner and Böhme 2008). *2* Long Fall horizon in Medicine Hat Brick and Tile Quarry, Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; Frenchman Formation (Fox 1990). *3* FR-1,

Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; Frenchman Formation (Johnston 1980). *4* "Scotty" Quarry (RSMNH loc. 72F07-0022) Frenchmen River Valley, south of Shaunavon, southwestern Saskatchewan, Canada; Frenchman Formation (Tokaryk and Bryant 2004). *5* Wounded Knee locality, Frenchmen River Valley, south of Shaunavon, southwestern Saskatchewan, Canada; Frenchman Formation (Fox 1989; Gardner 2000a, 2003a; Gardner and Böhme 2008). *6* Gryde locality (= RSMNH loc. 72F08-0012), Frenchmen River Valley, south of Shaunavon, southwestern Saskatchewan, Canada; Frenchman Formation (Gardner 2000a; Gardner and Böhme 2008; Storer 1991). *7* Morgan Creek Badlands (= Killdeer Badlands), south-central Saskatchewan, Canada; Frenchman Formation (Sternberg 1924). *8* Localities in Garfield County, northeastern Montana, USA; Hell Creek Formation (Bryant 1989; DeMar 2011, 2013; DeMar and Wilson, unpublished observation; Wilson et al. 2014). *9* Localities in Slope and Bowman counties, southwestern North Dakota, USA; Hell Creek Formation (Gardner and Pearson, unpublished observation; Pearson et al. 2002). *10* NDSFC loc. L064, Logan County, south-central North Dakota, USA; Iron Lightning Member, Fox Hills Formation (Hoganson et al. 2007). *11* SDSMT localities, Harding County, northwestern South Dakota, USA; Hell Creek Formation (Greenwald 1971). *12* "Sue" Quarry, Cheyenne River Indian Reservation, northwestern South Dakota, USA; Hell Creek Formation (Gates et al. 2010; T. Gates, personal communication). *13* Type Lance localities and Greasewood Creek, all Niobrara County, east-central Wyoming, USA; Lance Formation (Auffenberg 1961; Auffenberg and Goin 1959; Estes 1964, 1965, 1969b, 1981; Estes and Sanchíz 1982; Fox 1976b; Gardner 2000a, b, 2003a, 2005, 2008, 2012; Gilmore 1928b; Goin and Auffenberg 1958; Naylor 1979; Whitmore and Martin 1986). *14* Robber's Roost locality (UW V-79032), Sweetwater County, south-central Wyoming, USA; Lance Formation (Breithaupt 1982; Gardner 2000a, unpublished observation). *15* Localities in the Hanna Basin, southeastern Wyoming, USA; lower part of Ferris Formation (Lillegraven and Eberle 1999; Wroblewski 1997). *16* Localities in the Cheyenne Basin, northeastern Colorado, USA; Laramie Formation and D1 Sequence of Denver Formation (Carpenter 1979; Gardner 2000a; G. Wilson unpublished observation). *17* OMNH loc. V812, central Utah, USA; lower part of North Horn Formation (Cifelli et al. 1999b). Taxonomic authorships provided only for species named on material from the indicated time interval. See text and ESM Appendix 6 for further information about taxonomic identifications presented in this faunal list

History Museum, Los Angeles County, Los Angeles, California, USA; LSUMG=Louisiana State University Museum of Geology, Baton Rouge, Louisiana, USA; MCZ=Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNA= Museum of Northern Arizona, Flagstaff, Arizona, USA; MOR=Museum of the Rockies, Montana State University, Bozeman, Montana, USA; NCSM=North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA; NDGS=North Dakota Geological Survey, Bismarck, North Dakota, USA; NDSFC=Noth Dakota State Fossil Collection, North Dakota Heritage Center, Bismarck, North Dakota, USA; NJSM=New Jersey State Museum, Trenton, New Jersey, USA; OMNH=Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, USA; PTRM=Pioneer Trials Regional Museum, Bowman, North Dakota, USA; PU=Princeton University Collection [now at Yale Peabody Museum (YPM)]; RSMNH=Royal

Table 7 Mixed latest Maastrichtian (Lancian NALMA) and earliest Palaeocene (Puercan NALMA) lissamphibian occurrences from the Bug Creek Anthills locality, McCone County, northeastern Montana, USA; Hell Creek Formation[a]

Albanerpetontidae
Albanerpeton nexuosum
Gen. et sp. indet.
Urodela
Scapherpetontidae
Scapherpeton tectum
Lisserpeton bairdi Estes, 1965
Piceoerpeton naylori Gardner, 2012
Gen. et sp. nov. 1
Batrachosauroididae
Opisthotriton kayi
Prodesmodon copei
Sirenidae
Habrosaurus dilatus
Amphiumidae
Proamphiuma cretacea Estes, 1969c
?Cryptobranchidae
Gen. et sp. indet.
Anura
Palaeobatrachidae
Palaeobatrachus? *occidentalis*
Family incertae sedis
Scotiophryne pustulosa Estes, 1969b
cf. *Eopelobates* sp.
Gen. et sp. indet. (multiple taxa)

[a] This locality is plotted as "BCA" on the Lancian locality map (Fig. 8). Bug Creek Anthills is the type locality for taxa in bold. References for these occurrences are as follows: DeMar and Wilson (unpublished observation); Estes (1965, 1969b, c, 1981); Estes and Berberian (1970); Estes et al. (1969); Gardner (2000a, b, 2003a, b, 2008, 2012, unpublished observation); and Naylor (1983). Taxonomic authorships are provided only for species named on material from Bug Creek Anthills. See text and ESM Appendix 7 for further information about taxonomic identifications presented in this faunal list

Saskatchewan Museum of Natural History, Regina, Saskatchewan, Canada; SDSMT=South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; SEPCP=Coordinación de Paleontología, Museo del Desierto, Paleontological Collection-Vertebrates, Saltillo, Coahuila, Mexico; SMM=Science Museum of Minnesota, St. Paul, Minnesota, USA; SMU=Southern Methodist University, Dallas, Texas, USA; TMM=Texas Memorial Museum, Austin, Texas, USA; TMP=Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALP=University of Arizona Laboratory of Paleontology, Tucson, Arizona, USA; UALVP=University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; UC=University of Chicago, Chicago, Illinois,

USA; UCM=University of Colorado Museum, Boulder, Colorado, USA; UCMP=University of California Museum of Paleontology, Berkeley, California, USA; UM=University of Michigan, Ann Arbor, Michigan, USA; UMNH=Utah Museum of Natural History, Salt Lake City, Utah, USA; USNM=National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UW=University of Wyoming Collection of Fossil Vertebrates, University of Wyoming, Laramie, Wyoming, USA; UWBM=University of Washington Burke Museum of Natural History and Culture, Seattle, Washington, USA; YPM=Yale Peabody Museum, New Haven, Connecticut, USA.

Other abbreviations

BCA=Bug Creek Anthills locality; ESM = electronic supplementary material; loc. = locality; locs. = localities; Ma=million years ago; Myr=millions of years; UK = United Kingdom.

Chronological Review of the North American Mesozoic and Palaeocene Lissamphibian Fossil Record

Introductory remarks

Below we present a chronological review of the lissamphibian record in North America from the Mesozoic Era and Palaeocene Epoch. Our review is augmented by photos of some representative specimens and taxa (Figs. 1 and 2), locality maps and time charts (Figs. 3, 4, 5, 6, 7, 8, 9, and 10) and faunal lists (Tables 1, 2, 3, 4, 5, 6, 7, 8, and 9), all in the text, and by ESM Appendices 1–9. Useful summaries of lissamphibian records outside the temporal and geographic scope of our review can be found in the following publications: Báez (2000: South American Tertiary anurans); Estes (1981: global gymnophionan, caudate and albanerpetontid records); Gardner and Böhme (2008: global albanerpetontid record); Holman (2003, 2006: North American anuran and caudate records, respectively); Milner (2000: global caudate and albanerpetontid records); Roček (2000: global Mesozoic anuran record; 2013, this issue: Laurasian Mesozoic and Tertiary anuran record); Roček and Rage (2000: Tertiary anurans from continents other than South America); Sanchiz (1998: global anuran records); Skutschas (2013, this issue: Mesozoic caudates and albanerpetontids of Middle Asia, Kazakhstan and Siberia); Szentesi et al. (2013: European Late Cretaceous lissamphibians); Wang (2004: Mesozoic anurans and caudates of China). Informative summaries of geography, climate, environments and other relevant topics for the interval and continent covered in our review are presented in chapters in edited volumes by Brett-Surman et al. (2012) and Weishampel

Table 8 Early Palaeocene (Puercan and Torrejonian NALMAs) lissamphibian occurrences[a] in North America

Puercan

Lissamphibia

  Order, family, genus, and species indet. [3]

Urodela

  Scapherpetontidae

    Scapherpeton tectum [4, 5, 6, 8]

    Lisserpeton bairdi [4, 5, 6]

    Gen. et sp. indet. [9]

  Batrachosauroididae

    Opisthotriton kayi [1, 2, 4, 5, 6, 9, 10, 12]

    Prodesmodon copei [4, 5, 10]

  Sirenidae

    Habrosaurus dilatus [4, 8]

    Habrosaurus sp. [10, 12]

  Amphiumidae

    Proamphiuma cretacea [4]

  Family incertae sedis

    Gen. et sp. indet. [2, 7, 10, 11]

Anura

  Family incertae sedis

    Gen. et sp. indet. [2, 4, 6, 12]

Torrejonian

Albanerpetontidae

  Gen. et sp. indet. [14]

Urodela

  Scapherpetontidae

    Scapherpeton tectum [15*, 16, 18, 19]

    cf. *Scapherpeton tectum* [17]

    Lisserpeton bairdi [16, 18]

  Batrachosauroididae

    Opisthotriton kayi [13, 16, 17, 18, 19]

    Opisthotriton gidleyi nomen dubium (Sullivan, 1991) [**17**]

  Sirenidae

    Habrosaurus dilatus [16, 17, 18, 20]

    Habrosaurus sp. [19]

Anura

  Family incertae sedis

    cf. *Scotiophryne* sp. [16]

    Gen. et sp. indet. [16]

Puercan or Torrejonian

Anura

  Palaeobatrachidae

    Palaeobatrachus occidentalis [21]

  Family incertae sedis

    Gen. et sp. indet. [21]

[a] Localities are denoted by the same *numbers* (*1–21*) used in the corresponding locality map (Fig. 9) and ESM Appendix 8. Localities are grouped by NALMA (Puercan: *1–12*; Torrejonian: *13–20*; Puercan or

Torrejonian: *21*). Numbers in square brackets denote localities: bold numbers denote holotype localities; numbers with an asterisk denote only genus reported; underlined numbers denote occurrences needing verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* UALVP Genesee #2 locality, central Alberta, Canada; upper part of Scollard Formation (Gardner 2000b; Naylor 1981a). *2* Rav W-1 horizon in Medicine Hat Brick and Tile Quarry, Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; lower part of Ravenscrag Formation (Fox 1990; Johnston and Fox 1984; Naylor 1981a). *3* Croc Pot, Frenchmen River Valley, northwest of Ravenscrag, southwestern Saskatchewan, Canada; lower part of Ravenscrag Formation (Fox 1990). *4* Localities in Garfield County, northeastern Montana, USA; Tullock Formation (Bryant 1989; DeMar 2011; DeMar and Wilson, unpublished observation; Wilson et al. 2014). *5* Purgatory Hill, McCone County, northeastern Montana, USA; Tullock Formation (Van Valen and Sloan 1965). *6* PTRM localities, Slope and Bowman counties, southwestern North Dakota; Fort Union Formation (Gardner and Pearson, unpublished observation). *7* Unnamed locality, Bighorn Basin, Park County, north-central Wyoming, USA; "Hunt Creek member", Fort Union Formation (Johnson 1986). *8* Bugger-to-get-to (UW loc. V-82010), Washakie County, north-central Wyoming, USA; Polecat Bench Formation (Hartman 1986). *9* Alexander locality (UCM loc. 77267), Arapahoe County, north-central Colorado, USA; Denver Formation (Gardner, unpublished observation; Middleton and Dewar 2004). *10* West Bijou Creek locality (UCM loc. No. 78191), Denver Basin, Elbert County, northeastern Colorado, USA; Denver Formation (Gardner, unpublished observation). *11* Kimbetoh E (UCMP loc. V1312), San Juan County, northwestern New Mexico, USA; Nacimiento Formation (Sullivan and Lucas 1986; Williamson and Lucas 1993). *12* Localities in Big Bend National Park, Brewster County, southwestern Texas, USA; upper part of Javelina Member, Tornillo Formation (Standhardt 1986). *13* Diss, west-central Alberta, Canada; Coalspur Formation (Fox 1990). *14* ?Who Nose, Calgary, southern Alberta, Canada; Paskapoo Formation (Gardner and Böhme 2008). *15* Locality 2E (sensu Russell 1929), Elbow River, Calgary, southern Alberta, Canada; Paskapoo (= Porcupine Hills) Formation (Russell 1929). *16* Medicine Rocks I localities, Carter County, southeastern Montana, USA; Fort Union Formation (= Tongue River Formation) (Estes 1976). *17* Gidley Quarry, Sweetgrass County, south-central Montana, USA; Lebo Formation (Sullivan 1991); note a *Habrosaurus dilatus* palatine reported by Gardner (2003a) comes from the same county and formation, but is not certainly from Gidley Quarry (see ESM Appendix 8). *18* Rock Bench Quarry, Park County, northwestern Wyoming, USA; Fort Union Formation (Krause 1980). *19* Swain Quarry, Carbon County, south-central Wyoming, USA; Fort Union Formation (Sullivan 1980, 1991). *20* Kutz Canyon, San Juan County, northwestern New Mexico, USA; Nacimiento Formation (Sullivan and Lucas 1986). *21* Sheep Pass Canyon, southern Egan Range, east-central Nevada, USA; Member B, Sheep Pass Formation (Bonde et al. 2011; Shirk et al. 2009). Taxonomic authorships provided only for species named on material from the indicated time interval. See text and ESM Appendix 8 for further information about taxonomic identifications presented in this faunal list

et al. (2004) for the Mesozoic and by Janis et al. (1998) for the Palaeocene.

Late Triassic

There are two equivocal reports of Late Triassic lissamphibians from the Newark Supergroup in the eastern USA (Fig. 3, Table 1): a fragmentary jaw from the Tomahawk locality, in the middle Carnian age Vinita Formation, east-central Virginia

Table 9 Late Palaeocene (Tiffanian and Clarkforkian NALMAs) lissamphibian occurrences[a] in North America

Tiffanian

Albanerpetontidae

  Albanerpeton sp. nov. [2, 4]

Urodela

  Scapherpetontidae

    Scapherpeton tectum [2*, 5*, 7*, 13]

    Lisserpeton bairdi [14]

    Piceoerpeton willwoodense [3, 5, 7, 8, 10, 11, 12, 14]

  Batrachosauroididae

    Opisthotriton kayi [2*, 5, 13, 15]

  Amphiumidae

    Amphiuma jepseni Estes, 1975 [13]

    Gen. et sp. indet. [5]

  Cryptobranchidae

    Cryptobranchus saskatchewanensis Naylor, 1981b [5]

  Dicamptodontidae

    Dicamptodon antiquus Naylor and Fox, 1993 [1]

    Ambystomichnus montanensis (Gilmore, 1928a) [9]

  Proteidae

    Necturus krausei Naylor, 1978b [5]

  Family indet.

    Gen. et sp. indet. [1, 5, 6, 7]

Anura

  Rhinophrynidae

    Eorhinophrynus sp. [13]

  Family indet.

    Gen. et sp. indet. [2, 5, 7, 13]

Clarkforkian

Urodela

  Scapherpetontidae

    Piceoerpeton willwoodense (Meszoely, 1967) [17, 18]

  Batrachosauroididae

    Opisthotriton kayi [16*, 17]

  Cryptobranchidae

    Cryptobranchus saskatchewanensis [19]

  Family indet.

    Gen et sp. indet. [20, 21]

Anura

  Family indet.

    Gen. et sp. indet. [20]

late Palaeocene or early Eocene

Anura

  Family indet.

    Eorubeta nevadensis [22]

    Gen. et sp. indet. [22]

[a] Localities are denoted by the same *numbers* (*1–22*) used in the corresponding locality map (Fig. 10) and ESM Appendix 9. Localities are grouped by NALMA (Tiffanian: *1–15*; Clarkforkian: *16–21*; late

Palaeocene or early Eocene: *22*). Numbers in square brackets denote localities: bold numbers denote holotype localities; numbers with an asterisk denote only genus reported; underlined numbers denote occurrences needing verification (e.g. no voucher specimen listed, described or figured; problematic specimens; provenance suspect). *Localities*: *1* UALVP Smoky Tower #1 locality, west-central Alberta, Canada; Paskapoo Formation (Gardner, unpublished observation; Naylor and Fox 1993). *2* UALVP DW localities along Blindman River, central Alberta, Canada; Paskapoo Formation (Fox 1984; Fox and Naylor 1982; Gardner 2000c; Gardner and Böhme 2008). *3* Canyon Ski Quarry along Red Deer River, central Alberta, Canada; Paskapoo Formation (Fox 1984; Naylor and Krause 1981). *4* Cochrane 2, south-central Alberta, Canada; Paskapoo (= Porcupine Hills) Formation (Gardner and Böhme 2008). *5* Roche Percée localities, southeastern Saskatchewan, Canada; upper part of Ravenscrag Formation (Gardner 2003b, 2012; Naylor 1978b, 1981a, b; Naylor and Krause 1981). *6* Almont locality, Morton County, central North Dakota, USA; Sentinel Butte Formation (Gardner and Newbrey unpublished observation). *7* Wannagan Creek Quarry, Billings County, southwestern North Dakota, USA; Tongue River (= Bullion Creek) Formation (Erickson 1991, 1999, 2012; Gardner 2012; Naylor and Krause 1981). *8* Brisbane locality, Grant County, southwestern North Dakota, USA; Tongue River Formation (Gardner 2012; Naylor and Krause 1981). *9* Unspecified locality, Bear Butte, Sweetgrass County, south-central Montana, USA; Fort Union Formation (Gilmore 1928a; Peabody 1954, 1959). *10* Highway Blowout locality, Carter County, southeastern Montana, USA; Tongue River Formation (Naylor and Krause 1981). *11* Olive locality, southeastern Montana, USA; Tongue River Formation (Naylor and Krause 1981). *12* UM loc. SC-198 (Fossil Hollow) and UM loc. SC-273, both Park County, northwestern Wyoming, USA; Polecat Bench Formation (Krause 1980; Naylor and Krause 1981). *13* Princeton Quarry local fauna (Princeton [= Silver Coulee], Fritz, and Schaff quarries), Park County, northwestern Wyoming, USA; Fort Union (= Polecat Bench) Formation (Estes 1969c, d, 1975). *14* Cedar Point Quarry, Bighorn County, northwestern Wyoming, USA; Fort Union (= Polecat Bench) Formation (Gardner 2012; Krause 1980; Naylor and Krause 1981). *15* UM loc. SC-270, Park County, northwestern Wyoming, USA; Fort Union Formation (Krause 1980). *16* Bear Creek local fauna, Carbon County, south-central Montana, USA; Willwood Formation (Auffenberg 1961). *17* UM loc. FG-6, Foster Gulch, Bighorn County, northwestern Wyoming, USA; ?Polecat Bench Formation (Gardner 2012; Naylor and Krause 1981). *18* UM loc. SC-171 and unnamed locality (= type locality for *Piceoerpeton willwoodense*), Park County, northwestern Wyoming, USA; Willwood Formation (Gardner 2012; Meszoely 1967; Naylor and Krause 1981). *19* ?UM loc. SC-227, Park County, northwestern Wyoming, USA; Willwood Formation (Krause 1980; Naylor 1981b). *20* SC-29 Discovery Site (carbonate lens J), Park County, northwestern Wyoming, USA; Willwood Formation (Gingerich 1987). *21* Big Multi Quarry, Sweetwater County, southwestern Wyoming, USA; Fort Union Formation (Wilf et al. 1998). *22* Sheep Pass Canyon, southern Egan Range, east-central Nevada, USA; Member C, Sheep Pass Formation (Shirk et al. 2009; Bonde et al. 2011); note this member straddles the Paleocene/Eocene boundary, but the occurrence is included here for completeness. Taxonomic authorships provided only for species named on material from the indicated time interval. See text and ESM Appendix 9 for further information about taxonomic identifications presented in this faunal list. designate localities

(Sues and Olsen 1990) and an atlantal centrum and fragmentary ilia from the Moncure locality, in the early Norian age Cumnock Formation, central North Carolina (Heckert et al. 2012). Although the small size and structure of these specimens are suggestive of lissamphibians, none is unambiguously diagnostic for Lissamphibia (Heckert et al. 2012; Milner 1994; Sues and Olsen 1990). The Newark Supergroup contains

numerous fossiliferous localities in rift basins along the eastern coast of North America that collectively have yielded a diversity of Triassic freshwater and terrestrial vertebrate taxa (e.g. Sues and Fraser 2010; Sues et al. 1994b). Heckert et al. (2012) noted that compared to other localities in the Newark Supergroup, the Tomahawk and Moncure localities are similar in their lithofacies (mud and siltstones), in their inferred depositional environments (lacustrine or marginal lacustrine) and in that both localities have yielded abundant small fossils recovered by surface collecting and screenwashing. That combination of factors may at least partly explain why out of the entire Newark Supergroup, only that pair of localities has produced possible lissamphibian fossils. It is worth mentioning that fossiliferous, continental Late Triassic age beds are also widely exposed in the western USA (see review by Sues and Fraser 2010). In that region, certain localities, such as the Placerias Quarry and SMU loc. 252, both in the Chinle Formation of Arizona, were deposited under wet palaeoenvironments seemingly suitable for lissamphibians and have yielded abundant, small vertebrate bones (e.g. Kaye and Padian 1994; Polcyn et al. 2002), but there is no indication of lissamphibians.

Early Jurassic

The oldest, unequivocal records of lissamphibians in North America are from the Kayenta Formation, the age of which is poorly constrained to the Sinemurian–Pliensbachian based on its palynoflora, scutes of the dinosaur *Scelidosaurus* and magnetostratigraphic evidence (see summary by Curtis and Padian 1999). Small-bodied tetrapods are known from several localities in the Kayenta Formation (e.g. Curtis and Padian 1999; Sues et al. 1994a), but lissamphibians only have been reported from one locality, namely Gold Spring Quarry 1 in northeastern Arizona (Fig. 3, Table 1). Hand quarrying at that locality from 1977 to 1983 yielded numerous skulls, skeletons and isolated bones (e.g. Fig. 1a) of the world's oldest known stem caecilian *Eocaecilia micropodia* Jenkins and Walsh, 1993, which is notable for retaining girdles and limbs that have been lost in crown caecilians, and several partially associated skeletons of the world's oldest known crown frog *Prosalirus bitis* Shubin and Jenkins, 1995. Both taxa have been described, figured and interpreted in detail (e.g. Jenkins and Shubin 1998; Jenkins and Walsh 1993; Jenkins et al. 2007; Maddin et al. 2012; Shubin and Jenkins 1995). Screenwashing of a spoil pile at Gold Spring Quarry 1 also recovered a modest collection of isolated elements, including lissamphibian jaws, atlantes and trunk vertebrae, ilia and limb bones, which was described by Curtis and Padian (1999). Now that *Prosalirus* and *Eocaecilia* have been more fully described, it seems evident that many of the lissamphibian specimens described and figured by Curtis and Padian (1999) likely pertain to those genera. The identity of the supposed urodele atlantes reported

by those authors deserves further comment. If that identification is correct, those specimens would be the oldest global record for caudates. In this context, we disregard the problematic *Triassurus sixtelae* Ivachnenko, 1978 from the Late Triassic of Kirghizia; although that species originally was described as a caudate, it is no longer regarded as such (e.g. Estes 1981; Milner 1994; Skutschas 2013, this issue). While Holman (2006) accepted the Kayenta atlantes as being from urodeles, others have questioned that identification (Sues et al. 1994a). Several workers have suggested that those atlantes may instead pertain to albanerpetontids (Averianov et al. 2008; Gardner and Böhme 2008; Skutschas 2007; Sweetman and Gardner 2013), which if correct would be the oldest global record for Albanerpetontidae. Recent examination of those atlantes indicates they likely are assignable to *Eocaecilia* (Gardner, Skutschas and Sweetman unpublished observation); a more detailed consideration of those specimens is in preparation and will be presented elsewhere.

Late Jurassic

Following a substantial hiatus of at least 30 million years in the North American fossil record, lissamphibians next are documented from localities scattered across Wyoming, Utah, and Colorado within the Morrison Formation (Fig. 3). All known lissamphibian localities are in the upper part of the formation, within deposits of predominantly lacustrine or paludal origins in the Brushy Basin Member or equivalents and are widely considered to be Kimmeridgian–earliest Tithonian in age (e.g. Foster 2007; Kielan-Jaworowska et al. 2004). Caudates and anurans are represented by rare articulated and associated skeletons recovered through quarrying and also by isolated bones obtained through quarrying, surface collecting and screenwashing. In terms of the quality and abundance of specimens and identifiable taxa, the most productive and important localities in the Morrison Formation are Quarry 9 at Como Bluff, southeastern Wyoming, and the Rainbow Park localities, in the Utah portion of Dinosaur National Monument; good overviews of those areas are provided by Carrano and Velez-Juarbe (2006) and Foster (2007). On the basis of specimens from Quarry 9 and Rainbow Park, the lissamphibian assemblage from the upper part of the Morrison Formation (see Table 1) contains at least seven anuran species (only two of which are formally named), one named urodele species and one undescribed caudate species of uncertain affinities. Additionally, three nomina dubia species (two anurans and one caudate) have been named on material from Quarry 9, and there are unverified reports of stem salamanders at both Quarry 9 and Rainbow Park.

Quarry 9 has yielded only isolated lissamphibian bones, including those of the anuran *Eobatrachus agilis* nomen dubium (Marsh, 1887), a taxon that has the distinction of being the first Mesozoic frog to be described from anywhere in the

world. Subsequent work has convincingly demonstrated that the isolated bones originally assigned to that taxon (holotype humerus and referred atlas, tibiofibula, urostyle and ilium: Marsh 1887; Moodie 1912, 1914) pertain to an assortment of taxa, including one or more anurans, a caudate and an indeterminate reptile (Hecht and Estes 1960). Furthermore, the holotype humerus is not diagnostic beyond Anura, which renders the name *E. agilis* a nomen dubium (Evans and Milner 1993; = nomen vanum according to Sanchiz 1998). Two other lissamphibian taxa, both of which are now also considered nomina dubia (Evans and Milner 1993), have been named for isolated limb bones from Quarry 9: the caudate *Comonecturoides marshi* Hecht and Estes, 1960 and the anuran *Comobatrachus aenigmatis* Hecht and Estes, 1960. The only currently named and accepted lissamphibian species from Quarry 9 is the anuran *Enneabatrachus hechti* Evans and Milner, 1993, which is based on an incomplete ilium and may be a discoglossid sensu lato. Also from Quarry 9, Evans and Milner (1993) briefly described a second ilium as belonging to a possible pelobatid sensu lato, two indeterminate anuran humeri and vertebrae pertaining to one or more indeterminate caudates. In their abundance table for Quarry 9, Carrano and Velez-Juarbe (2006, table 2) reported 110 "Amphibia" specimens. Many of those specimens remain undescribed, which raises the possibility that additional lissamphibian taxa or more informative specimens of previously reported lissamphibian taxa may be represented in existing collections.

Farther to the west in northeastern Utah, important collections of small-bodied tetrapods have been obtained by hand quarrying and screenwashing at localities in Rainbow Park, northeastern Utah (see Foster 2007). The first detailed report of lissamphibians from Rainbow Park was by Henrici (1998a), who preliminarily recognised the following five anuran taxa: (1) an indeterminate genus and species on the basis of an isolated ilium; (2) a second indeterminate genus and species on the basis of an associated pair of ilia; (3) an indeterminate, possible discoglossid on the basis of an isolated ilium; (4) cf. *Enneabatrachus hechti*, identified from associated postcranial bones on a slab; (5) an undescribed new genus and species of pipoid represented by several partially disarticulated skeletons of metamorphic and recently transformed individuals. The last of those taxa was formally described as *Rhadinosteus parvus* Henrici, 1998b and tentatively assigned to the Rhinophrynidae, a family of endemic North American anurans known by three monotypic genera—two Palaeogene and one Recent. Although its familial affinities are not known with certainty, *Rhadinosteus* documents the oldest North American occurrence for Pipoidea, which in addition to containing Rhinophrynidae also includes the South American and African Pipidae and the extinct European and western Asian Palaeobatrachidae (e.g. Ford and Cannatella 1993; Henrici 1998b; Sanchiz 1998). The other named lissamphibian from Rainbow Park is the

Fig. 11 Diversity curves depicting temporal lissamphibian taxonomic richness during the Mesozoic and Palaeocene of North America, based on occurrences documented for this review. Taxonomic richness is equal to the number of species per 5-Myr bin and depicted for each major lissamphibian clade (Anura, Caudata, Albanerpetontidae and Gymnophiona) and collectively summarised for Lissamphibia (*far left curve*). *Values* at the *top of each curve* are numbers of species. *Values* at the *bottom of the Lissamphibia curve* are total numbers of published lissamphibian records, including our unpublished observations documented in this paper per 5-Myr time bin (see ESM Appendix 12 for the raw data). These values crudely reflect the amount of 'sampling' or research effort afforded for each time interval and are used as a means to roughly estimate sampling bias. Raw taxic or species richness is indicated by the *vertical solid black line*. Minimal lineage level richness is represented by the *vertical dotted black line*. *Total records* refers to the level of 'sampling' or research effort per bin and is illustrated by the *vertical solid grey line* in the Lissamphibia curve. Fossiliferous intervals are *shaded*. Putative lissamphibians from the Late Triassic (see text for details) are represented by a *question mark below the Lissamphibia curve*. The *solid horizontal black line near the top of the figure* denotes the K-Pg boundary, which for the purposes of our study we placed at 65.5 Ma. One hypothesis of evolutionary relationships among the major lissamphibian clades is shown in the cladogram on the *bottom right of the figure* and with each clade depicted by a *silhouette below their respective richness curves*. The albanerpetontid silhouette is modified from McGowan and Evans (1995, fig. 2a). Boundary dates are based on the Geologic Time Scale assembled by Walker and Geissman (2009). See text and ESM Appendices 10 and 11 for details on methodology and data used to calculate the temporal taxonomic richness curves

urodele *Iridotriton hechti* Evans et al., 2005. It is known by an incomplete skeleton and was one of the first lissamphibian fossils to be described, in part, using the then-new imaging technology of micro-computed tomography. *Iridotriton* was interpreted by Evans et al. (2005) as a probable stem salamandroid, but more recently Gao and Shubin (2012) suggested it is a cryptobranchid. Regardless of its exact phylogenetic position, *Iridotriton* documents the earliest unequivocal appearance of a crown salamander in North America. A second, undescribed caudate from Rainbow Park is represented by several partially disarticulated skeletons preserved together (e.g. Fig. 1c); because study of these specimens is at a preliminary stage (Gardner and Chure, work in progress), here we conservatively identify this taxon only to the level of Caudata.

There are two unverified reports of possible stem salamander atlantes from the Morrison Formation. In a conference abstract, Nessov (1992) mentioned one or more isolated atlantes from Dinosaur National Monument as exhibiting features diagnostic for Karauridae, a family of stem salamanders known only from the Middle Jurassic of Kyrgyzstan and the Late Jurassic of Kazakhstan (e.g. Skutschas and Martin 2011; Skutschas 2013, this issue). Although intriguing, this identification cannot be verified because the relevant specimens were not described or figured, nor were any institutional catalogue numbers provided to help locate them. Among the small collection of indeterminate caudate vertebrae reported by Evans and Milner (1993) from
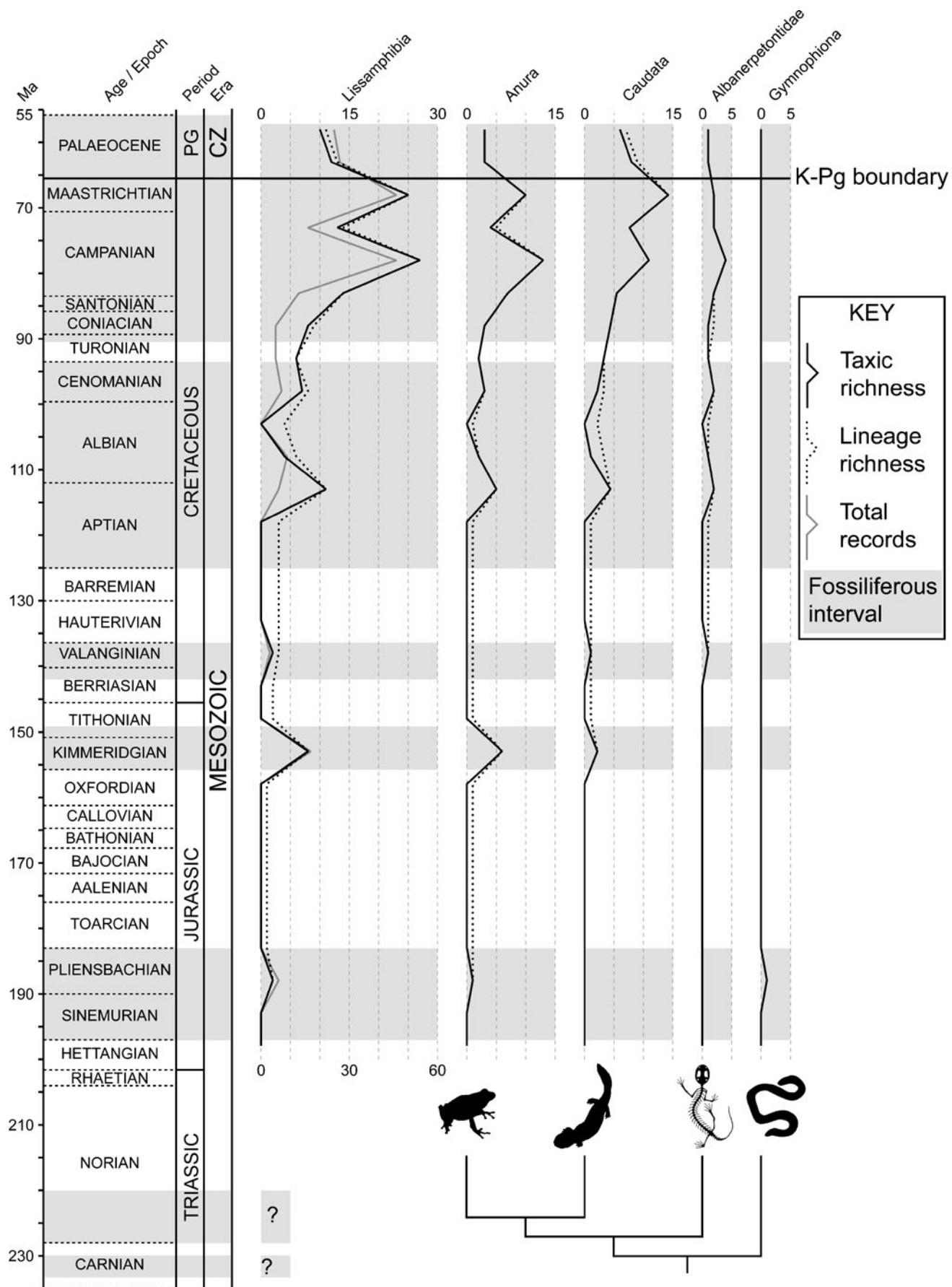
Quarry 9 was an incomplete bone that they interpreted as an atlantal centrum (Evans and Milner 1993, fig. 5). They further noted that it closely resembled atlantes described by Evans et al. (1988) for the Middle Jurassic stem salamander *Marmorerpeton* from the UK. Although we have not seen the Quarry 9 specimen firsthand, our colleague Pavel Skutschas has and is of the opinion that it may be a broken piece of turtle skull bone (P. Skutschas personal communication). While the Late Jurassic age of the Morrison Formation is within the temporal range for which stem salamanders may be expected to occur, their presence in that formation is not confirmed.

The remaining lissamphibian-bearing localities in Colorado (Fruita, Garden Park, Small Quarry and Wolf Creek Quarry: Callison 1987; Foster 2007) and Wyoming (Little Houston Quarry, Mile 175 and Ninemile Hill: Foster 2001, 2007; Foster and Heckert 2011) have produced indeterminate, undescribed anuran and caudate material. Although albanerpetontids are known from older (Bathonian of UK and France) and contemporaneous (Portugal) deposits in Europe (see review by Gardner and Böhme 2008, table 12.2), no diagnostic fossils of that clade have yet been recognised from the Morrison Formation.

Early Cretaceous

The first half of the North American lissamphibian record during the Early Cretaceous is limited, but it improves through the latter half of the epoch. North American lissamphibians of exclusively Early Cretaceous age are known from three and, possibly, as many as five stratigraphic units and regions in the USA (Fig. 4, Table 2): certainly from the Lakota Formation of South Dakota, the Cloverly Formation of Montana and Wyoming and the Trinity Group of Texas and Oklahoma, and possibly from the Wayan Formation of Idaho and the Potomac Formation of Virginia. We also arbitrarily include the Cedar Mountain Formation of Utah in our Early Cretaceous account because the fossiliferous, upper portion of that unit straddles the Early–Late Cretaceous boundary.

A locality (OMNH V1243) dated as late Berriasian–Valanginian (see Cifelli et al. in press) in exposures of the lower part of the Lakota Formation in the Black Hills region of South Dakota has yielded two undescribed lissamphibian fossils: a urodele trunk vertebra (Fig. 1b) and an albanerpetontid jaw fragment. Although neither specimen currently can be identified more precisely, they are notable for being the only pre-Aptian records for Early Cretaceous lissamphibians in North America. The albanerpetontid jaw fragment also documents the first appearance for that clade in North America. Research on the vertebrate assemblage from the Lakota Formation is ongoing (see Cifelli et al. in press), so there is a reasonable expectation that additional lissamphibian specimens and taxa may be identified from that formation.

A moderately diverse lissamphibian assemblage is coming to light from exposures of the Cloverly Formation, in the Bighorn Basin of Montana and Wyoming. The age of the Cloverly Formation is poorly constrained, but conventionally it is dated as Aptian–Albian (e.g. Kielan-Jaworowska et al. 2004; Oreska et al. 2013; Ostrom 1970). The first lissamphibian material reported from the Cloverly Formation was fragmentary, indeterminate albanerpetontid jaws (Gardner 1999a). Oreska et al. (2013) have recently described and figured more informative albanerpetontid specimens, including frontals (Oreska et al. 2013, fig. 6C, D) that are diagnostic for the genus *Albanerpeton*, plus the first urodeles and anurans to be reported from the formation. The urodele specimens identified by Oreska et al. (2013) consist of indeterminate batrachosauroidid vertebrae, possible scapherpetontid vertebrae and jaws and indeterminate jaws, vertebrae, limb and girdle bones. Their figured example (Oreska et al. 2013, fig. 7B) of what they regarded as a possible scapherpetontid atlantal centrum does indeed appear to be diagnostic for that family. The Cloverly Formation thus records the earliest appearances of batrachosauroidids and scapherpetontids, two urodele families that were prominent components of North American lissamphibian assemblages through the rest of the Cretaceous and into the Palaeocene. On the basis of external ornament patterns on maxillary specimens, Oreska et al. (2013) identified at least two toothed anurans: a *Scotiophryne*-like taxon bearing a pustulate ornament and a second taxon bearing a pit-and-ridge ornament. They also reported indeterminate anuran skull and postcranial bones. Undescribed urodele and anuran specimens are also present in OMNH collections from the Cloverly Formation. Among the most notable is a trio of atlantal centra (bulk catalogued as OMNH 23259: Fig. 1d) that are not clearly referable to any salamander family currently known from the North American Early Cretaceous. In terms of their larger size (when compared to other salamander atlantes known from the North American Early Cretaceous) and general form, the three atlantes are vaguely reminiscent of some stem salamander atlantal centra (see, for example, Skutschas 2013, this issue). To highlight the distinctiveness of these three atlantes and to reflect our uncertainty about their affinities, here we list them as Caudata indet. The OMNH collection includes some fragmentary anuran maxillae bearing pit-and-ridge ornamentation similar to that on the second anuran taxon identified by Oreska et al. (2013). Most of the OMNH anuran maxillae are comparable in size to those reported by Oreska et al. (2013), but one (OMNH 32305; unfigured) is noticeably larger. The tripartite combination of albanerpetontids, urodeles and anurans that is first encountered in the Western Interior in the Cloverly Formation persists in lissamphibian assemblages within the region throughout the remainder of the Cretaceous and into the Palaeocene.

Approximately correlative with the Cloverly Formation is a complex of non-marine deposits in eastern Idaho and western Wyoming that has produced sparse vertebrate material (e.g. Dorr 1985; Krumenacker 2005). The only reported lissamphibian fossils from those latter deposits are undescribed, possible frog long bones that were recovered by screenwashing a microvertebrate locality in the Wayan Formation (Albian) of southeastern Idaho (Dorr 1985). The recovery of a lizard jaw from a locality farther to the northeast in Idaho, within older (Aptian) rocks of the Gannett Group (Krumenacker 2005), suggests this unit may also be a potential source of lissamphibian fossils.

Lissamphibians are known from three of the four formations comprising the Trinity Group (Aptian–Albian) in Texas and Oklahoma. In central Texas, the Trinity Group contains in ascending sequence the Twin Mountains, Glen Rose and Paluxy formations. Farther north in Texas and into southeastern Oklahoma, the Glen Rose Formation pinches out and, in that region, the remaining portion of the Trinity Group is called the Antlers Formation. Good reviews of the geology, vertebrate assemblages and history of work in the Trinity Group are provided by Winkler et al. (1989, 1990) for Texas and by Cifelli et al. (1997a) for Oklahoma. Age determinations for most non-marine localities in the Trinity Group are challenging, but by using various lines of evidence and regional correlations (e.g. Cifelli et al. 1997a; Jacobs et al. 1991; Winkler et al. 1989, 1990) the lissamphibian-bearing localities within the group can be arranged in an approximate age sequence extending from the late Aptian into the early–middle Albian (see time chart in Fig. 4). In terms of the number and quality of specimens and diversity of taxa represented, the most important lissamphibian-bearing localities are Butler Farm and Greenwood Canyon, both in north-central Texas and in the upper part (early–middle Albian) of the Antlers Formation. Unfortunately, these localities have been inaccessible for several decades (Winkler et al. 1989). Greenwood Canyon is historically significant for having yielded the first reported Cretaceous anurans in North America (Zangerl and Denison 1950). That anuran collection consists of numerous isolated bones that have yet to be studied in detail. Notable features of anuran bones from Greenwood Canyon, and indeed from all the Trinity Group localities, include the following: the specimens are from relatively small-bodied anurans; maxillae bear teeth; a pit-and-ridge style ornament covers the external surfaces of skull roof bones, squamosals and maxillae. Preliminary work by Gardner (1995) recognised several maxillary morphs within the Greenwood Canyon collection on the basis of proportions, lingual structures and external ornament patterns. Those maxillary morphs suggest multiple anuran taxa are present. Higher level affinities of the anurans from Greenwood Canyon and the rest of the Trinity Group are uncertain. Previous suggestions that at least some specimens pertain to leptodactylids, discoglossids or gobiatids (e.g. Hecht 1960,

1963; Lynch 1971; Roček 2000; Roček and Nessov 1993; Sanchiz 1998; Winkler et al. 1990) are unsubstantiated. Greenwood Canyon also is the type locality for the urodele *Prosiren elinorae* Goin and Auffenberg, 1958 (see the holotype trunk vertebra depicted in Fig. 1e) and the albanerpetontid *Albanerpeton arthridion* Fox and Naylor, 1982. Both species also are known from Butler Farm and some other Trinity Group localities. *Prosiren elinorae* was described in moderate detail by Estes, (1969a, 1981), but note that the jaws and a humerus referred by him to the species subsequently were transferred to *A. arthridion* (see Fox and Naylor 1982; Gardner 1999a). Mostly because of historical precedence and inertia, *P. elinorae* and *Ramonellus longispinus* Nevo and Estes, 1969 (Early Cretaceous, Israel) continue to be placed as the only two species within the family Prosirenidae. Milner's (2000) intriguing suggestion that *P. elinorae* instead may be a batrachosauroidid has yet to be tested. *A. arthridion* is better understood: Gardner (1999a) presented a more detailed description and expanded diagnosis for the species, and several cladistic analyses have consistently placed it as the basalmost species in the genus (e.g. Gardner 2002; Sweetman and Gardner 2013; Venczel and Gardner 2005). Other localities in the Trinity Group have yielded fewer lissamphibian specimens, and the diversities do not appear to be as great, although that could be an artifact of the smaller sample sizes from those localities. As reported by Winkler et al. (1990), localities in the Twin Mountains Formation (Paluxy Church; late Aptian) and Paluxy Formation (Huggins #1 and #2, Pecan Valley Estates; early Albian) have yielded rare vertebrae of *P. elinorae* and skull and postcranial bones of indeterminate anurans. The final locality of interest, McLeod Honor Farm, occurs in approximately the middle portion (late Aptian–early Albian) of the Antlers Formation in southeastern Oklahoma and has yielded moderate numbers of *A. arthridion* and indeterminate anuran bones (Cifelli et al. 1997a; Gardner 1999a; this paper, Fig. 2h). A questionable caudate was also included in a faunal list (Cifelli et al. 1997a, table 1); however, re-examination of the trunk vertebra that was the basis for that identification indicates that this likely is from a squamate (Gardner unpublished observation). With the once-productive Greenwood Canyon and Butler Farm localities now inaccessible, McLeod Honor Farm appears to hold the most promise for producing additional lissamphibian specimens from the Trinity Group.

The only report of North American Early Cretaceous lissamphibians outside of the Western Interior is from northeastern Virginia, where a possible anuran trackway was described by Weems and Bachman (1997) from the early Aptian age Patuxent facies in the Potomac Formation. Although the trackway is of the appropriate size to have been made by an anuran and the overall placement of prints are suggestive of a saltatory (i.e. hopping or jumping) gait, the

prints themselves as described and figured by Weems and Bachman (1997, figs. 3–6) seem too poorly preserved to be meaningfully compared with those of extant anurans (cf. Brown et al. 1984, p. 194; Murie 1974, figs. 183a–c, 184a, b). While we do not discount that this trackway was made by an anuran, we regard its anuran origins as unverified. It is worth noting that slightly farther to the north in Maryland, laterally equivalent oxbow lake deposits of the Arundel Clay facies within the same formation (see Lipka et al. 2006) are a more promising, potential source of lissamphibian body fossils. Those deposits have yielded a small collection of dinosaur teeth, freshwater shark teeth and spines and a mammal jaw and isolated tooth (e.g. Cifelli et al. 1999a; Cifelli et al. 2013; Lipka 1998), but to date no diagnostic lissamphibian bones have been recovered (T. Lipka, personal communication).

The Cedar Mountain Formation is a thick unit of Barremian–early Cenomanian age that crops out in central Utah and is divided into several members (e.g. Cifelli et al. 1999c and references therein). Screenwashing and hand quarrying in the uppermost unit, the Mussentuchit Member, has yielded a taxonomically diverse assemblage of small-bodied vertebrates that has been dubbed the Mussentuchit local fauna (Cifelli et al. 1999c). Radiometric dates place the Mussentuchit local fauna around the Early–Late Cretaceous boundary (Cifelli et al. 1997b; Garrison et al. 2007). Albanerpetontids, urodeles and anurans are present and are mostly represented by isolated bones. Gardner (1999b) recognised two kinds of albanerpetontids on the basis of fragmentary jaws: (1) an *Albanerpeton nexuosum*-like species having fused premaxillae and (2) an indeterminate, but more primitive taxon having smaller, unfused premaxillae. The cf. *A. nexuosum* material (Gardner 1999b, fig. 3A–E; this study, ESM Appendix 2) documents the first appearance of the so-called "robust-snouted" subclade of *Albanerpeton* species, a group that extends through the Late Cretaceous and includes the only Cenozoic albanerpetontids (e.g. Gardner 2002; Gardner and Böhme 2008; Venczel and Gardner 2005). Material reported for the other albanerpetontid taxon lacks derived features seen in more advanced species of *Albanerpeton* and instead is more typical of *A. arthridion* or one of the other albanerpetontid genera; the latter are restricted to the Middle Jurassic–Early Cretaceous of Europe (*Anoualerpeton*, *Celtedens* and *Wesserpeton*) and the Early Cretaceous of North Africa (*Anoualerpeton*) (see Gardner and Böhme 2008; Sweetman and Gardner 2013). To date, urodeles and anurans from the Mussentuchit local fauna have not been considered in as much detail as albanerpetontids. As mentioned by Cifelli et al. (1999c), an indeterminate scapherpetontid can be recognised on the basis of a small number of isolated vertebrae and dentaries; an earlier suggestion that some of those specimens pertained to a batrachosauroidid (Gardner 1994) is incorrect. Anurans are known by moderate numbers of isolated skull and postcranial

bones and also by several incomplete skeletons. Several distinctive maxillary morphs can be recognised on the basis of differences in form, ornament patterns and lingual structures (e.g. Fig. 2i vs. j), and these suggest the presence of several anuran taxa (Cifelli et al. 1999c; Gardner 1994, 1995). Although anuran maxillae from the Mussentuchit Member are somewhat similar to those from the slightly older Trinity Group (e.g. ornamented externally and bear teeth), they differ in details of ornament and structure. Most noticeably, virtually all of the Mussentuchit specimens are from substantially larger-bodied anurans. Other localities in the Mussentuchit Member have yielded rare, indeterminate anuran and caudate bones (Fiorillo 1999, table 2; Garrison et al. 2007, table 5).

Late Cretaceous

Beginning with the above-mentioned occurrences in the upper part of the Cedar Mountain Formation around the Albian–Cenomanian boundary in central Utah, there is a reasonably continuous sequence of lissamphibian occurrences through the Late Cretaceous in North America. Fossils are almost exclusively in the form of isolated bones recovered by screenwashing and surface collecting. Historically, collecting and research efforts have focused on the more richly fossiliferous Campanian and Maastrichtian deposits in the northern USA (especially Wyoming and Montana) and deposits of late Santonian and Campanian age in southern Alberta, Canada, but starting in the 1980s field work in other deposits and regions has provided greater stratigraphic and geographic coverage. The North American Late Cretaceous record is largely confined to the Western Interior, with localities occurring between northern Mexico into central Alberta and from every stage in the epoch. There are also three occurrences, all Campanian in age, outside of the Western Interior—one each in Baja California, New Jersey and North Carolina. The Late Cretaceous dominates the North American Mesozoic and Palaeocene lissamphibian record, to the extent that slightly more than 60% of all occurrences documented here (i.e. total number of taxa reported from each of the localities in Tables 1, 2, 3, 4, 5, 6, 7, 8, and 9) unambiguously fall within the Late Cretaceous. To accommodate this large number of occurrences, here we subdivide our survey of North American Late Cretaceous lissamphibians into five smaller, more time-constrained intervals.

It is important to note that from the beginning of the Late Cretaceous until the late Maastrichtian, the Western Interior Seaway was continuous from north-to-south and completely bisected the North American continent. All lissamphibian localities in the Western Interior dating from when the seaway was complete are from the area that was then a strip of land between the emerging Rocky Mountains and the western margin of the seaway. Some of the late Maastrichtian age

localities in present-day Saskatchewan, Montana and the Dakotas formed on land that began re-emerging between the northern and southern arms of the retreating seaway. This newly emergent land was the first connection in several tens of millions of years between the formerly isolated eastern and western portions of the North American continent. That connection broadened into the Palaeogene, as the seaway continued to retreat and the eastern and western portions of the continent once again became fully continuous throughout the entire Western Interior.

Middle/late Cenomanian–early/middle Campanian

In North America, the lissamphibian record for the middle/late Cenomanian to early/middle Campanian is centered largely in southern Utah, but also includes occurrences in north-central Texas, in southeastern Alberta and possibly in northwestern New Mexico (Fig. 5, Table 3). It also includes lissamphibians from two rock units (upper part of the John Henry Member, Straight Cliffs Formation, Utah, and the Deadhorse Coulee Member, Milk River Formation, Alberta) that fall within the Aquilan NALMA, which is the chronologically oldest (late Santonian–early Campanian) of the conventionally accepted NALMAs.

The unequivocally oldest lissamphibians to be considered in this account occur in the middle Cenomanian Woodbine Formation, where localities in the Dallas and Fort Worth area of north-central Texas have yielded undescribed, indeterminate anuran and urodele bones (Bennett et al. 2011; 2012; G. Bennett personal communication; Lee 1997; Winkler and Jacobs 2002).

A thick sequence of Upper Cretaceous rocks exposed on the Markagunt, Paunsaugunt and Kaiparowits plateaus in south-central and southwestern Utah contains a series of vertebrate microfossil localities (e.g. Eaton and Cifelli 1988; Eaton et al. 1997, 1999) that have produced lissamphibian fossils. On these plateaus, lissamphibian-bearing localities occur in the following rock units (listed in approximate ascending sequence): the unnamed middle member (middle? and late Cenomanian) of the Dakota Formation; the Smoky Hollow (late Turonian) and John Henry (Coniacian–late Santonian) members of the Straight Cliffs Formation; an undifferentiated sequence within the Straight Cliffs Formation (Coniacian age locality MNA 1260); the upper part (likely late Santonian or early Campanian) of the Iron Springs Formation and a locality (UMNH VP 10) of comparable age in an unidentified formation; the Wahweap Formation (early–middle Campanian). A final lissamphibian-bearing unit, the Kaiparowits Formation (middle–late Campanian) also occurs on the Kaiparowits Plateau, but this unit is considered in the following section. More detailed treatments of the above-listed rock units and their lissamphibian-bearing localities can be found in recent papers by Roček et al. (2010) and

Gardner et al. (2013). Although the Utah localities considered in this account differ markedly in the number and quality of specimens they have produced, collectively they are critical for filling a temporal gap in about the first half (i.e. up to early/middle Campanian) of the North American Late Cretaceous lissamphibian record.

All adequately sampled rock units of middle/late Cenomanian to early/middle Campanian age in southern Utah contain the typical mix of albanerpetontids, urodeles and anurans. Albanerpetontids from the Straight Cliffs Formation were treated in a preliminary fashion by Gardner (1999b), whereas more comprehensive treatments of the anuran and urodele records have been presented by Roček et al. (2010) and Gardner et al. (2013), respectively. Albanerpetontids are known by isolated vertebrae, jaws and rare frontals (e.g. Fig. 2a, b) from most of the above-listed units, except the Iron Springs Formation (Table 3). Each of the other units typically contains several albanerpetontid premaxillary morphs, suggesting the presence of more than one albanerpetontid species. Both the Dakota Formation and the John Henry Member of the Straight Cliffs Formation have produced fused premaxillae (e.g. Fig. 2b) comparable to those of the late Santonian–Maastrichtian species *Albanerpeton nexuosum* (Estes, 1981). Other premaxillary specimens are unfused. Many of the latter have been conservatively identified only as Albanerpetontidae indet. (Gardner 1999b; this paper), but we anticipate that with more detailed study at least some of that material will prove identifiable to genus or species. At present, the sole diagnosable albanerpetontid species from this interval and region is *A. cifellii* Gardner, 1999b, which is known only by its distinctive holotype premaxilla from the late Turonian age Smoky Hollow Member of the Straight Cliffs Formation.

As documented by Gardner et al. (2013), most of the lissamphibian-bearing rock units of middle/late Cenomanian to early/middle Campanian age in southern Utah contain multiple urodele taxa, which mostly are represented by vertebrae and some jaws. Scapherpetontids and batrachosauroidids occur throughout the entire interval. The scapherpetontid record consists of *Scapherpeton* vertebrae (?Coniacian–early/middle Campanian), with occurrences in the basal (?Coniacian) and middle (early Santonian) parts of the John Henry Member of the Straight Cliffs Formation being the earliest appearances of that taxon in North America. Other scapherpetontids reported by Gardner et al. (2013) are *Lisserpeton*-like vertebrae from the ?Coniacian and late Cenomanian, *Piceoerpeton*-like vertebrae from the ?Coniacian and vertebrae of a probable new genus and species from the late Cenomanian (Gardner et al. 2013); these are collectively listed as "gen. et sp. indet. (multiple taxa)" in our Table 3. Batrachosauroidids are represented by *Opisthotriton* (Santonian–early/middle Campanian) and by a pair of new monotypic genera, one each from the late Cenomanian and

the late Turonian (Table 3: gen. et sp. nov. 1 and 2, respectively). The existence in older (i.e. pre-Santonian) Cretaceous deposits in Utah and Wyoming (Gardner et al. 2013; Oreska et al. 2013) of scapherpetontid and batrachosauroidid specimens that cannot be assigned to known later Cretaceous and Paleogene genera indicates that both families were already diversifying by the early Late Cretaceous. Atlantal centra diagnostic for *Habrosaurus* have been identified from the upper part (late Santonian) of the John Henry Member of the Straight Cliffs Formation (Gardner et al. 2013). This is the oldest, unequivocal appearance in North America of Sirenidae, a family that was a characteristic component of lowland urodele assemblages throughout the remainder of the Cretaceous and into the Paleogene in the Western Interior and which survives today in the southeastern USA. An unnamed new urodele genus and species was reported by Gardner et al. (2013) on the basis of distinctive trunk vertebrae (e.g. Fig. 1f) and atlantal centra recovered from several units of late Turonian to early or middle Campanian age. The familial affinities of that new taxon are uncertain, although Gardner et al. (2013) noted that its vertebrae showed some resemblance to those of sirenids. Additional, indeterminate urodele taxa are represented by trunk vertebrae from the late Cenomanian, late Turonian and ?Coniacian (Gardner et al. 2013). A final occurrence not included in the Gardner et al. (2013) paper is that of the incertae sedis urodele (sensu Gardner et al. 2010) *Nezpercius dodsoni* Blob et al., 2001, which is known by four ilia from the early–middle Campanian age Wahweap Formation (Roček et al. 2010).

Roček et al.'s (2010) treatment of the anuran record in southern Utah focused on documenting and describing specimens and on recognising broad temporal patterns in osteological features, rather than trying to identify and diagnose taxa. Nevertheless, some insights into anuran diversities can be gleaned from their work, using distinctive morphs that were reported and figured for certain bones. Roček et al. (2010) recognised three basic kinds of ilia in their samples (dorsal tubercle present; oblique or spiral groove present; neither of those features present), each of which could be further subdivided into numerous variants or morphotypes that were described in more detail in a follow-up paper by Roček et al. (2013). Roček et al. (2010) reported between two and 14 iliac morphotypes for the four best sampled localities within the middle/late Cenomanian to early/middle Campanian interval. Considering that many of those iliac morphotypes are represented by one or only a few examples and that differences described among some of them are extremely subtle, caution is advisable in equating each morphotype with a distinct biological taxon. If maxillary morphs are counted among the specimens figured by Roček et al. (2010), counts drop to a more modest range of one to four morphotypes depending on the unit. As with older North American Cretaceous examples, all of the anuran maxillae

reported by Roček et al. (2010) from the middle/late Cenomanian to early/middle Campanian of Utah are sculpted externally and bear teeth. The only anuran species that Roček et al. (2010) specifically identified for this portion of the Utah record was *Scotiophryne pustulosa* Estes, 1969b, on the basis of one ilium from the Santonian portion of the John Henry Member of the Straight Cliffs Formation and seven ilia from the early–middle Campanian age Wahweap Formation. In keeping with the taxonomically conservative approach of their study, Roček et al. (2010) did not assign or even suggest to which families or supra-familial groups any of the Utah fossils might belong. Recently, Jean-Claude Rage (personal communication) suggested that judging by the photographs published by Roček et al. (2010), several of the Utah specimens may be assignable to Pipomorpha; this intriguing possibility and other aspects of the anuran record from this interval in southern Utah deserve further study.

Outside of Utah, the only other late Santonian age lissamphibian-bearing localities known to us are in Verdigris Coulee in south-central Alberta, in exposures of the Deadhorse Coulee Member, in the upper part of the Milk River Formation. The upper part of the Milk River Formation (= "Upper Milk River Formation" of some authors) was originally considered to be early Campanian in age (e.g. Clemens et al. 1979; Fox 1972, 1978; Lillegraven and McKenna 1986; Russell 1964, 1975), and the mammalian assemblage from the unit characterises the Aquilan NALMA (Fox 1978; Lillegraven and McKenna 1986; Russell 1975). Subsequent magnetostratigraphic and palynological studies (Braman 2001; Leahy and Lerbekmo 1995; Payenberg et al. 2002) of correlative sections through the upper part of the formation, farther to the west along Verdigris Coulee, suggest a slightly older age of late Santonian for the Deadhorse Coulee Member and, by extension, for the early portion of the Aquilan NALMA (Cifelli et al. 2004; Kielan-Jaworowska et al. 2004). Screenwashed localities from the upper part of the Milk River Formation have produced abundant albanerpetontid jaws (e.g. Fig. 2c, d) and fewer frontals, parietals and atlantes (Fox and Naylor 1982; Gardner 2000a). These collections were instrumental in formulating the proposal by Fox and Naylor (1982) that *Albanerpeton* (then the only recognised genus) was not an odd salamander, but instead belonged to a distinct group of possible lissamphibians, for which Fox and Naylor (1982) coined the family- and order-level names Albanerpetontidae and Allocaudata, respectively. In the same paper, Fox and Naylor (1982) also named the new species *A. galaktion* Fox and Naylor, 1982 for a distinctive premaxilla (see holotype depicted in Fig. 2d) from the Milk River Formation and referred all other jaws, frontals, parietals and atlantes from the same unit to that species. Gardner (2000a) subsequently revised that species, transferred some of the previously referred jaws and frontals

to *A. nexuosum*, and regarded the parietals and atlantes as indeterminate beyond the family level. On the basis of diagnostic vertebrae, two families and three species of urodeles are definitely present in the upper part of the Milk River Formation (Fox 1972; Gardner 2000b, 2005; Naylor 1981a, 1983): the scapherpetontid *Scapherpeton tectum* Cope, 1876; the batrachosauroidid *Opisthotriton kayi* Auffenberg, 1961; and a second, as yet unnamed batrachosauroidid (gen. et sp. nov. 3 in Table 3) that was first noted by Naylor (1983). Anurans from the upper part of the Milk River Formation are represented by a small number of isolated skull and postcranial bones; these have not been studied in any detail and, for the time being, are best identified as Anura indet.

The presence of lissamphibians in the Allison Member (late Santonian–early Campanian) of the Menefee Formation in northwestern New Mexico is unclear. In a trio of conference abstracts published in consecutive years, Lewis et al. (2006, 2007, 2008) first reported teeth and jaws of *Albanerpeton*, then downgraded that identification to "possible lissamphibian remains", and in the final abstract made no mention of lissamphibians.

Middle–late Campanian (Judithian NALMA)

Lissamphibian-bearing formations of unequivocal middle–late Campanian age (Judithian NALMA) in North America are restricted to the Western Interior of Canada and the USA, as follows (Fig. 6, Table 4): the Foremost, Oldman and Dinosaur Park formations of Alberta; the Dinosaur Park Formation and, possibly, the Oldman Formation of Saskatchewan; the Judith River and Two Medicine formations of Montana; the Mesaverde Formation of Wyoming; the Kaiparowits Formation of Utah; the Aguja Formation of Texas. Here we also include the Fruitland Formation of New Mexico within the Judithian, following more recent reassessments (e.g. Keilan-Jaworowska et al. 2004) of the age of that formation. Roberts et al. (2005, figs. 6, 8) provided a useful regional correlation chart depicting many of those formations. Judithian lissamphibian material has been known for over a century in both the USA (Cope 1876) and Canada (Lambe 1902), but our understanding of lissamphibians from this interval has lagged behind those from the late Maastrichtian (Lancian). Historically, Judithian lissamphibian assemblages have been regarded as an impoverished version of those from the Lancian (e.g. Armstrong-Ziegler 1980; Fox 1976a; Rowe et al. 1992; Sahni 1972). As more specimens and localities come to light, it is becoming apparent that Judithian lissamphibian assemblages are similar in diversity to those of the Lancian (e.g. compare Campanian vs. Maastrichtian richness peaks, respectively, in Fig. 11) and contain a mix of some taxa known from the Lancian and some taxa that appear to be unique to the Judithian (e.g. Gardner 2000a, 2003a; Roček et al. 2010).

The Judithian NALMA is about 5 or 6 million years in duration (cf. Weil 1999 vs. Cifelli et al. 2004, fig. 2.1) and was founded on mammalian taxa from the type area of the Judith River Formation (Fox 1978; Kielan-Jaworowska et al. 2004; Lillegraven and McKenna 1986; Russell 1975), which is located in the Missouri River Valley of north-central Montana (e.g. Rogers and Brady 2010, fig. 1; Sahni 1972, fig. 2). The first North American fossil salamanders were recognised from that area on the basis of isolated vertebrae surface collected by J.B. Hatcher and subsequently examined by Cope (1876) who named five species in two genera for that material: *Scapherpeton tectum*, *S. laticolle*, *S. excisum*, *S. favosum* and *Hemitrypus jordanianus*. *Scapherpeton tectum* continues to be recognised as a diagnosable urodele species (e.g. Auffenberg and Goin 1959; Estes 1964, 1981; Gardner 2000b, 2012), but the remaining names proposed by Cope (1876) are considered to be junior subjective synonyms of *S. tectum*. The first descriptive account of a Judithian age lissamphibian assemblage was provided almost a century later by Sahni (1972), as part of his monographic treatment of the entire vertebrate assemblage from the type area of the Judith River Formation. Sahni's (1972) lissamphibian material consisted of a moderate number of isolated bones obtained by screenwashing three localities, the most productive being Clambank Hollow, in the upper part of the formation. On the basis of anuran maxillae, ilia and humeri, Sahni (1972) informally recognised three species of discoglossids sensu lato and one species of pelobatid sensu lato. Examination of those specimens by one of us (Gardner, unpublished observation) indicates that none can be assigned to a known anuran family and that differences among the humeri and iliac morphs are minor and of questionable taxonomic significance. However, the three maxillary morphs are more convincing and lend support to Sahni's (1972) suggestion that multiple anuran species are represented. For urodeles, Sahni (1972) reported the scapherpetontids *S. tectum* and *Lisserpeton bairdi* Estes, 1965, the batrachosauroidids *Opisthotriton kayi* Auffenberg, 1961 and *Prodesmodon copei* Estes, 1964, and the sirenid *Habrosaurus dilatus* Gilmore, 1928b. The first three identifications are correct, but the *P. copei* identification was based on fragmentary jaws of an indeterminate albanerpetontid (Gardner 2000a), and the *H. dilatus* identification was based on fragmentary jaws identifiable only to genus level (Gardner 2003a). Additional vertebrate microfossil localities containing lissamphibian fossils are now known from the same area, but lower in the section (see Rogers 1995; Rogers and Brady 2010, figs. 1b, 11), and also farther south in Montana at Top Cat Quarry (Fiorillo 1989). Specimens and taxa from those localities have not been considered in much detail. The one exception is a trio of ilia from the type area that Blob et al. (2001) interpreted as belonging to an anuran they called *Nezpercius dodsoni*; in a subsequent work, Gardner et al. (2010) argued that these ilia

are from an incertae sedis urodele. Judging from a published photo of representative vertebrate microfossils from one locality (UC-914: Rogers and Brady 2010, fig. 6B) and unpublished photographs provided to us by R.R. Rogers and D.B. Brinkman of select specimens, these newer localities in the type area contain some well-preserved specimens that should provide further insights into the lissamphibian assemblage of the Judith River Formation.

Compared to the type Judith River Formation, other Judithian lissamphibian assemblages are broadly similar in containing a mix of the following taxa (Table 4): one to three species of *Albanerpeton*; multiple species of urodeles, predominantly *Scapherpeton*, *Lisserpeton* and *Opisthotriton* and less commonly *Prodesmodon* and *Habrosaurus*; multiple anuran species. One of the most stratigraphically and geographically extensive records for Judithian lissamphibians occurs in the Belly River Group of southeastern Alberta and southwestern Saskatchewan. In this region, dozens of vertebrate microfossil localities are distributed through, in ascending order, the Foremost, Oldman and Dinosaur Park formations. Much of the published information on Belly River Group lissamphibians is in the form of occurrence lists for microvertebrate localities, formation-level faunal lists and brief descriptive accounts for material from specific localities and areas (e.g. Brinkman 1990; Brinkman et al. 2004; Dodson 1983; Eberth and Brinkman 1997; Eberth et al. 1990, 2001; Fox 1976a; Frampton 2006; Gardner 2005; Lambe 1902; Peng et al. 1995, 2001; Storer 1993; Tokaryk 1988). Due to a limited number of localities and less research focus, lissamphibians of the Belly River Group are not as well known from the Foremost Formation of Alberta or from the Oldman and Dinosaur Park formations of Saskatchewan.

The rest of the Albertan portion of the Belly River Group contains a denser sequence of more productive localities within the following units and areas: (1) the Oldman and Dinosaur Park formations in the eastern part of the Milk River Valley and Onefour areas; (2) the uppermost portion of the Oldman Formation and the entire Dinosaur Park Formation in the Dinosaur Provincial Park area; (3) the Irvine locality in the upper portion of the Dinosaur Park Formation. Two lissamphibians are named for material from the Dinosaur Park Formation of Alberta: the albanerpetontid *Albanerpeton gracile* (Gardner, 2000a; this paper, Fig. 2e–g) from Dinosaur Provincial Park and the urodele *Habrosaurus prodilatus* Gardner, 2003a from Irvine. To date, the lissamphibian assemblage from the Irvine locality has received the most attention, thanks to a large collection of vertebrate microfossils made there by the UALVP during the mid-1960s to mid-1970s (e.g. Gardner 2000b, 2003a, 2005; Gardner and Brinkman in press). Irvine contains a diversity of anuran (e.g. Fig. 2k, m) and urodele taxa, including several undescribed, new species. Other lissamphibian-bearing localities in the Belly River Group are stratigraphically lower than Irvine, and

although those non-Irvine localities are not as well studied, it is clear that at least some of them contain similarly diverse, but not identical lissamphibian assemblages to the one at Irvine. For example, an unnamed anuran characterised by unsculpted and edentate maxillae (Anuran gen. et sp. nov. 3; see Fig. 2l) that is unknown from Irvine occurs at localities near the base of the Dinosaur Park Formation, in Dinosaur Provincial Park. Also, the albanerpetontids *A. galaktion*, *A nexuosum* and *A. gracile* are present in some combination at many localities in the Oldman and Dinosaur Park formations, yet for reasons unknown no albanerpetontid specimens have been identified from Irvine.

A comparably diverse lissamphibian assemblage is coming to light from the Kaiparowits Formation, on the Kaiparowits Plateau of south-central Utah. Preliminary work on specimens obtained by screenwashing a moderate number of localities distributed throughout the vertical extent of the formation is revealing a diversity of albanerpetontids, anurans and urodeles (Eaton et al. 1999; Gardner 2000a; Gardner et al. 2013; Roček et al. 2010; this paper, Fig. 2n–p, r). A notable occurrence in the Kaiparowits Formation is an undescribed, new species of *Theatonius*, a genus that until recently was known from only one Lancian locality in Wyoming (Fox 1976b; Gardner 2008). The *Theatonius* species from the Kaiparowits Formation and the above-mentioned species (Anuran gen. et sp. nov. 3) from the basal Dinosaur Park Formation of Alberta are the first appearances of edentate anurans in the North American fossil record and, to the best of our knowledge, also the oldest global records for edentate anurans.

Less extensively sampled, Judithian age lissamphibian assemblages are known from screenwashed localities in the Mesaverde Formation ("Mesaverde" Formation sensu Lillegraven and McKenna 1986) of central Wyoming (Breithaupt 1985; DeMar and Breithaupt 2006, 2008; Gardner 2000a), in the Fruitland Formation of northwestern New Mexico (Armstrong-Ziegler 1978, 1980; Gao and Fox 1996; Gardner 2000a; Hunt and Lucas 1993) and in the Aguja Formation of southwestern Texas (Gardner 2000a; Langston et al. 1989; Rowe et al. 1992; Sankey 1998, 2008; Standhardt 1986).

The final Judithian formation known to contain lissamphibians is the Two Medicine Formation of north-central Montana, where one locality (MOR TM-088) has produced several anuran skeletons in varying degrees of completeness and articulation (Varricchio 2002). The most exciting of these is a nearly complete, articulated skeleton (Fig. 2q) that is the best preserved anuran yet recorded from the Mesozoic of North American. It pertains to a new genus and species (here informally designated as gen. et sp. nov. 1), which also is represented by disarticulated skull bones from the approximately contemporaneous Dinosaur Park Formation in Alberta. Recent discoveries of rare articulated specimens of lizards from the Egg Mountain locality in the

Two Medicine Formation (e.g. DeMar et al. 2012) provide hope that lissamphibian specimens may be recovered in the future from that locality as well.

Before concluding this section, we must briefly deal with unsubstantiated reports of two Lancian aspect lissamphibians in the Judithian of the Western Interior, specifically of the anuran *Palaeobatrachus occidentalis* Estes and Sanchíz, 1982 (Archibald and Bryant 1990, table 1; Blob et al. 2001; Bryant 1989, table 2) and of the urodele *Proamphiuma cretacea* Estes, 1969c (Archibald and Bryant 1990, table 1; Fox 1976a, p. 8; MacLeod et al. 1997, p. 281; Naylor 1978a, p. 507). Except for Blob et al. (2001), who cited Bryant (1989) as their source, none of these publications provided any details (e.g. described, figured or listed voucher specimens; citations of other publications) to support the reported occurrences. To the best of our knowledge, no diagnostic specimens of either species have been recovered from any Judithian age locality in the Western Interior. In the apparent absence of any evidence to the contrary, we thus disregard previous claims that *Palaeobatrachus* or *Proamphiuma* were present during the Judithian.

Late Campanian–early Maastrichtian ("Edmontonian" NALMA)

The late Campanian to early Maastrichtian interval in North America represents the last major transgression of the Western Interior Seaway. Consequently, during that time only limited amounts of terrigenous rocks were deposited along the western margin of that seaway, and relatively few fossiliferous localities for small-bodied, non-marine vertebrates are known from those rocks. Russell (1964, 1975) erected the "Edmontonian" NALMA for the interval between the older Judithian and younger Lancian NALMAs. The "Edmontonian" NALMA was criticised by Lillegraven and McKenna (1986), who argued that this interval could not be characterised or defined with the same degree of rigor as the other latest Cretaceous NALMAs, mainly because its then-known mammalian assemblage consisted of only a small number of taxa, some of which were conspecific with Lancian taxa and others that were too poorly known to be temporally informative. More recent discoveries (e.g. Fox and Naylor 1986; Hunter et al. 2010; Lillegraven 1987) have identified additional mammalian taxa that may prove to be diagnostic for the "Edmontonian". Pending wider acceptance of that NALMA, here we follow the current convention of enclosing the name "Edmontonian" in quotes to indicate its informal status (e.g. Cifelli et al. 2004; Hunter et al. 2010; Kielan-Jaworowska et al. 2004; Lillegraven and McKenna 1986). Up to seven million years may separate the Lancian and Judithian, but because the upper and lower limits of the

"Edmontonian" cannot be established it is uncertain how much of that intervening, seven million year interval is spanned by the "Edmontonian" (Cifelli et al. 2004).

Compared to lissamphibian assemblages from the Judithian and Lancian, "Edmontonian" lissamphibians are poorly known and none appears to be unique to that interval. Fragmentary lissamphibian bones recovered by surface collecting and screenwashing and putative lissamphibian footprints have been reported from just five "Edmontonian" formations in the northern and central portion of the Western Interior (Fig. 7, Table 5).

The first "Edmontonian" lissamphibians were reported by Langston (1975, 1976) who briefly described fragmentary jaws and vertebrae of *Opisthotriton* from a microvertebrate locality in an isolated patch of the St. Mary River Formation exposed at Scabby Butte, southwestern Alberta. According to Sloan and Russell (1974), the Scabby Butte exposures are within the lower part of the St. Mary River Formation. The Scabby Butte local fauna is of historical interest because it was the basis for Russell's (1964, 1975) initial concept of the "Edmontonian". Gardner (2003a) also reported a fragmentary, indeterminate albanerpetontid dentary from Scabby Butte. Elsewhere in the St. Mary River Formation, smaller collections of microvertebrate elements have been obtained from a locality closer to the top of the formation along the Oldman River in southwestern Alberta (Sloan and Russell 1974) and from a locality in the lower third of the formation in north-central Montana (Hunter et al. 2010), but no lissamphibians were reported from either of those localities.

The most diverse "Edmontonian" lissamphibian assemblage currently known was reported by Larson et al. (2010) from five localities in the upper part (= Morrin and Tolman members sensu Eberth and Braman 2012; see also Eberth et al. 2013) or early Maastrichtian portion of the Horseshoe Canyon Formation, where it is exposed along the Red Deer River Valley, northwest of Drumheller, Alberta. According to Larson et al. (2010, table 1), the inventory of specimens and taxa consists of fragmentary and mostly indeterminate anuran skull and postcranial bones, *Opisthotriton* and *Scapherpeton* vertebral centra and one vertebra of an indeterminate, larger-bodied scapherpetontid. Larson et al. (2010, p. 1168, fig. 8A, B caption) also identified a fragmentary anuran ilium and, less certainly, a urostyle as "(?)*Palaeobatrachus occidentalis*". Judging from their published photograph of the ilium (Larson et al. 2010, fig. 8A), we are skeptical about that taxonomic identification (see also comments by Wuttke et al. 2012), but because we have not personally examined that specimen we record it in our "Edmontonian" faunal list (Table 5) as an unverified occurrence of that species. For the remaining anuran bones, Larson et al. (2010) reported only one pattern of cranial ornament and, on that basis, suggested that only one indeterminate anuran taxon was represented. Sparse vertebrate

microfossil localities are known from the lower or late Campanian portion of the Horseshoe Canyon Formation (see Larson et al. 2010), but to our knowledge the presence of lissamphibians in that part of the formation has not been documented in print. Eberth et al. (2001, table 3) also listed *Scapherpeton tectum* and indeterminate anurans in a faunal list for the Horseshoe Canyon Formation, but without any details about the specimens or their stratigraphic occurrences within the formation.

Farther northwards in west-central Alberta, there are reports of lissamphibians from two localities in the middle part (latest Campanian) of the Wapiti Formation. Northeast of Grande Prairie, an isolated patch of badlands called Kleskun Hill Park (see Nydam et al. 2010) contains a vertebrate microfossil locality that reportedly has produced lissamphibian material: Tanke (2004, p. 22) mentioned the presence of "salamanders"; Fanti and Miyashita (2009, table 4) reported one salamander quadrate, oddly under the heading "Squamata"; Nydam et al. (2010, p. 1091) simply mentioned "amphibians" as being represented. Considering that several articulated lizard skulls have been collected from Kleskun Hill Park (Nydam et al. 2010), there is reason to hope that this could become an important locality for small-bodied "Edmontonian" tetrapods, including lissamphibians. The second occurrence is west of Grande Prairie, close to the Alberta–British Columbia border, where a trio of isolated prints was recovered from slumped sandstone slabs at Red Willow Falls along the Red Willow River. As described by Fanti et al. (2013), the prints are small, natural casts that each preserves four digits. In the comparative section of their paper, Fanti et al. (2013, p. 262) favored a urodele origin for the prints, yet elsewhere in the same paper they seemed less sure. In different places in their paper, the specimens were identified as "small tetrapod tracks" (fig. 2 caption) or "amphibian or lacertilian tracks" (p. 267) or were attributed to "amphibians" (p. 267) or "dubious amphibians" (p. 261). The fact that each print preserves four digits is suggestive of lissamphibians, because four digits are primitively present on the manus of living anurans and urodeles (e.g. Duellman and Trueb 1986) and also on the manus of a well-preserved albanerpetontid skeleton from the Lower Cretaceous of Spain (McGowan and Evans 1995). The prints from Red Willow Falls may well be from lissamphibians, but this cannot be verified with certainty. If one or both of the above-cited occurrences from the Wapiti Formation are from lissamphibians, these would be the most northerly occurrences for Mesozoic lissamphibians in North America.

As an aside, it is worth mentioning that small-bodied, non-marine vertebrate fossils are known from much farther northwards along the North Slope of Alaska (see inset map in Fig. 7). These fossils occur in strata of the Prince Creek Formation that have been regarded as late Campanian–early Maastrichtian in age (e.g. Gangloff and Fiorillo 2010), which would be approximately "Edmontonian" equivalent, or slightly younger, perhaps early Lancian equivalent (e.g. Cifelli et al. 2004). The Alaskan localities document a moderately diverse vertebrate assemblage consisting of fish, dinosaurs and mammals, but to date no reptiles other than dinosaurs and no lissamphibians have been found (e.g. Clemens and Nelms 1993; Fiorillo 2008; Gangloff and Fiorillo 2010). As noted by Clemens and Nelms (1993, p. 505), despite intensive screenwashing of multiple localities from different depositional settings, the failure to recover any diagnostic examples of the latter two groups "strongly suggests that, in the Maastrichtian, amphibians and nondinosaurian reptiles either were not members of the fauna of the North Slope or were present in much smaller abundances than in middle paleolatitudes."

The final and most southerly report of "Edmontonian" lissamphibians is from the Williams Fork Formation of northwestern Colorado. In a preliminary faunal list for the formation, Archibald (1987, table 1) listed "1 species of frog" and "2 species of salamander". We are unaware of any further publications dealing with those occurrences.

Campanian and Maastrichtian occurrences not assignable to NALMAs

Here we comment on lissamphibian assemblages from six localities in the USA and Mexico (Fig. 7, Table 5) that are of unequivocal or probable Campanian age and one locality in the USA of unequivocal Maastrichtian age. None of these seven localities can reliably be assigned to a NALMA, either because they entirely lack mammalian taxa or contain mammalian taxa that are unknown from the NALMAs in the Western Interior or because there are no other reliable means (e.g. stratigraphic correlations, radiometric dates, magnetostratigraphic or palynological zonations) to correlate them with a NALMA.

Two localities lie well outside of the Western Interior, in the eastern USA. The richer and better documented of the pair is the Ellisdale locality, New Jersey, which lies in the lower part of the Marshalltown Formation. The Ellisdale locality is interpreted as a storm deposit within a debris-choked tidal channel, and it contains a mix of marine, freshwater and terrestrial vertebrate fossils (see Denton and O'Neill 1998 and references therein). A Campanian age generally has been accepted for Ellisdale (see review by Kielan-Jaworowska et al. 2004); here we follow Denton and O'Neill (2012) in regarding the locality as approximately middle Campanian in age. Denton and O'Neill (2012) further suggested that Ellisdale might be equivalent to the Aquilan and Judithian NALMAs, but considering that evidence for that age assessment has yet to be presented and given the vast geographic distance between New Jersey and well-corroborated Judithian and Aquilan localities in the Western Interior, for the time being

we favor the middle Campanian age estimate. Regardless of its precise age, Ellisdale is notable for having produced the most taxonomically diverse Mesozoic lissamphibian assemblage on the continent outside of the Western Interior and, thus, it provides the best insight into Late Cretaceous lissamphibian diversity in eastern North America. As documented by Denton and O'Neill (1998), Ellisdale contains a diversity of urodeles, anurans and possibly albanerpetontids, all represented by isolated elements recovered by screenwashing. To date, the described specimens and taxa are limited to the following (all from Denton and O'Neill 1998): dentaries and vertebrae of the endemic batrachosauroidid *Parrisia neocesariensis* Denton and O'Neill, 1998 and two anuran ilia, one of a possible discoglossid sensu lato and one of a possible pelobatid sensu lato. The remaining urodeles may include a *Habrosaurus*-like sirenid and a *Proamphiuma*-like amphiumid, whereas the anurans may include *Scotiophryne*- and *Theatonius*-like taxa and possibly a hylid sensu lato (Denton and O'Neill 1998).

The second locality in the eastern USA is in North Carolina and is called the Bladen County Landfill Annex. This bonebed near the top of the Bladen Formation has produced a diverse, but as yet not formally described assemblage of terrestrial, brackish, and freshwater vertebrate taxa (e.g. Crane 2011, 2012). Work on the Bladen Formation farther to the south and in the subsurface of South Carolina has favored a late Campanian age (Gohn 1992); here we follow Crane (2011, 2012) in regarding the Bladen Formation exposures in North Carolina as simply Campanian. According to Crane's (2012) conference abstract, the only lissamphibian present at the Bladen Count Landfill Annex is *Albanerpeton*, but she did not indicate what material was used to make that identification.

Although many of the above-cited preliminary identifications from the two Campanian age localities in the eastern USA are tantalizing, pending descriptions of the relevant specimens they remain unverified. Even so, it is striking that collectively these two eastern localities appear to contain the usual tripartite mix of albanerpetontids, urodeles and anurans seen in Late Cretaceous assemblages in the Western Interior. It will be interesting to see whether those similarities hold true at lower taxonomic levels (e.g. genus and species), once the Ellisdale and Bladen County Landfill Annex lissamphibians are more fully described. The apparent absence in these eastern localities of scapherpetontids is especially intriguing, considering how ubiquitous that family was during the Cretaceous and Palaeocene in the Western Interior.

The third occurrence outside of the Western Interior is in the "El Gallo Formation", near the northwestern coast of Baja California, Mexico. As summarised by Kielan-Jaworowska et al. (2004), radiometric dates for a tuff within the formation and marine invertebrates from within

and above the formation favor a Campanian age, possibly "Edmontonian" equivalent, for the "El Gallo Formation". In a pair of descriptive papers on fossil mammals from the "El Gallo Formation", the presence of amphibians and, more specifically, frogs was mentioned (Lillegraven 1972 and 1976, respectively). The mammal fossils reported by Lillegraven (1972, 1976) came from three localities in the middle third of the formation, and although not explicitly stated by the author in either paper, the lissamphibian specimens presumably are from one or more of those localities. None of the lissamphibian material from the "El Gallo Formation" has been described.

Until recently, Mesozoic lissamphibians were unknown from the rest of Mexico (see review by Reynoso 2006). However, recent work in the Parras Basin, in the northeastern part of the country, has resulted in discoveries in the middle and upper parts of the Cerro del Pueblo Formation of at least seven vertebrate microfossil localities that contain a moderately diverse assemblage of fish and tetrapods (Aguillon Martinez 2010). This assemblage is biogeographically interesting because it constitutes the southernmost record for Campanian age, non-marine vertebrates in the Western Interior. On the basis of palaeomagnetic studies and marine invertebrates, a late Campanian age is favored for the Cerro del Pueblo Formation (e.g. Aguillon Martinez 2010; Eberth et al. 2004). To the best of our knowledge, the few mammalian specimens recovered from the Cerro del Pueblo Formation (Aguillon Martinez 2010) are not informative for assigning the formation to a NALMA. Aguillon Martinez (2010, pp. 14–17, table 6) reported lissamphibians from all four of her La Parrita microsites: one *Lisserpeton* vertebra from Parrita M2 and six indeterminate anuran postcranial bones collectively from Parrita M1–4.

The remaining three records considered here lie within the American portion of the Western Interior. For the two Campanian occurrences, the more northern is a possible anuran manus and pes print preserved as natural casts on a siltstone slab that was recovered from a rubble pile at an abandoned coal strip mine in Meetinghouse Canyon, east-central Utah (Robison 1991). According to Robison (1991), the lithology of the slab matched nearby in situ rock within the basal part of the Blackhawk Formation. Robison (1991) reported the Blackhawk Formation simply as Campanian in age, which we follow here, although we note that some other workers (e.g. Johnson et al. 2005) have given a more precise age of early Campanian. The other supposed Campanian record is by Ratkevich and Duffek (1996), who briefly reported on a diverse mollusc and microvertebrate assemblage obtained by screenwashing a silty lens reportedly from the Fort Crittenden Formation, in Adobe Canyon, southeastern Arizona. The microvertebrate portion of that assemblage is notable for including a number of small-bodied taxa that are not known from elsewhere in the Fort Crittenden Formation,

including the urodeles cf. *Scapherpeton* sp. and cf. *Opisthotriton* sp. Ratkevich and Duffek's (1996) short paper included no descriptions and only a few figures of specimens, which makes it impossible to evaluate most of their published identifications. McCord et al. (2001) and Lucas and Heckert (2005) questioned not only many of Ratkevich and Duffek's (1996) identifications but, more significantly, whether those specimens actually came from the Fort Crittenden Formation. No unequivocal localities elsewhere within the Fort Crittenden Formation have produced lissamphibians (Heckert et al. 2003; Lucas and Heckert 2005; McCord et al. 2001), although some have yielded isolated elements of small-bodied vertebrates, such as fish and lizards, that suggest lissamphibian fossils may eventually be recovered from the formation. For the time being, however, we consider the presence of lissamphibians within that unit unproven. Heckert et al. (2003) suggested a late Campanian age, possibly equivalent to the Judithian, for the Fort Crittenden Formation on the basis of lithostratigraphic correlations with other formations that have been radiometrically dated.

The sole Maastrichtian age lissamphibian locality that cannot be assigned to a NALMA is the Harebell vertebrate locality, in northwestern Wyoming, within the Bobcat Member of the Harebell Formation. This locality has yielded a sparse assemblage of non-mammalian vertebrates that has been reported in faunal lists by Love (1973, p. A27) and McKenna (1980, p. 323). Both of those papers (see also Breithaupt 1985, p. 167) list the urodele *Prodesmodon* as being present, but no further details were provided. A Maastrichtian age for the Harebell Formation is founded on lithostratigraphic correlations, radiometric dates, magnetostratigraphy and vertebrate and palynomorph biostratigraphy (e.g. Harris et al. 1996; Love 1973; McKenna 1980), but a more precise age for the Harebell vertebrate locality is not available.

Late Maastrichtian (Lancian NALMA)

The Lancian NALMA correlates to the latter part of the Maastrichtian. The Lancian lissamphibian record in North America is comparable in its overall taxonomic diversity to that of the Judithian (e.g. compare Maastrichtian versus Campanian richness peaks, respectively, in Fig. 11), but it is limited to a more geographically restricted portion of the Western Interior that extends from southern Alberta and Saskatchewan southwards only as far as northeastern Colorado and central Utah (Fig. 8). Within that region, lissamphibians have been reported from nine formations (Table 6). Wilson et al. (2010) recently provided a regional overview of Lancian age localities and formations; as indicated in their regional correlation chart (Wilson et al. 2010, fig. 1), many of the fossil localities are concentrated in the latter two-thirds of the Lancian. On a global scale, the North American late Maastrichtian (Lancian) record is important because it contains one of the most diverse lissamphibian assemblages known for the Late Cretaceous, and it is one of the few well-documented, terminal Cretaceous lissamphibian assemblages. Elsewhere, the next most diverse lissamphibian assemblage of comparable age occurs in the late Maastrichtian of India, but this assemblage is limited entirely to anurans (e.g. Prasad and Rage 2004). The Lancian is the best sampled and studied interval for Mesozoic lissamphibians in North America and two Lancian rock units—the Lance and Hell Creek formations—are among the most richly fossiliferous units anywhere for Cretaceous lissamphibians. Both of those formations contain numerous vertebrate microfossil localities that have yielded abundant, well-preserved lissamphibian bones. For example, there are more than 60 localities in the Hell Creek Formation of Garfield County, Montana, that collectively have produced several thousand lissamphibian bones (e.g. DeMar and Wilson unpublished observation; Wilson et al. 2014). Over half (13 of 22) of the formally named and accepted lissamphibian species from the North American Mesozoic have Lancian occurrences (Table 6). Although not considered in any detail in this paper, another important contribution of the Lancian record is the insights it provides into lissamphibian communities leading up to the K-Pg boundary (for a more comprehensive treatment, see Wilson et al. 2014). A potentially significant biogeographic event for lissamphibians occurred on the North American continent during the Lancian: as the Interior Seaway began retreating to the north and south, land re-emerged in the central part of the Western Interior and would have allowed for the mixing of non-marine faunas between the formerly isolated western and eastern portions of the continent for the first time in about 25 million years.

Lancian lissamphibians are best documented from the type area of the Lance Formation, in Niobrara County, east-central Wyoming (e.g. Auffenberg 1961; Auffenberg and Goin 1959; Estes 1964, 1965, 1969b, 1981; Estes and Sanchíz 1982; Fox 1976b; Gardner 2000a, b, 2003a, 2008, 2012; Gilmore 1928b; Goin and Auffenberg 1958; this paper, Figs. 1m, q–r, 2s–t). Mammal taxa recognised from that area are the basis for the Lancian NALMA (e.g. Cifelli et al. 2004; Clemens et al. 1979; Lillegraven and McKenna 1986; Russell 1975). This is a richly fossiliferous area for the Lance Formation, with a history of collecting that extends back to the late 1880s when surface collecting and dry sieving for small vertebrate fossils began there, largely in pursuit of mammal jaws and teeth (see review by Kielan-Jaworowska et al. 2004). These efforts also produced isolated, non-mammalian specimens, including urodele bones that were featured in several publications between the late 1920s and early 1960s, as follows: (1) Gilmore (1928b) named and regarded *Habrosaurus dilatus* as a lizard on account of the bulbous and non-pedicellate teeth on the holotype dentary (see Estes 1964, upper image in pl. 3), but later Estes (1964) convincingly argued it was a sirenid; (2) Goin and Auffenberg (1958) named *Adelphesiren olivae*

and correctly assigned it to Sirenidae on account of its characteristic sirenid trunk vertebrae, then later Estes (1964) synonymised it with *H. dilatus*; (3) Auffenberg and Goin (1959) included vertebrae from the type Lance Formation and other units in a paper in which they synonymised three of Cope's (1876) species of *Scapherpeton* (i.e. *S. excisum*, *S. favosum* and *S. laticolle*) with *S. tectum* and erected the family Scapherpetonidae (note that family name was later emended to Scapherpetontidae by Kuhn [1967]); (4) Auffenberg (1961) named *Opisthotriton kayi* on the basis of vertebrae and a maxilla. Intensive screenwashing efforts that began in the mid-1950s in the type Lance Formation, again mostly for mammal fossils (see Cifelli et al. 2004; Estes 1964), dramatically increased the number of recovered fossil specimens. Less than a decade later, when Estes (1964) published his monograph on non-mammalian vertebrates from the type area of the Lance Formation, he stated (p. 2) that screenwashing had resulted in the recovery of over 30,000 small vertebrate fossils. Countless more specimens have been recovered in the subsequent decades, as screenwashing efforts have continued in the type area of the Lance Formation. Estes' (1964) monograph contained the first formation level account of an entire non-mammalian assemblage, and it demonstrated the wealth of information that could be gleaned from detailed study and comparison of isolated bones, teeth and scales recovered from vertebrate microfossil localities. It is no understatement to say that Estes' (1964) monograph opened the way to a new approach for studying small-bodied, non-mammalian fossil vertebrates and the ecosystems of which they were a part.

For the lissamphibian portion of his study, Estes (1964) recognised four named species of urodeles and informally recognised five kinds of anurans. Since then, the number of formally named lissamphibian species recognised from the type area of the Lance Formation has increased (Table 6, ESM Appendix 6) to 11 named species—one albanerpetontid, six urodeles and four anurans—plus additional, unnamed and indeterminate taxa (e.g. Estes 1965, 1969b, 1981; Estes and Sanchíz 1982; Fox 1976b; Gardner 2000a, b, 2003a, 2008, 2012). Outside of the type area in Wyoming, smaller collections of lissamphibian specimens and less diverse assemblages have been reported from farther north within Niobrara County (Whitmore and Martin 1986) and in Sweetwater County in south-central Wyoming (Breithaupt 1982). The latter assemblage includes an albanerpetontid, *A. galaktion* (see Gardner 2000a), not currently known from the type area. Of the dozen named species recognised from the Lance Formation, seven are founded on holotypes from the type area, as follows: the albanerpetontid *Albanerpeton nexuosum* (Estes, 1981), the batrachosauroidid *Prodesmodon copei* Estes, 1964, and the anuran *Palaeobatrachus occidentalis* Estes and Sanchíz, 1982, all from Lull 2 (= UCMP loc. V-5620); the anurans *Theatonius lancensis* Fox, 1976b and *Paradiscoglossus*

americanus Estes and Sanchíz, 1982, both from Bushy Tailed Blowout (= UCMP loc. V-5711); the sirenid *H. dilatus* Gilmore, 1928b and the batrachosauroidid *Opisthotriton kayi* Auffenberg, 1961, both from unrecorded localities.

The albanerpetontid and urodele portion of the Lance Formation are broadly similar in overall species-level diversity and composition to those from the Judithian, in that both assemblages share two species of albanerpetontids (*Albanerpeton nexuosum* and *A. galaktion*), the scapherpetontids *Scapherpeton tectum* and *Lisserpeton bairdi*, the batrachosauroidids *Opisthotriton kayi* and *Prodesmodon copei* and the sirenid genus *Habrosaurus*. Differences are that the Judithian has a third albanerpetontid (*A. gracile*), an unnamed new scapherpetontid (gen. et sp. nov. 1) and *H. prodilatus*, whereas the Lance Formation has the scapherpetontid *Piceoerpeton naylori*, an unnamed new batrachosauroidid (gen. et sp. nov. 4) and *H. dilatus*. Anurans are more challenging to compare because our understanding of that component in the Judithian and Lancian lissamphibian assemblages is less satisfactory. Both assemblages contain multiple anuran taxa and may contain similar numbers of species. Some of the same anuran taxa are present in both assemblages (e.g. *Scotiophryne pustulosa*, *Theatonius* spp. and the probable wastebasket taxon "cf. *Eopelobates* sp."), but each assemblage also contains different taxa. In a recent review of anurans from the Lance Formation, Gardner (2008) suggested that as many as 12 taxa might be represented on the basis of distinctive maxillary and iliac morphs. Three anuran species have been named on the basis of bones from the Lance Formation. *Theatonius lancensis* was the first edentate anuran reported from the Mesozoic, and its affinities remain as obscure as when it was first described (Fox 1976b; Gardner 2008; Holman 2003; Sanchíz 1998). *Paradiscoglossus americanus* and *Palaeobatrachus occidentalis* were originally interpreted (Estes and Sanchíz 1982) as members of the Eurasian families Discoglossidae sensu lato and Palaeobatrachidae, respectively. At that time, the latter familial assignment was notable for being one of the oldest reports of palaeobatrachids and the only record (along with some referred Bug Creek Anthills bones) from outside of Europe and western Asia. Both species continue to be accepted, but their higher level taxonomies have come into question. Assignment of *Palaeobatrachus occidentalis* to what otherwise is largely a Tertiary age Eurasian genus was first questioned by Sanchiz (1998), but he did not offer any alternatives. Here we follow the current convention (e.g. Sanchiz 1998; Gardner 2008) of writing the name as "*Palaeobatrachus*? *occidentalis*" to indicate uncertainty about the generic placement of that species. Both species were described on the basis of ilia, yet as pointed out by Gardner (2008; see also Roček 2013, this issue) for *Paradiscoglossus americanus* and more recently by Wuttke et al. (2012) for *Palaeobatrachus*? *occidentalis*, none of the holotype or

referred iliac specimens exhibit features that are compellingly diagnostic for either family. Here we follow Gardner (2008) in regarding *Paradiscoglossus americanus* as an incertae sedis taxon, but provisionally retain *Palaeobatrachus? occidentalis* in the Palaeobatrachidae. We note, however, that the apparent absence of more convincingly diagnostic palaeobatrachid elements, such as rectangular and fused frontoparietals and upper jaws bearing non-pedicellate teeth and small osseous knobs between tooth loci, in collections from the Lance Formation lend support to the notion that palaeobatrachids may not have been present in the Lance Formation.

Although less well documented, the Hell Creek Formation—exclusive of the Bug Creek Anthills (see following account)—has yielded abundant lissamphibian fossils from localities in northeastern Montana (e.g. Bryant 1989; DeMar 2011, 2013; Lupton et al. 1980; Wilson et al. 2014; Wilson 2008; this paper, Fig. 1h, j–k), in southwestern North Dakota (e.g. Pearson et al. 2002; this paper, Fig. 1i) and in northwestern South Dakota (e.g. Gates et al. 2010; Greenwald 1971). In recent years, field-based studies aimed at examining vertebrate communities across the K-Pg boundary have identified and screenwashed numerous vertebrate microfossil localities throughout most of the approximately 90-m thickness of the Hell Creek Formation in Garfield County, northeastern Montana, and in Bowman and Slope counties, southwestern North Dakota. Although mostly only preliminary details about the lissamphibian components from those study areas have been published (Montana: Carter 2009; Carter et al. 2007; DeMar 2011, 2013; Wilson et al. 2014; North Dakota: Pearson et al. 2002), on the basis of those publications and specimens examined by us, we can say with confidence that these localities will be critical for furthering our understanding of Lancian lissamphibians. Already, notable findings from the Montana collections include: (1) recognition of the first specimen (a maxilla) of the anuran *Theatonius lancensis* outside of its type locality in the Lance Formation of Wyoming (DeMar and Wilson, unpublished observation) and (2) the description of a new urodele, namely the proteid *Paranecturus garbanii* DeMar, 2013, on the basis of atlantes and trunk vertebrae (Fig. 1j, k). The latter discovery is significant for being the first pre-late Palaeocene record for Proteidae in North America and, depending on the familial affinities of "*Bishara backa*" from the Santonian–early Campanian of Kazakhstan (see Skutschas 2013, this issue), may also be the oldest global occurrence for that family. Among the North Dakota collections, a notable finding is the first unequivocal Cretaceous specimen (a trunk vertebra, see Fig. 1i) of the amphiumid *Proamphiuma cretacea* (Gardner and Pearson, unpublished observation). Comparisons between the Lance and Hell Creek formations cannot meaningfully be made for anurans because that group has not been examined in much detail yet for the Hell Creek Formation. The two anuran species recognised from that unit,

namely *T. lancensis* and *Scotiophryne pustulosa*, are also present in the Lance Formation. The apparent absence in collections from the Hell Creek Formation of diagnostic specimens of the other two named Lancian anurans (*Palaeobatrachus? occidentalis* and *Paradiscoglossus americanus*) is not surprising, considering each species is known by just two ilia from the Lance Formation. The same two species of albanerpetontids (*Albanerpeton galaktion* and *A. nexuosum*) occur in both formations. Compared to the Lance Formation, the urodele assemblage from the Hell Creek Formation is more diverse, with as many as 12 diagnosable or potentially diagnosable species among five families being present, whereas in the Lance Formation there are seven diagnosable or potentially diagnosable species among three families. Both formations share three scapherpetontids (*Scapherpeton tectum*, *Lisserpeton bairdi* and *Piceoerpeton naylori*), two batrachosauroidids (*Opisthotriton kayi* and *Prodesmodon copei*) and one sirenid (*Habrosaurus dilatus*). The only urodele unique to the Lance Formation is an unnamed species of batrachosauroidid (gen. et sp. nov. 4 in Table 6). By contrast, the Hell Creek Formation contains another six urodeles not known from the Lance Formation, as follows: three scapherpetontids, namely a large bodied taxon (here informally identified as cf. *Piceoerpeton* sp. in Table 6) and two unnamed new genera and species (here informally identified as gen. et sp. nov. 1 and 2; see Table 6); a sirenid (*H. prodilatus*); a proteid (*Paranecturus garbanii*); an amphiumid (*Proamphiuma cretacea*). With an inventory of 11 diagnosable or potentially diagnosable urodele species, the Montana portion of the Hell Creek Formation contains the most diverse urodele assemblage known for the Lancian and, indeed, for any of the Jurassic–Palaeocene intervals covered in this review. Amphiumids and proteids are living families that are moderately species rich in the eastern USA. Their appearances in the Lancian of North Dakota (*Proamphiuma*) and Montana (*Paranecturus*) could be explained by these families having moved from the eastern subcontinent into the Western Interior across the newly re-established land connection.

Outside of the Lance and Hell Creek formations, less well-studied lissamphibian assemblages of Lancian age that contain some combination of albanerpetontids, urodeles and anurans have been reported from the following six horizons and areas: (1) the lower part of the Scollard Formation, south-central Alberta (Eberth et al. 2001; Gardner 2000a); (2) the Frenchman Formation, southwestern and south-central Saskatchewan (e.g. Fox 1989, 1990; Gardner 2000a, 2003a; Johnson 1986; Sternberg 1924; Storer 1991; Tokaryk 1997; Tokaryk and Bryant 2004); (3) the Iron Lightning Member of the Fox Hills Formation, south-central North Dakota (Hoganson et al. 2007); (4) the lower part of the Ferris Formation, southeastern Wyoming (Lillegraven and Eberle

1999; Wroblewski 1997); (5) the Laramie Formation in northeastern Colorado (Carpenter 1979; Gardner 2000a); (6) the D1 Sequence of the Denver Formation in northeastern Colorado (G. Wilson, personal communication). None of those units contains any lissamphibian taxa not already known from the Lance or Hell Creek formations. There is one final Lancian record of note—an incomplete and indeterminate anuran skeleton briefly reported on by Cifelli et al. (1999b) from the lower part (latest Cretaceous) of the North Horn Formation, central Utah. Although that anuran skeleton is not particularly informative, it is the only example of an articulated lissamphibian specimen from the Lancian.

Bug Creek Anthills (mixed late Maastrichtian and early Palaeocene)

Bug Creek Anthills is part of a cluster of vertebrate microfossil localities in McCone County, northeastern Montana, within the upper part of the Hell Creek Formation (see Clemens et al. 1979; Lofgren 1995; Sloan and Van Valen 1965; Van Valen and Sloan 1965; this study, Fig. 8, plotted as "BCA"). These localities have been important for studies of North American fossil vertebrates due to the abundant and often well-preserved specimens that have been recovered from there since the early 1960s. Although palaeomammalogists recognised early on that Bug Creek Anthills contained a mixture of late Maastrichtian and early Palaeocene aspect mammalian taxa (e.g. see reviews by Cifelli et al. 2004; Clemens et al. 1979; Kielan-Jaworowska et al. 2004; Lofgren 1995), early palaeoherpetological studies regarded Bug Creek Anthills as contemporaneous with localities in the Lance Formation and, thus, Lancian in age (e.g. Estes 1965; Estes and Berberian 1970; Estes et al. 1969). More recent work has argued convincingly that Bug Creek Anthills is a temporally mixed assemblage, consisting of Puercan and reworked Lancian fossils (Lofgren 1995). Two important implications of that interpretation are: (1) for any given fossil from Bug Creek Anthills, there currently is no way to determine whether it is from an animal that lived during the Lancian or the Puercan and (2) consequently, Bug Creek Anthills cannot with confidence be used to date first or last appearances of taxa relative to the K-Pg boundary (Cifelli et al. 2004). These limitations are somewhat offset by the wealth of osteological information that often can be obtained from the abundant and well-preserved fossils from Bug Creek Anthills (e.g. Estes 1965, 1969b, c; Estes at el. 1969; Gardner 2000b, 2003a, b, 2008, 2012; Naylor 1983; this paper, Fig. 1l, n–p, s).

The lissamphibian assemblage from Bug Creek Anthills consists of ten named species, plus additional unnamed and indeterminate species (Table 7). Four currently recognised species are based on holotypes from Bug Creek Anthills: the scaperpetontids *Lisserpeton bairdi* Estes, 1965 and

Piceoerpeton naylori Gardner, 2012; the amphiumid *Proamphiuma cretacea* Estes, 1969b; the anuran *Scotiophryne pustulosa* Estes, 1969a. Aside from a possible cryptobranchid represented by one small, undescribed vertebra (Gardner unpublished observation), all Bug Creek Anthills lissamphibian species occur in the Lancian or Judithian, and some extend into the Palaeocene. Unlike the pattern seen with mammals, there is no good indication of exclusively Palaeocene aspect lissamphibians at Bug Creek Anthills. Little if any weight probably should be attached to that observation, considering that lissamphibians are not especially well documented from the early Palaeocene in North America (Table 8). Until recently, the only lissamphibian considered unique to Bug Creek Anthills was *Proamphiuma cretacea* (Estes 1969b; Gardner 2003a). Recent identifications of diagnostic *P. cretacea* vertebrae (Fig. 1i, u, respectively) from an unequivocal Lancian locality in the Hell Creek Formation of North Dakota (Gardner and Pearson unpublished observation) and from several unequivocal Puercan localities in the Tullock Formation of Montana (DeMar 2011; Wilson et al. 2014) demonstrate that species ranged across the K-Pg boundary and establish that Amphiumidae had appeared by the late Maastrichtian. The unsubstantiated statement by MacLeod et al. (1997, p. 281) that *P. cretacea* made its last appearance in the Judithian of Montana is best disregarded. Further refinements to age ranges for taxa known only from Bug Creek Anthills can be expected with improved sampling and with documentation of Lancian and Puercan assemblages that bracket and overlap with the Bug Creek Anthills.

Palaeocene

The Palaeocene Epoch is a transitional interval between the devastation of the K-Pg mass extinction event and the establishment of mammalian- and angiosperm-dominated terrestrial ecosystems and biotas characteristic of the Cenozoic. The Palaeocene saw an explosive radiation of mammalian groups (e.g. Clemens 2002; Wilson 2014), and much of what we know about that interval of mammalian history is based on fossils recovered from hundreds of Palaeocene age localities distributed through the North American Western Interior (e.g. see review by Lofgren et al. 2004). Many of these localities have yielded fossils of other vertebrates, including lissamphibians.

As documented here, 15 formations in the Western Interior have yielded Palaeocene age lissamphibian fossils. Many of these formations and their localities are included in the regional correlation chart provided by Lofgren et al. (2004, fig. 3.2). Compared to the Mesozoic, Palaeocene non-marine vertebrate localities in the Western Interior generally are more plentiful and have a stratigraphically denser distribution; in addition, their ages can often be resolved more precisely thanks to the presence of age-diagnostic mammalian taxa at

many localities and the high-resolution system of NALMAs for the Cenozoic. From oldest to youngest, the Palaeocene is divided into four NALMAs: Puercan, Torrejonian, Tiffanian and Clarkforkian. Some of the formations listed here span several NALMAs. Overviews of the Palaeocene NALMAs and related matters are provided by Prothero (1998), Lofgren et al. (2004) and Rose (2006).

As was the case for the Cretaceous, Palaeocene age lissamphibian-bearing formations in the Western Interior were deposited in fluvial and associated (e.g. floodplains, swamps and ponds) environments under similarly warm, subtropical climatic conditions. The Palaeocene lissamphibian fossil record is biased towards isolated bones. Screenwashing continues to be an important method of obtaining fossils, but a greater emphasis on hand quarrying, mainly in pursuit of mammal, fish and plant fossils, also has produced some exquisitely preserved lissamphibian bones and skeletons (e.g. Fig. 1t, y).

Comparisons of lissamphibian occurrences for the Late Cretaceous versus the Palaeocene (Tables 3–6 vs. 8 and 9) would seem to indicate that during the Palaeocene anurans and albanerpetontids were noticeably less common. For example, for the eight unequivocal Torrejonian localities or groups of localities listed here, urodeles are known from seven localities, whereas anurans and albanerpetontids are each known from just one locality. The scarcity of Palaeocene albanerpetontids may be a real pattern. Albanerpetontid fossils are relatively uncommon in most well-sampled Lancian localities (e.g. Wilson et al. 2014), especially when compared to Judithian or older Cretaceous localities in North America. These differences in relative abundances suggest that albanerpetontids may already have been declining on the continent near the end of the Cretaceous. Palaeocene albanerpetontids in North America are limited to one Torrejonian locality and several Tiffanian localities in Alberta, with only one species present. The apparent scarcity of anurans in the Western Interior during the Palaeocene is less easy to explain. The lack of any mention of anurans from localities where other components of the herpetofauna appear to have been thoroughly documented (e.g. the Torrejonian age Gidley and Swain quarries: Sullivan 1980, 1991) and the rarity of anurans from other localities (e.g. the Tiffanian age Roche Percée localities: Naylor 1981b) suggest that, for reasons unknown, during the Palaeocene anurans were less common in the region than during the Late Cretaceous. By contrast, urodeles have a relatively strong presence in the Western Interior throughout the Palaeocene, with multiple taxa being represented.

Early Palaeocene (Puercan and Torrejonian NALMAs)

The Puercan and Torrejonian NALMAs constitute slightly less than half of the Palaeocene; the Puercan is about 1 million years in duration, whereas the Torrejonian is about 3 million years in duration (Lofgren et al. 2004). Both of these NALMAs are based on mammalian assemblages from the San Juan Basin of New Mexico, an area that has yielded few lissamphibian fossils.

Puercan age lissamphibians are known from at least eight formations, with localities extending from central Alberta southwards to southwestern Texas (Fig. 9, Table 8). An intact skeleton of the batrachosauroidid *Opisthotriton kayi* is known from a plant locality in the upper part of the Scollard Formation in central Alberta (Naylor 1981b; this paper, Fig. 1t) and presumed urodele trackways have been described from the Fort Union Formation in north-central Wyoming (Johnson 1986). All other Puercan occurrences are in the form of isolated bones. Some of those come from formations and areas where only a few lissamphibian-bearing localities are known. These include the following: Rav W-1 horizon and Croc Pot, southwestern Saskatchewan, lower part of Ravenscrag Formation (Fox 1990; Johnston and Fox 1984; Naylor 1981b); UW loc. V-82010, north-central Wyoming, Polecat Bench Formation (Hartman 1986); UCM locs. 77267 and 78191, north-central and northeastern Colorado, respectively, Denver Formation (Gardner unpublished observation; Middleton and Dewar 2004); UCMP loc. V1312, northwestern New Mexico, Nacimiento Formation (Sullivan and Lucas 1986; Williamson and Lucas 1993); and LSUMG locs. V-108 and V111, southwestern Texas, Tornillo Formation (Standhardt 1986). Isolated lissamphibian bones have also been recovered from larger numbers of vertebrate microfossil localities in the Tullock Formation of northeastern Montana (e.g. Bryant 1989; DeMar 2011; DeMar and Wilson, unpublished observation; Wilson et al. 2014; Van Valen and Sloan 1965) and in the lower part of the Fort Union Formation of southwestern North Dakota (Gardner and Pearson, unpublished observation). As documented by Wilson et al. (2014), recent work on a locality just above the K-Pg boundary, in the base of the Tullock Formation in Montana, has revealed the existence of a highly uneven and taxonomically depauperate urodele assemblage, the composition of which is typical of plant and animal assemblages following a major ecological disturbance or mass extinction event (e.g. Dornelas et al. 2011; Harries et al. 1996).

Lissamphibians of Torrejonian age have been reported from five formations extending from central Alberta southwards to northwestern New Mexico (Fig. 9, Table 8), as follows: Coalspur and Paskapoo formations, Alberta (Fox 1990; Gardner and Böhme 2008; Russell 1929; Scott 2003); Fort Union Formation, Montana and Wyoming (Estes 1976; Krause 1980; Naylor and Krause 1981; Sullivan 1980, 1991); Lebo Formation, Wyoming (Gardner 2003a; Sullivan 1991); Nacimiento Formation, New Mexico (Sullivan and Lucas 1986). Most of the documented lissamphibian-bearing localities from this interval have produced only isolated bones, many of which were recovered during hand quarrying. Two undescribed, fragmentary albanerpetontid jaws from a

single Paskapoo locality (?Who Nose, in the City of Calgary, Alberta) represent the only known early Palaeocene occurrence for this group in North America (Gardner and Böhme 2008). Two other localities in different formations are notable for having yielded urodele skeletal specimens. Fox (1990) mentioned a skull of *Opisthotriton kayi* from the Diss locality, in the Coalspur Formation of west-central Alberta. Sullivan (1991) described the holotype skull of *O. gidleyi* nomen dubium (Sullivan, 1991) and the anterior part of a skeleton of *Habrosaurus dilatus*, both from Gidley Quarry, in the Lebo Formation of south-central Montana. Gardner (2000b) suggested that considering the crushed nature of the holotype skull and the doubtful reliability of the features used by Sullivan (1991) to erect his new species of *Opisthotriton*, that the name *O. gidleyi* be considered a junior subjective synonym of the type species *O. kayi*. The incomplete *H. dilatus* skeleton from Gidley Quarry is the only articulated example of that long-lived (Santonian–Palaeocene) sirenid genus.

The final occurrences to be considered here are anuran fossils reported in two conference abstracts (Bonde et al. 2011; Shirk et al. 2009) from Member B of the Sheep Pass Formation (Maastrichtian–Eocene) in east-central Nevada. A Maastrichtian–Palaeocene age has been given for Member B (e.g. Bonde et al. 2011; Druschke 2009; Shirk et al. 2009), but the position of the anuran-bearing horizon has not been reported. Here we provisionally regard the occurrence as probably early Palaeocene in age because (1) radiometric dates for the base of Member B are approximately coincident with the K-Pg boundary (Druschke et al. 2009) and (2) judging from a stratigraphic section presented by Druschke (2009, chapter 4, fig. 2) much of Member B is depicted as being within the lower part of the Palaeocene. Two kinds of anuran fossils have been reported from Member B: a pair of *Palaeobatrachus occidentalis* skeletons (Shirk et al. 2009) and taxonomically unidentified, partially disarticulated skeletons and isolated, reworked bones (Bonde et al. 2011). The possibility of the skeletons belonging to *P. occidentalis* is potentially exciting, considering that species otherwise is known by just a few isolated bones from the Lance Formation and Bug Creek Anthills (Estes and Sanchíz 1982; Gardner 2008) and given recent doubts about its higher level affinities (Wuttke et al. 2012). Regardless of their precise age and identities, the anuran fossils from Member B should prove illuminating once they are formally described and interpreted; that work is in progress (A. Henrici, personal communication).

The early Palaeocene lissamphibian assemblage in the Western Interior contains no species that are not known from the Lancian. Anurans appear to be noticeably less diverse during the early Palaeocene compared to the Lancian. Of the four named anuran species recognised from the Lancian, none is unequivocally present during the early Palaeocene; nor are any of the maxillary or iliac morphs recognised from the Lance Formation (Gardner 2008) currently known from the early Palaeocene. There are two potential exceptions, those being postcranial bones of *Scotiophryne pustulosa* and "cf. *Scotiophryne*" from Montana (Bryant 1989 and Estes 1976, respectively) and skeletons of *Palaeobatrachus occidentalis* from Nevada (Shirk et al. 2009). Bryant's (1989) report of *Scotiophryne pustulosa* in the Puercan–earliest Torrejonian age Tullock Formation of Montana was based on an undescribed and unfigured humerus. We regard that specimen as Anura indet. because we consider the humerus diagnostically unreliable for anuran species. Estes (1976) identified "cf. *Scotiophryne*" from a Torrejonian locality in the Fort Union Formation of Montana on the basis of an ilium and humeri. Considering that the holotype of *S. pustulosa* is an ilium and that this species was described by the same author (Estes 1969b), we have somewhat more confidence in the published identification of that Montana ilium. Shirk et al.'s (2009) report of *P. occidentalis* skeletons in probable early Paleocene age deposits in Nevada cannot be verified until these specimens are described. Finally, we note that reports of *Palaeobatrachus* in the Torrejonian (Archibald and Bryant 1990, table 1; Bryant 1989, table 2; MacLeod et al. 1997, p. 281) are unsubstantiated because no details about those occurrences were provided. Other occurrences known to us for early Palaeocene anurans in the Western Interior are limited to the Puercan and these consist of unstudied bones (e.g. Fig. 2u). Further work is clearly needed to better document the diversity of North American early Palaeocene anurans. The early Palaeocene albanerpetontid record is even less informative because it is limited to two indeterminate jaw fragments from one Torrejonian locality in Alberta. The much better documented and diverse urodele assemblage during the early Palaeocene in the Western Interior resembles that from the latest Cretaceous in containing scapherpetontids, batrachosauroidids, sirenids and amphiumids. This resemblance is greatest for the Puercan, when the batrachosauroidid *Prodesmodon copei* and the amphiumid *Proamphiuma cretacea* are both known. Neither of these species has been recorded from the Torrejonian or younger intervals.

Late Palaeocene (Tiffanian and Clarkforkian NALMAs)

The Tiffanian is about 5 million years in duration, whereas the Clarkforkian is slightly less than 1 million years in duration (Lofgren et al. 2004). These NALMAs are based on mammalian assemblages from southern Colorado and northwestern Wyoming, respectively; only the latter area is known to have yielded lissamphibian fossils.

Considering it is the longest of the four Palaeocene NALMAs, it perhaps is not surprising that the Tiffanian has produced the most diverse lissamphibian assemblage for the epoch (Table 9). Lissamphibian-bearing localities of Tiffanian

age are known from six formations in the northern and central parts of the Western Interior (Fig. 10). The DW localities and Cochrane 2, all in the Paskapoo Formation of central and south-central Alberta, have produced jaws and skull roof bones belonging to an unnamed species of *Albanerpeton* (e.g. Fox and Naylor 1982, table 1; Gardner 2000c, fig. 1C; Gardner and Böhme 2008). Those fossils document the geologically youngest records for Albanerpetontidae in North America. The anuran record is marginally better, consisting of rare isolated and mostly indeterminate bones from the DW localities in the Paskapoo Formation (Fox 1984), the Roche Percée localities in the upper part of the Ravenscrag Formation, southeastern Saskatchewan (Naylor 1981b; this paper, Fig. 2v) and the Wannagan Creek Quarry in the Tongue River (= Bullion Creek) Formation, southwestern North Dakota (Erickson 1991, 1999, 2012). The Princeton Quarry local fauna, which consists of several quarries in the Fort Union (= Polecat Bench) Formation, northwestern Wyoming, has produced bones of indeterminate anurans and of the rhinophrynid *Eorhinophrynus* sp. (Estes 1975). The latter is the oldest Cenozoic occurrence for that otherwise Eocene age genus (e.g. Holman 2003; Sanchiz 1998) and, depending on the affinities of *Rhadinosteus* from the Late Jurassic age Morrison Formation (Henrici 1998b), it also may be the oldest global record for the family. The Princeton Quarry local fauna is further notable for having produced the first articulated and associated urodele skeletons to be described from the North American Palaeocene. These are two incomplete skeletons of *Opisthotriton kayi* and an incomplete postcranium and skull of *Amphiuma jepseni* Estes, 1969c (Estes 1969c, d, 1975). The *O. kayi* skeletal specimens were important for corroborating associations proposed earlier by Auffenberg (1961) and Estes (1964) for isolated, late Maastrichtian (Lancian) age vertebrae and skull bones from the Lance Formation. Although not as thoroughly described, the most taxonomically diverse urodele assemblage for the entire Palaeocene reportedly comes from the Roche Percée localities, in the upper part of the Ravenscrag Formation, southeastern Saskatchewan (Naylor 1981b). All of the Roche Percée lissamphibian specimens are isolated bones (e.g. Figs. 1w, x, 2v) salvaged from spoil piles at a former open pit coal mine. The Roche Percée urodele assemblage consists of at least six species in five families: the scapherpetontids *Piceoerpeton willwoodense* (Meszoely, 1967) and cf. *Scapherpeton* sp.; the batrachosauroidid *Opisthotriton kayi*; the cryptobranchid *Cryptobranchus saskatchewanensis* Naylor, 1981b; the proteid *Necturus krausei* Naylor, 1978b; an indeterminate amphiumid (Gardner 2003b; Naylor 1978b, 1981b; Naylor and Krause 1981). Additionally, Naylor (1981b, p. 76) stated "one or two new species of uncertain affinities" may also be present. The giant scapherpetontid *P. willwoodense* makes its first appearance in the Tiffanian. Besides occurring at Roche Percée, *P. willwoodense* also is known by isolated vertebrae (e.g.

Fig. 1v) and skull bones from numerous Tiffanian age localities in Alberta, Montana, Wyoming, and North Dakota (Erickson 1991, 1999, 2012; Gardner 2012; Krause 1980; Naylor and Krause 1981). One of the *Piceoerpeton*-bearing localities in Wyoming, Cedar Point Quarry in the Fort Union (= Polecat Bench) Formation, also reportedly contains *Lisserpeton* (Krause 1980; Naylor and Krause 1981). Another of the *Piceoerpeton*-bearing localities, the famous Wannagan Creek Quarry in the Tongue River (= Bullion Creek) Formation of southwestern North Dakota, also reportedly contains *Scapherpeton* (Erickson 1991, 1999, 2012). The Wannagan Creek Quarry has also yielded an undescribed, indeterminate urodele skeleton (Erickson 2012, fig. 23). Two other Tiffanian localities that are better known for their fish and plant fossils have also produced several urodele skeletons: (1) the fish beds at Almont (see Newbrey and Bozek 2000; Zetter et al. 2011), in the Sentinel Butte Formation of central North Dakota, have yielded an unidentified urodele skeleton (Gardner and Newbrey unpublished observation) and (2) Smoky Tower (see Christophel 1976; Wilson 1980), in the Paskapoo Formation of west-central Alberta, has yielded the holotype skeleton of *Dicamptodon antiquus* Naylor and Fox 1993 (e.g. see Fig. 1y) and a pair of unidentified skeletons (Gardner unpublished observation). The holotype skeleton of *D. antiquus* is the oldest body fossil record for Dicamptodontidae in North America and may be the only unequivocal fossil occurrence for the family (for differing opinions, see Estes 1981 vs. Milner 2000). Approximately contemporaneous trackways interpreted as having been made by a dicamptodontid (Estes 1981; Peabody 1954, 1959) were described from the Fort Union Formation of south-central Montana (Gilmore 1928b; Peabody 1954, 1959) and are the holotype for the ichnotaxon *Ambystomichnus montanensis* (Gilmore, 1928a).

Lissamphibians of Clarkforkian age are limited to a few localities in Montana and Wyoming (Fig. 10, Table 9). The best documented Clarkforkian lissamphibian is the scapherpetontid *Piceoerpeton willwoodense*, which is known by the holotype trunk vertebra from the Willwood Formation and by referred trunk vertebrae and an exoccipital from the ?Polecat Bench Formation, both in northwestern Wyoming (Krause 1980; Meszoely 1967; Naylor and Krause 1981). Another locality in the Willwood Formation produced a fragmentary and worn maxilla that Naylor (1981b) questionably referred to the cryptobranchid *Cryptobranchus saskatchewanensis*. There are two unverified reports of the batrachosauroidid *Opisthotriton* sp. from the Clarkforkian. The first is a trunk vertebra briefly described by Auffenberg (1961) from the Bear Creek local fauna in the Willwood Formation. Unfortunately, the published line drawing of that specimen (Auffenberg 1961, fig. 5) is not especially informative, and the specimen now appears to have been lost (A.

Henrici, personal communication). The other reported Clarkforkian occurrence of *Opisthotriton* sp., at UM loc. FG-6 in the ?Polecat Bench Formation of northwestern Wyoming, is founded on an undescribed specimen listed by Krause (1980, table 1, footnote 13). Big Multi Quarry, in the Fort Union Formation of southwestern Wyoming, reportedly contains urodeles (Wilf et al. 1998). Freshwater limestone deposits in the Clarkforkian portion of the Willwood Formation, in northwestern Wyoming, are richly fossiliferous and have yielded some exquisite, small-bodied tetrapod skeletons, especially of mammals (e.g. Bloch and Boyer 2001; Gingerich 1987). The only reports of lissamphibians from those deposits, however, are of a fragmentary anuran humerus and some small urodele vertebrae, all from carbonate lens J at SC-29 Discovery Site (Gingerich 1987).

For completeness, we also include here preliminary reports of anuran skeletons and an anuran bonebed from a unit that straddles the Palaeocene–Eocene boundary, namely Member C of the Sheep Pass Formation, in east-central Nevada. The skeletons provisionally were identified (Shirk et al. 2009) as belonging to the incertae sedis anuran *Eorubeta nevadensis* Hecht, 1960, but no taxonomic identifications have been provided for the isolated bones contained in the bonebed (Bonde et al. 2011; Shirk et al. 2009). Work on anurans from the Sheep Pass Formation is in progress (A. Henrici, personal communication).

Taken at face value, the late Palaeocene lissamphibian assemblage in the Western Interior continues the trend seen in the Torrejonian, with losses of some latest Cretaceous urodele taxa in a stepwise fashion. Most striking is the absence of the sirenid *Habrosaurus* from any of the late Palaeocene localities. Regarding scapherpetontids, *Scapherpeton* has four unverified occurrences and *Lisserpeton* has one unverified occurrence in the Tiffanian; neither is recorded from the Clarkforkian. *Opisthotriton* is reliably known by skeletons from the Tiffanian age Princeton Quarry local fauna, but other reported occurrences in the Tiffanian and Clarkforkian are unverified. To our knowledge, those four genera are unknown from the Eocene. Although this apparent stepwise loss of latest Cretaceous aspect urodeles through the Palaeocene is appealing, it is important to emphasise that the observed pattern is founded on relatively few localities and specimens and that some of the taxonomic identifications are unverified. Other urodele taxa appear or re-appear in the Tiffanian record, as follows: (1) *Piceoerpeton willwoodense* is the first appearance of that species and a re-appearance (from the Lancian) of the genus; (2) *Dicamptodon antiquus* is the first appearance of that extant genus and, assuming Milner (2000) is correct, for the family; (3) *Amphiuma jepseni* is the first appearance of that extant genus and a re-appearance (from the Lancian–Puercan) of Amphiumidae; (4) *Necturus krausei* is the first appearance of that extant genus and a re-appearance

(from the Lancian) of Proteidae; (5) *Cryptobranchus saskatchewanensis* is the first appearance of that extant genus and, depending on the affinities of the vertebra mentioned above from Bug Creek Anthills, is either the first appearance or a re-appearance in North America of Cryptobranchidae. *Piceoerpeton willwoodense* survived into the early Eocene; after that time, scapherpetontids are absent from the fossil record (e.g. Gardner 2012; Naylor and Krause 1981). By contrast, the other four urodele genera that made their first appearances in the Tiffanian (i.e. *Amphiuma*, *Cryptobranchus*, *Dicamptodon* and *Necturus*) survive to the present day in North America. Albanerpetontids briefly re-appeared during the Tiffanian in the form of one undescribed species of *Albanerpeton*, then vanished from the North American record. *Albanerpeton* persisted in Europe until the late Pliocene (e.g. Delfino and Sala 2007; Gardner and Böhme 2008). The late Palaeocene anuran record in the Western Interior is relatively uninformative, except for establishing the unequivocal presence during that time of Rhinophrynidae, a taxonomically impoverished family that is endemic to North America and contains one living species.

Temporal lissamphibian richness during the Mesozoic and Palaeocene in North America

Of the 36 5-Myr temporal intervals or bins required for the interval covered by our analysis, only 16 are fossiliferous. Even fewer bins (14) contain unequivocal lissamphibians, beginning approximately at the Sinemurian/Pliensbachian boundary (ESM Appendix 10, bin 10) for the Kayenta Formation occurrences and extending through to the terminal Palaeocene (ESM Appendix 10, bin 36) for the Clarkforkian and the Palaeocene/Eocene boundary occurrences (Fig. 11). Of the approximately 120 lissamphibian localities and groups of localities documented here (Tables 1–9), four were not included for richness estimates; these were the two Late Triassic localities in the eastern USA, the Tincup Creek locality in Idaho and Bug Creek Anthills in Montana (see Methodology and conventions). Based on our taxonomic decisions, a total of 107 discrete taxonomic entities (1 gymnophionan, 57 anurans, 38 caudates and 11 albanerpetontids), consisting of diagnosable or potentially diagnosable species and of specifically indeterminate occurrences, were distributed among the raw 141 binned occurrences. The eight species range-through occurrences in bin 33 (approximately equivalent to the late Campanian–early Maastrichtian or "Edmontonian") were not included in the total binned occurrences value (see ESM Appendix 10 for details). A total of 183 minimal lineage level occurrences are estimated, a richness increase of 42 binned occurrences or nearly 30% above the raw taxic value.

Figure 11 illustrates temporal taxic and minimal lineage level richness patterns for each of the four major lissamphibian clades and for Lissamphibia as a whole during the Jurassic to Palaeocene in North America. The raw taxic richness curve for Lissamphibia demonstrates the heterogeneous occurrences of taxa through the approximately 140 Myr interval studied here. Much of the variation in the richness curve is driven by anurans and caudates. Albanerpetontids have relatively low richness values throughout the entire interval of study; their one peak richness is during the middle–late Campanian (Judithian), with a total of four taxa (three named species + one indeterminate; Table 4). A general pattern of increasing taxonomic richness occurs leading up to the K-Pg boundary and declines thereafter. More than 70% of taxic occurrences are during the last approximately 28 Myr (Campanian–Palaeocene) of the entire sampled interval, which equates to about 68% (73 of 107) of the total number of discrete taxonomic entities. The minimal lineage level richness curve largely mimics the raw taxic richness pattern, although it is important to emphasise that for each individual clade (excluding Gymnophiona) the corresponding curve predicts slightly higher richness values (between one and four additional inferred lineages) between successive taxic peaks, and these often coincide with intervals where actual fossil occurrences are lacking. The majority of lineage level contributions to the richness curve (69%) occur prior to the Cenomanian, an interval when major and minor temporal gaps fragment the lissamphibian fossil record. Of the remaining binned intervals during the Cenomanian to the terminal Palaeocene and where we could apply the minimal lineage level approach (bins 30, 33, 35 and 36), the number of additional predicted lineages decreases to only one per interval, a pattern partially driven by several occurrences of undescribed taxa, particularly anurans (e.g. Gardner 2008; Roček et al. 2010) and a lesser number of caudate taxa (e.g. Gardner et al. 2013), that currently are of uncertain taxonomic affinities. The occurrences of these numerous indeterminate and undescribed taxa, plus the various uncertainties in higher taxonomic affinities for described taxa (e.g. anurans; Gardner 2008), hinder our ability to apply additional lineage extensions for several taxa during this interval (e.g. across the trough spanning the Campanian/Maastrichtian boundary). As stated above (see Methodology and conventions section), the lineage level method was not applicable to Gymnophiona due to that clade's absence from the North American record between the Early Jurassic and Quaternary. Given such an extensive hiatus (approximately 190 Myr) in the North American gymnophionan record, it is unreasonable to assume evolutionary continuity, even at a continental scale, because of the possibility of migration events, range contractions and local extinctions (Fara 2004).

Overall, both of the richness curves (taxic and minimal lineage level) depict relatively low richness values (0–8 taxa)

during approximately the first half of the temporal interval under study (Sinemurian–Barremian). Only a few minor peaks and one moderate spike in richness are plotted for that interval. The first minor peak (two taxic and two minimal lineages) at approximately the Sinemurian/Pliensbachian boundary (ESM Appendix 10, bin 10) represents the first unequivocal appearances of lissamphibians in North America, namely the crown frog *Prosalirus* and the stem caecilian *Eocaecilia* in the Kayenta Formation of Arizona (Table 1). The moderate richness peak (eight taxic and eight minimal lineages) occurring during the Kimmeridgian–earliest Tithonian (ESM Appendix 10, bin 17), is founded exclusively on specimens from two richly fossiliferous and moderately well-studied localities (Quarry 9 in Wyoming and Rainbow Park in Utah) in the Morrison Formation (Table 1) that collectively contain about a half dozen taxa of anurans and a few caudates, including the earliest North American urodele (i.e. *Iridotriton*). The next minor peak (two taxic and three lineages) during the late Berriasian–Valanginian includes the first North American occurrence of Albanerpetontidae and of an indeterminate, but distinctive urodele (Fig. 1b) from the Lakota Formation in South Dakota (Table 2).

Following the relatively lissamphibian-poor Sinemurian–Barremian interval, richness values rise to 11 taxa in North America at approximately the Aptian/Albian boundary, thanks largely to recently documented assemblages from the Cloverly Formation of Montana and Wyoming and earlier studies of assemblages from the Trinity Group of Texas and Oklahoma (Table 2). Lissamphibian samples collected from several Cloverly Formation localities by Oreska et al. (2013) are substantial in size (>700 specimens), but include specimens mostly indeterminate below the ordinal level. Nevertheless, these samples include the earliest appearances of a *Scotiophryne*-like anuran (i.e. cf. *Scotiophryne* sp.), the genus *Albanerpeton* and indeterminate batrachosauroidid and scapherpetontid salamanders. The two urodele occurrences (i.e. Batrachosauroididae gen. et sp. indet. and Scapherpetontidae gen. et sp. indet.: Table 2) mark the first appearances of two clades that are inferred to span most of the Albian and early Cenomanian (see Caudata "Lineage richness" curve in Fig. 11; ESM Appendix 10, bins 26–28) and then carry on with numerous fossil occurrences through to the end (i.e. terminal Palaeocene) of the studied interval.

Richness values for all lissamphibian clades begin rising approximately from the middle/late Cenomanian through to the early–middle Campanian. Collectively, Lissamphibia taxic richness increases from a minimum of six to 14 taxa during this interval (Fig. 11; ESM Appendix 10, bins 28–31). This increasing richness pattern is chiefly driven by collections from multiple Verdigris Coulee localities in the Milk River Formation of south-central Alberta and by more recent collections from as many as 28 localities spanning the Dakota, Straight Cliffs, Iron Springs and Wahweap formations

exposed on the Markagunt, Paunsaugunt and Kaiparowits plateaus in southern Utah (Fig. 5, Table 3). Current research (Gardner et al. 2013; Roček et al. 2010), including several unpublished observations by one of us (JDG) and colleagues (see Table 3), on lissamphibians from these formations indicates the presence of several distinctive anurans based principally on maxillary and iliac morphs that likely represent novel taxa: five urodeles based on vertebrae (e.g. Fig. 1f), and several albanerpetontids based on premaxillae (e.g. Fig. 2b). Cumulative fossil sample sizes from the aforementioned southern Utah localities for the anuran and urodele occurrences consist of several hundred published specimens, including 68 maxillae and 183 ilia for anurans (Roček et al. 2010, fig. 3 graph) and about 80 vertebrae and dentaries for urodeles (Gardner et al. 2013). Future systematic work on these specimens will undoubtedly provide a better understanding of the taxonomic diversity necessary for calculating more accurate richness estimates for that time interval.

Peak lissamphibian richnesses occurred during the Campanian (27 taxic and 27 minimal lineages) and again during the Maastrichtian (25 taxic and 25 minimal lineages) (ESM Appendix 10, bins 32 and 34, respectively). The vast majority of taxonomic occurrences from those intervals are derived from confirmed Judithian and Lancian age deposits (Tables 4, 6). Albanerpetontids reached their highest richness (four taxic and four minimal lineages) during the middle–late Campanian (Judithian). Anurans, composed primarily of multiple undescribed and indeterminate but discrete taxa, also reached their peak richness (13 taxic and 13 minimal lineages) during the Judithian, whereas urodeles peaked (13 taxic and 13 minimal lineages) during the late Maastrichtian (Lancian). Lancian age urodeles are mostly described and ubiquitous species (e.g. *Scapherpeton tectum*, *Opisthotriton kayi*), although several new taxa have come to light and are included in our richness estimate. Historically, the Judithian and Lancian NALMAs have been the primary focus for collecting and research efforts (e.g. see "Total records" curve in Fig. 11; ESM Appendix 12) because of the richly fossiliferous deposits in Alberta, Canada, and the northern USA (Wyoming and Montana). Consequently, the peak richnesses revealed in the Campanian and Maastrichtian most likely are a reflection of those biased efforts, although a portion of the true richness pattern may still be present. Clearly, additional research effort is warranted from the surrounding time intervals to corroborate these findings.

The relatively low taxic and minimal lineage level richness values between the peaks of the Campanian and Maastrichtian primarily reflect the poorly sampled "Edmontonian" or late Campanian–early Maastrichtian interval. That interval (ESM Appendix 10, bin 33) was the only one in which we incorporated species range-through occurrences in the raw taxic richness estimate. Eight species range-through occurrences were added to the five raw occurrences (see Lissamphibia value in parentheses in ESM Appendix 10, bin 33) during this interval for a total of 13 taxa, which is approximately half that in the surrounding time intervals. This occurrence of low taxic richness is slightly elevated when inferring minimal numbers of lineages (14 taxa). Due to uncertainties in the higher level relationships for most of the specifically indeterminate occurrences (e.g. multiple undescribed, but distinct indeterminate anuran taxa) in the surrounding temporal bins (i.e. bins 32 and 34), we could not infer additional lineages for this poorly sampled interval.

A seemingly compelling trend of decreasing lissamphibian richness across the K-Pg boundary is shown in Fig. 11, with a 52% decline in total lissamphibian richness (i.e. from 25 to 12 taxic occurrences; ESM Appendix 10, bins 34 and 35, respectively). The minimal lineage level method predicts a slightly lower decline in richness (48%) with only 13 of 25 Maastrichtian lineages being present during the first 5 Myr of the Palaeocene. The single lineage extension across the K-Pg boundary is the inferred proteid ghost lineage between the Lancian age *Paranecturus garbanii* and its late Palaeocene (Tiffanian) sister taxon *Necturus krausei* (Tables 6 and 9, respectively). Richness values for the three lissamphibian clades that crossed the K-Pg boundary in North America are as follows: anurans decrease from 10 to 3 or 70% for both taxic and lineage; caudates decrease from 13 to 8 or 38% for taxic and from 13 to 9 or 31% for lineage; albanerpetontids decrease from 2 to 1 or 50% for both taxic and lineage. Although these patterns suggest high extinction levels for lissamphibians during the K-Pg mass extinction, it is important to bear in mind that the large size of the temporal bins (5 Myr) used to generate those curves tends to obscure finer temporal patterns around the K-Pg boundary. For example, some of the species occurring in bin 34 make their last stratigraphic occurrence and, hence, their final temporal appearance well in advance of the K-Pg boundary (e.g. *Habrosaurus prodilatus*). Given that such taxa drop out of the fossil record prior to the K-Pg boundary, they are unlikely to have been victims of the K-Pg mass extinction event (Wilson et al. 2014). When more finely resolved stratigraphic distributions like these are considered, proportional species-level extinctions of urodeles and albanerpetontids are inferred to have been considerably lower (22%; Wilson et al. 2014) than estimates predicted here for those two clades combined (40% taxic, 33% lineage). The proportionately high richness decline for anurans (70%) across the K-Pg boundary is most certainly attributable to the near lack of research on that group from the early Palaeocene (e.g. see "Total records" curve in Fig. 11; ESM Appendix 12). As such, the dramatic decrease plotted on Fig. 11 for Anura, and for Lissamphibia as a whole, across the K-Pg boundary

may, to some extent, be an artifact of our methodology and, more significantly, of our relatively poor knowledge about North American early Palaeocene lissamphibians, rather than a true reflection of diversity patterns during that interval.

The last temporal bin (bin 36) in our temporal richness analysis, which encompasses the late (Tiffanian) and latest (Clarkforkian) Palaeocene, includes the occurrence of an anuran at approximately the Palaeocene/Eocene boundary (i.e. *Eorubeta nevadensis*; Table 9). Richnesses continued to drop from the early Palaeocene (bin 35) as several batrachosauroidid, scapherpetontid and sirenid species go extinct (e.g. *Prodesmodon copei*, *Lisserpeton bairdi* and *Habrosaurus dilatus*, respectively). Richness is buffered, however, by the first unequivocal appearances of several new families of urodeles (Cryptobranchidae and Dicamptodontidae) and one family of anurans (Rhinophrynidae), plus appearances of species and genera from pre-existing families (e.g. the amphiumid *Amphiuma jepseni* and the proteid *Necturus krausei*). The occurrence data assembled here implies that the scapherpetontid *Piceoerpeton willwoodense* was the dominant lissamphibian species during the late Palaeocene, with unequivocal occurrences at nine out of the 21 Tiffanian and Clarkforkian localities listed in Table 9. However, we caution that the apparent prominence of *P. willwoodense* during that interval almost certainly is driven by one publication in which that species and its occurrences were thoroughly documented (Naylor and Krause 1981). We suspect that if similarly detailed surveys of institutional collections were done for other relatively common species, such as *Opisthotriton kayi* or *Scapherpeton tectum*, these too might be shown to have been at least as ubiquitous as *P. willwoodense*. Although sirenids are absent from the latter part of the Palaeocene (Table 9), we inferred a single sirenid lineage for this interval because the family reappears during the Eocene and extends through to the present day in North America (e.g. Estes 1981; Gardner 2003a; Holman 2006).

Considering that only slightly more than one-third of the 5-Myr bins used in our analysis contained lissamphibians and that diversities are not adequately documented for even the best sampled and studied assemblages, it is unreasonable to expect that the resultant curves will accurately reflect true biological patterns through time. The relative magnitudes in each of the corresponding peaks in richness versus research effort per time bin are hauntingly similar throughout the curve (Fig. 11: Lissamphibia "Taxic" and Lineage" richness lines versus the "Total records" line, respectively). Furthermore, if the same richness curve had been constructed three decades ago—i.e. prior to discoveries of lissamphibian-bearing rocks in the Early Jurassic of Arizona, the Early Cretaceous of South Dakota, Wyoming, and Montana, and the latest Albian–Maastrichtian of Utah and prior to renewed interest in lissamphibian assemblages from the Late Jurassic age Morrison Formation of Utah, the middle–late Campanian Belly River Group of

Alberta and the latest Maastrichtian age Lance Formation of Wyoming—the richness curve would have been flatter, with fewer and lower peaks. As both our sampling of temporal intervals and our understanding of the taxonomy and evolutionary relationships of the involved taxa improves, we predict that the curves will become smoother as some of the current troughs begin to fill. If nothing else, the current curves depicted in Fig. 11 highlight intervals and taxonomic groups that warrant further attention.

Concluding remarks

All four lissamphibian clades are represented in the North American record: Gymnophiona (Early Jurassic, Quaternary and Recent); Anura (Early Jurassic to Recent); Caudata (Late Jurassic to Recent); Albanerpetontidae (basal Cretaceous to late Palaeocene). Our review has documented over 400 occurrences of lissamphibians or purported lissamphibians from 61 geological formations of Late Triassic to terminal Palaeocene age in North America. Although plagued by the usual problems of a record that is temporally and geographically patchy and is biased towards isolated bones, the North American Mesozoic and Palaeocene lissamphibian record provides important insights into the evolution of lissamphibian clades and assemblages on the continent. Thirty-two formally named species are recognised, and additional diagnosable, but unnamed species can also be recognised on the basis of material in existing collections. Much of the North American Mesozoic and Palaeocene lissamphibian record is concentrated in the Western Interior. That region contains the most stratigraphically continuous late Early Cretaceous to Palaeocene record for lissamphibians from anywhere in the world, including several geographically restricted and dense sequences across the Cretaceous-Paleogene boundary. Notable "firsts" from the Western Interior portion of the continent's record include: (1) the geologically oldest record for crown frogs (Anura) and the geologically oldest and most primitive stem caecilian, both in the Early Jurassic of Arizona; (2) the first occurrences of edentate anurans in the latest Cretaceous of Alberta and Montana; (3) the first occurrences of the endemic North American urodele families Sirenidae (Santonian in Utah), Amphiumidae (late Maastrichtian in North Dakota) and Dicamptodontidae (late Palaeocene in Alberta). Outside of the Western Interior, a small number of intriguing Late Cretaceous occurrences in Baja California and the eastern USA promise to provide a more continental perspective on lissamphibians during that interval.

Despite the numerous occurrences and reports documented here in our review, it is safe to say that we still have only a cursory understanding of the North American Mesozoic and Palaeocene lissamphibian record. The broad brush strokes are emerging, but many details remain tantalizingly obscure. Field

work directed at identifying and collecting new fossiliferous localities, placing those localities into stratigraphic context and interpreting their depositional histories will continue to be a priority. While there is merit in continuing to exploit known fossiliferous localities and units, especially those that produce high-quality specimens, targeting regions and intervals that are poorly known (such as the basal Cretaceous of the Western Interior) will be critical for helping fill gaps in the fossil record. Collections made from multiple stratigraphic levels within rock units, such as through the Belly River Group in Alberta (e.g. Brinkman 1990; Brinkman et al. 2004) and the Hell Creek Formation in Montana (Wilson et al. 2014) have shown the utility of that approach for documenting changes in lissamphibian assemblages over relatively short intervals. Although these kinds of studies are only feasible in richly fossiliferous units, where they can be undertaken they can provide detailed insights into palaeoenvironmental change and community dynamics, and can more precisely calibrate first and last appearances of taxa.

Existing collections include abundant lissamphibian material from the Mesozoic and Palaeocene of North America, much of which has not been studied in any detail or not at all. Many of the previously named lissamphibian taxa deserve to be re-evaluated in light of newer developments (e.g. additional specimens, recognition of other potentially diagnostic characters and of similar species, better appreciation for variability, improved stratigraphic control, new study techniques and approaches) and will benefit from being more rigorously diagnosed, described and illustrated. There also is a need to properly name and describe the many informally recognised taxa—including those mentioned in our review—because until those are properly named, diagnosed and described they remain essentially unavailable to the larger scientific community. As taxa become better documented, it will be informative to try to place them into some kind of phylogenetic context, as has been done for the proteid *Paranecturus garbanii* (DeMar 2013) and for Cretaceous and Palaeocene species of *Albanerpeton* (e.g. Gardner 2002; Venczel and Gardner 2005), to better understand how they fit into the "big picture" of lissamphibian evolution.

While compiling this review, it became glaringly obvious to us that we have barely scratched the surface of the North American Mesozoic and Palaeocene lissamphibian record. If the surge of new localities, specimens, taxa and ideas that have come to light in the five decades since Estes' (1964) monograph on non-mammalian vertebrates from the Lance Formation is any indication, the future holds many exciting new opportunities for the study of Mesozoic and Palaeocene lissamphibians in North America.

References

Aguillon Martinez MC (2010) Fossil vertebrates from the Cerro del Pueblo Formation, Coahuila, Mexico, and the distribution of late Campanian (Cretaceous) terrestrial vertebrate faunas. Phd dissertation. Southern Methodist University, Dallas

Alroy J (1996) Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. Palaeogeogr Palaeoclimatol Palaeoecol 127:285–311

AmphibiaWeb (2013): Information on amphibian biology and conservation. [web application]. Berkeley, California: AmphibiaWeb. Available at http://amphibiaweb.org/. Accessed 15 May 2013

Archibald JD (1987) Late Cretaceous (Judithian and Edmontonian) vertebrates and geology of the Williams Fork Formation, N.W. Colorado. In: Currie PJ, Koster EH (eds) Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers, Revised Edition, 10–14 August 1987, Drumheller, Alberta. pp. 7–11

Archibald JD, Bryant LJ (1990) Differential Cretaceous/Tertiary extinctions of nonmarine vertebrates; evidence from northeastern Montana. In: Sharpton VL, Ward PD (eds) Global catastrophes in Earth history; an interdisciplinary conference on impacts, volcanism, and mass mortality. Geol Soc Am Spec Pap 247L 49–562

Armstrong-Ziegler JG (1978) An aniliid snake and associated vertebrates from the Campanian of New Mexico. J Paleontol 52:480–483

Armstrong-Ziegler JG (1980) Amphibia and Reptilia from the Campanian of New Mexico. Fieldiana Geol, New Ser 4:1–39

Auffenberg W (1961) A new genus of fossil salamander from North America. Am Midl Nat 66:456–465

Auffenberg W, Goin CJ (1959) The status of the salamander genera *Scapherpeton* and *Hemitrypus* of Cope. Am Mus Novitates 1979:1–12

Averianov AO, Martin T, Skutschas PP, Rezvyi AS, Bakirov AA (2008) Amphibians from the Middle Jurassic Balabansai Svita in the Fergana Depression, Kyrgyzstan (Central Asia). Palaeontology 2008:1–15

Báez AM (2000) Tertiary anurans from South America. In: Heatwole H, Carroll RL (eds) Amphibian biology, vol 4. Palaeontology. Surrey Beatty & Sons, Chipping Norton, pp 1388–1401

Bennett GE III, Main D, Anderson BK, Peterson R. (2011) Microvertebrate paleoecology of the Cretaceous Woodbine Formation (Cenomanian) at the Arlington Archosaur Site, north-central Texas. Geological Society of America, 60th Annual Meeting, Southeastern Section, 23–25 March 2011, Wilmington, North Carolina, Abstracts with Programs 43(2), p. 89

Bennett GE III, Main D, Noto CR, Anderson BK, Vranken NV (2012) Microvertebrate paleoecology, wildfires and biodiversity of coastal Appalachia in the Cretaceous (Cenomanian) Woodbine Formation at the Arlington Archosaur Site, north Texas. Society of Vertebrate Paleontology, 72nd Annual Meeting, 17–20 October, Raleigh, North Carolina, Program and Abstracts. p. 63

Blob RW, Carrano MT, Rogers RR, Forster CA, Espinoza NR (2001) A new fossil frog from the Upper Cretaceous Judith River Formation of Montana. J Vertebr Paleontol 21:190–194

Bloch JI, Boyer DM (2001) Taphonomy of small mammals in freshwater limestones from the Paleocene of the Clarks Fork Basin. In: Gingerich PD (ed) Paleocene-Eocene stratigraphy and biotic changes in the Bighorn and Clarks Fork Basin, Wyoming. Univ Michigan Pap Paleontol 33: 185–198

Bonde J, Shirk A, Druschke P, Hilton R (2011) Frog taphonomy in a high elevation lake basin on the Nevadaplano, Late Cretaceous to Eocene, Sheep Pass Formation, east-central Nevada. Society of Vertebrate Paleontology, 71st Annual Meeting, 2–5 November 2011, Las Vegas, Nevada, Program and Abstracts. p. 74

Borsuk-Białynicka M, Cook E, Evans SE, Maryańska (1999) A microvertebrate assemblage from the Early Triassic of Poland. Acta Palaeontol Pol 44:167–188

Braman DR (2001) Terrestrial palynomorphs of the upper Santonian–?lowest Campanian Milk River Formation, southern Alberta, Canada. Palynology 25:57–107

Breithaupt BH (1982) Paleontology and paleoecology of the Lance Formation (Maastrichtian), east flank of Rock Springs Uplift, Sweetwater County, Wyoming. Univ Wyoming Contrib Geol 21: 123–151

Breithaupt BH (1985) Nonmammalian vertebrate faunas from the Late Cretaceous of Wyoming. In: Thirty-sixth annual field conference guidebook. Wyoming Geological Association, pp. 159–175

Brett-Surman MK, Holtz TR Jr, Farlow JO (2012) The complete dinosaur, 2nd edn. Indiana University Press, Bloomington

Brinkman DB (1990) Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. Palaeogeogr Palaeoclimatol Palaeoecol 78:37–54

Brinkman DB, Russell AP, Eberth DA, Peng J (2004) Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. Palaeogeogr Palaeoclimatol Palaeoecol 213:295–313

Brown RW, Lawrence MJ, Pope J (1984) The Larousse guide to animal tracks, trails and signs. Larousse & Co, New York

Bryant LJ (1989) Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. Univ Calif Publ Geol Sci 134:1–107

Callison G (1987) Fruita: a place for wee fossils. In: Averett WR (ed) Paleontology and geology of the Dinosaur Triangle. Guidebook for 1987 Field Trip, Sept. 18–20, 1987. Museum of Western Colorado, Grand Junction, pp 91–96

Cameron B, Estes R (1971) Fossil and Recent "tadpole nests": a discussion. J Sed Petrol 41:171–178

Carpenter K (1979) Vertebrate fauna of the Laramie Formation (Maestrichtian), Weld County, Colorado. Univ Wyoming Contrib Geol 17:37–49

Carrano MT, Valez-Juarbe J (2006) Paleoecology of the Quarry 9 vertebrate assemblage from Como Bluff, Wyoming (Morrison Formation, Late Jurassic). Palaeogeogr Palaeoclimatol Palaeoecol 237:147–159

Carter G (2009) Amphibian paleocommunity dynamics of the Hell Creek Formation in northeastern Montana and the Cretaceous-Tertiary extinction event. Ninth North American Paleontological Convention, 21–26 June 2009, Cincinnati, Ohio, Abstracts. Cincinnati Mus Cen Sci Contrib 3:331–332

Carter G, Wilson G, Piekarski T, Poltenovage M (2007) Amphibian paleocommunities as ecological indicators during the last 2 million years of the Cretaceous in northeastern Montana. J Vertebr Paleontol 27[Suppl 3]:56A

Chure DJ, Litwin R, Hasiotis ST, Evanoff E, Carpenter K (2006) The fauna and flora of the Morrison Formation. New Mexico Mus Nat Hist Sci Bull 36:233–249

Cifelli RL, Madsen SK, Larson EM (1996) Screen-washing and associated techniques for the recovery of microvertebrate fossils. In: Cifelli RL (ed) Techniques for recovery and preparation of microvertebrate fossils. Oklahoma Geol Surv Spec Publ 96-4:1–24

Cifelli RL, Gardner JD, Nydam RL, Brinkman DL (1997a) Additions to the vertebrate fauna of the Antlers Formation (Lower Cretaceous), southeastern Oklahoma. Oklahoma Geol Notes 57:124–131

Cifelli RL, Kirkland JI, Weil DAR, Kowallis BJ (1997b) High precision ^{40}Ar/^{39}AR geochronology and the advent of North America's Late Cretaceous terrestrial fauna. Proc Natl Acad Sci USA 94:11163–11167

Cifelli RL, Lipka TR, Schaff CR, Rowe TB (1999a) First Early Cretaceous mammal from the eastern seaboard of the United States. J Vertebr Paleontol 19:199–203

Cifelli RL, Nydam RL, Eaton JG, Gardner JD, Kirkland JI (1999b) Vertebrate faunas of the North Horn Formation (Upper Cretaceous–lower Paleocene), Emery and Sanpete counties, Utah. In: Gillette DD (ed) Vertebrate paleontology in Utah. Utah Geol Surv Misc Publ 99-1:377–388

Cifelli RL, Nydam RL, Gardner JD, Weil A, Eaton JG, Kirkland JI, Madsen SK (1999c) Medial Cretaceous vertebrates from the Cedar Mountain Formation, Emery County, Utah: the Mussentuchit Local Fauna. In: Gillette DD (ed) Vertebrate paleontology in Utah, Utah Geol Surv Misc Publ 99-1:219–242

Cifelli RL, Eberle JJ, Lofgren DL, Lillegraven JA, Clemens WA (2004) Mammalian biochronology of the latest Cretaceous. In: Woodburne MO (ed) Late Cretaceous and Cenozoic mammals of North America: biostratigraphy and geochronology. Columbia University Press, New York, pp 21–42

Cifelli RL, Gordon CL, Lipka TR (2013) New multituberculate mammal from the Early Cretaceous of eastern North America. Can J Earth Sci 50:315–323

Cifelli RL, Davis BM, Sames B (in press) Earliest Cretaceous mammals from the western United States. Acta Palaeontol Pol. doi:10.4202/app.2012.0089

Clemens WA (2002) Evolution of the mammalian fauna across the Cretaceous-Tertiary boundary in northeastern Montana and other areas of the Western Interior. In: Hartman JH, Johnson KR, Nichols DJ (eds) The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Geol Soc Am Spec Pap 361: 217–245

Clemens WA, Nelms LG (1993) Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. Geology 21:503–506

Clemens WA, Lillegraven JA, Lindsay EH, Simpson GG (1979) Where, when, and what—a survey of known Mesozoic mammal distribution. In: Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (eds) Mesozoic mammals: The first two-thirds of mammalian history. University of California Press, Berkeley, pp 7–58

Cope ED (1876) On some extinct reptiles and Batrachia from the Judith River and Fox Hills beds of Montana. Proc Acad Nat Sci Phila 28: 340–359

Crane CD (2011) Vertebrate paleontology and taphonomy of the Late Cretaceous (Campanian) Bladen Formation, Bladen County. Msc thesis. East Carolina University, Greenville

Crane CD (2012) Bridging the gap: North Carolina's role in Late Cretaceous (Campanian) research and its implications for regional paleobiogeography and faunal correlations. Society of Vertebrate Paleontology, 72nd Annual Meeting, 17–20 October, Raleigh, North Carolina, Program and Abstracts. p. 81

Cristophel DC (1976) Fossil floras of the Smoky Tower locality, Alberta, Canada. Palaeontogr Abt B 157:1–43

Curtis K, Padian K (1999) An Early Jurassic microvertebrate fauna from the Kayenta Formation of northeastern Arizona: microfaunal change across the Triassic-Jurassic boundary. PaleoBios 19(2):19–37

Delfino M, Sala B (2007) Late Pliocene Albanerpetontidae (Lissamphibia) from Italy. J Vertebr Paleontol 27:716–719

DeMar DG Jr (2011) New taxonomic, paleobiogeographic, and biostratigraphic records of fossil salamanders (Caudata) from the Hell Creek and Tullock formations of Garfield County, Montana. J Vertebr Paleontol 31[Suppl 3]:98A

DeMar DG Jr (2013) A new fossil salamander (Caudata, Proteidae) from the Upper Cretaceous (Maastrichtian) Hell Creek Formation, Montana, U.S.A. J Vertebr Paleontol 33:588–598

DeMar DG Jr, Breithaupt BH (2006) The nonmammalian vertebrate microfossil assemblages of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn basins, Wyoming. New Mexico Mus Nat Hist Sci Bull 35:33–53

DeMar DG Jr, Breithaupt BH (2008) Terrestrial and aquatic vertebrate paleocommunities of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn basins, Wyoming. In: Sankey JT, Baszio S (eds) Vertebrate microfossil assemblages: Their role in paleoecology and paleobiogeography. Indiana University Press, Bloomington, pp 78–103

DeMar DG Jr, Varricchio DJ, Head JJ, Moore JR, Wilson GP (2012) A nearly complete fossil iguanian from the Upper Cretaceous (Campanian) Two Medicine Formation of western Montana. Society of Vertebrate Paleontology, 72nd Annual Meeting, 17–20 October, Raleigh, North Carolina, Program and Abstracts. p. 86

Denton RK Jr, O'Neill RC (1998) *Parrisia neocesariensis*, a new batrachosauroidid salamander and other amphibians from the Campanian of eastern North America. J Vertebr Paleontol 18:484–494

Denton RK Jr, O'Neill RC (2012) Exploring the "lost continent" of Appalachia—the Ellisdalean land fauna and its implications for Late Cretaceous biogeography. Society of Vertebrate Paleontology, 72nd Annual Meeting, 17–20 October, Raleigh, North Carolina, Program and Abstracts. p. 86

Dodson P (1983) A faunal review of the Judith River (Oldman) Formation, Dinosaur Provincial Park, Alberta. The Mosasaur 1: 89–118

Dornelas M, Soykan CU, Ugland KI (2011) Biodiversity and disturbance. In: Magurran AE, McGill BJ (eds) Biological diversity: Frontiers in measurement and assessment. Oxford University Press, New York, pp 237–251

Dorr JA Jr (1985) Newfound Early Cretaceous dinosaurs and other fossils in southeastern Idaho and westernmost Wyoming. Univ Michigan Contribs Mus Paleontol 27:73–85

Druschke PA (2009) The Sheep Pass Formation, a record of Late Cretaceous and Paleogene extension within the Sevier Hinterland, east-central Nevada. PhD dissertation. University of Nevada, Las Vegas

Druschke PA, Hanson AD, Wells ML, Rasbury T, Stockli DF, Gehrels G (2009) Synconvergent surface-breaking normal faults of Late Cretaceous age within the Sevier hinterland, east-central Nevada. Geology 37:447–450

Duellman WE, Trueb L (1986) Biology of amphibians. McGraw-Hill, New York

Eaton JG (2004) New screen-washing approaches to biostratigraphy and paleoecology of nonmarine rocks, Cretaceous of Utah. Bull Carnegie Mus Nat Hist 36:21–30

Eaton JG, Cifelli RL (1988) Preliminary report on Late Cretaceous mammals of the Kaiparowits Plateau, southern Utah. Univ Wyoming Contrib Geol 26:45–55

Eaton JG, Kirkland JI, Hutchison JH, Denton R, O'Neill RC, Parrish JM (1997) Nonmarine extinction across the Cenomanian-Turonian boundary, southwestern Utah, with a comparison to the Cretaceous-Tertiary extinction event. Geol Soc Am Bull 109:560–567

Eaton JG, Cifelli RL, Hutchison JH, Kirkland JI, Parrish JM (1999) Cretaceous vertebrate faunas from the Kaiparowits Plateau, south-central Utah. In: Gillette DD (ed) Vertebrate Paleontology in Utah. Utah Geol Surv Misc Publ. 99-1:345–353

Eberth DA (1990) Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada. Palaeogeogr Palaeoclimatol Palaeoecol 78:1–36

Eberth DA, Braman DR (2012) A revised stratigraphy and depositional history for the Horseshoe Canyon Formation (Upper Cretaceous), southern Alberta Plains. Can J Earth Sci 49:1053–1086

Eberth DA, Brinkman DB (1997) Paleoecology of an estuarine, incised-valley fill in the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) of southern Alberta, Canada. Palaios 12:43–58

Eberth DA, Braman DR, Tokaryk TT (1990) Stratigraphy, sedimentology and vertebrate paleontology of the Judith River Formation (Campanian) near Muddy Lake, west-central Saskatchewan. Bull Can Petrol Geol 38:387–406

Eberth DA, Currie PJ, Brinkman DB, Ryan MJ, Braman DR, Gardner JD, Lam VD, Spivak DN, Neuman AG (2001) Alberta's dinosaurs and other fossil vertebrates: Judith River and Edmonton groups (Campanian-Maastrichtian). In: Hill CL (ed) Mesozoic and Cenozoic paleontology in the Western Plains and Rocky Mountains. Guidebook for the Field Trips of the Society of Vertebrate Paleontology 61st Annual Meeting. Mus Rockies Occ Paper 3:47–75

Eberth DA, Delgado-de Jesus R, Lerbekmo J, Brinkman D, Rodriguez-de la Rosa R, Sampson S (2004) Cerro del Pueblo Formation (Difunta Group, Upper Cretaceous), Parras Basin, southern Coahuila, Mexico: reference sections, age, and correlation. Revista Mexicana Ciencias Geol 21:335–352

Eberth DA, Evans DC, Brinkman DB, Therrien F, Tanke DH, Russell LS (2013) Dinosaur biostratigraphy of the Edmonton Group (Upper Cretaceous), Alberta, Canada: evidence for climatic influence. Can J Earth Sci 50:701–726

Erickson BR (1991) Flora and fauna of the Wannagan Creek Quarry: late Paleocene of North America. Sci Publ Science Mus Minnesota N Ser 7:1–19

Erickson BR (1999) Fossil Lake Wannagan (Paleocene: Tiffanian) Billings County, North Dakota. North Dakota Geol Surv Misc Ser 87:1–9

Erickson BR (2012) History of the Wannagan Creek expeditions. Sci Mus Minnesota Monograph, vol. 6. Paleontology:1–41

Estes R (1964) Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. Univ Calif Publ Geol Sci 49:1–180, + 5 plates

Estes R (1965) A new fossil salamander from Montana and Wyoming. Copeia 1965:90–95

Estes R (1969a) Prosirenidae, a new family of fossil salamanders. Nature 224:87–88

Estes R (1969b) A new fossil discoglossid frog from Montana and Wyoming. Breviora 328:1–7

Estes R (1969c) The fossil record of amphiumid salamanders. Breviora 322:1–11

Estes R (1969d) The Batrachosauroididae and Scapherpetontidae, Late Cretaceous and Early Cenozoic salamanders. Copeia 1969:225–234

Estes R (1975) Lower vertebrates from the Fort Union Formation, late Paleocene, Big Horn Basin, Wyoming. Herpetologica 31:365–385

Estes R (1976) Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. J Paleontol 50:500–520

Estes R (1981) Gymnophiona, Caudata. In: Wellnhofer P (ed) Encyclopedia of paleoherpetology, part 2. Gustav Fischer Verlag, Stuttgart, pp 1–115

Estes R, Berberian P (1970) Paleoecology of a Late Cretaceous vertebrate community from Montana. Breviora 343:1–35

Estes R, Hoffstetter R (1976) Les Urodèles du Miocène de La Grive-Saint-Alban (Isère, France). Bulletin du Muséum National d'Histoire Naturelle, 3e Série, no. 398. Sciences de la Terre 57:297–343

Estes R, Sanchíz B (1982) New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek formations. J Vertebr Paleontol 2:9–20

Estes R, Berberian P, Meszoely CAM (1969) Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County, Montana. Breviora 337:1–33

Estes R, Špinar ZV, Nevo E (1978) Early Cretaceous pipid tadpoles from Israel (Amphibia: Anura). Herpetologica 34:374–393

Evans SE, Milner AR (1993) Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. J Vert Paleontol 13:24–30

Evans SE, Milner AR, Mussett F (1988) The earliest known salamanders (Amphibia, Caudata): a record from the Middle Jurassic of England. Geobios 21:539–552

Evans SE, Lally C, Chure DC, Elder A, Maisano JA (2005) A Late Jurassic salamander (Amphibia: Caudata) from the Morrison Formation of North America. Zool J Linn Soc 143:599–616

Fanti F, Miyashita T (2009) A high latitude vertebrate fossil assemblage from the Late Cretaceous of west-central Alberta, Canada: evidence for dinosaur nesting and vertebrate latitudinal gradient. Palaeogeogr Palaeoclimatol Palaeoecol 275:37–53

Fanti F, Bell PR, Sissons RL (2013) A diverse, high-latitude ichnofauna from the Late Cretaceous Wapiti Formation, Alberta, Canada. Cret Res 41:256–269

Fara E (2004) Estimating minimum global species diversity for groups with a poor fossil record: a case study of Late Jurassic–Eocene lissamphibians. Palaeogeogr Palaeoclimatol Palaeoecol 207:59–82

Fiorillo AR (1989) The vertebrate fauna from the Judith River Formation (Late Cretaceous) of Wheatland and Golden Valley counties, Montana. The Mosasaur 4:127–142

Fiorillo AR (1999) Non-mammalian microvertebrate remains from the Robison Eggshell Site, Cedar Mountain Formation (Lower Cretaceous), Emery County, Utah. In: Gillette DD (ed) Vertebrate paleontology in Utah. Utah Geol Surv Misc Publ 99-1:259–268

Fiorillo AR (2008) On the occurrence of exceptionally large teeth of *Troodon* (Dinosauria: Saurischia) from the Late Cretaceous of northern Alaska. Palaios 23:322–328

Ford LS, Cannatella DC (1993) The major clades of frogs. Herpetol Mono 7:94–117

Foster J (2001) Taphonomy and paleoecology of a microvertebrate assemblage from the Morrison Formation (Upper Jurassic) of the Black Hills, Crook County, Wyoming. Brigham Young Univ Geol Stud 46:13–33

Foster J (2007) Jurassic West: The dinosaurs of the Morrison Formation and their world. Indiana University Press, Indianapolis

Foster J, Heckert AB (2011) Ichthyoliths and other microvertebrate remains from the Morrison Formation (Upper Jurassic) of northeastern Wyoming: a screen-washed sample indicates a significant aquatic component to the fauna. Palaeogeogr Palaeoclimatol Palaeoecol 305:264–279

Fox RC (1972) A primitive therian mammal from the Upper Cretaceous of Alberta. Can J Earth Sci 9:1479–1494

Fox RC (1976a) Upper Cretaceous and Paleocene vertebrate paleontology in Alberta. Geological Association of Canada, Mineralogical Association of Canada, and Edmonton Geological Society Annual Meeting19–21 May 1976, Edmonton, Alberta. Field Trip A-6 guidebook. pp 1–25 + 1 fig

Fox RC (1976b) An edentulous frog (*Theatonius lancensis*, new genus and species) from the Upper Cretaceous Lance Formation of Wyoming. Can J Earth Sci 13:1486–1490

Fox RC (1978) Upper Cretaceous terrestrial vertebrate stratigraphy of the Gobi Desert (Mongolian People's Republic) and western North America. In: Stelck CR, Chatterton BE (eds) Western and Arctic Canadian biostratigraphy. Geol Assoc Can Spec Pap 18:577–594

Fox RC (1984) First North American record of the Paleocene primate *Saxonella*. J Paleontol 58:892–894

Fox RC (1989) The Wounded Knee local fauna and mammalian evolution near the Cretaceous-Tertiary boundary, Saskatchewan, Canada. Palaeontographica Abt A 208:11–59

Fox RC (1990) The succession of Paleocene mammals in western Canada. In: Bown TM, Rose KD (eds) Dawn of the Age of Mammals in the northern part of the Rocky Mountain Interior. Geol Soc Am Spec Pap 243:51–70

Fox RC, Naylor BG (1982) A reconsideration of the relationships of the fossil amphibian *Albanerpeton*. Can J Earth Sci 19:118–128

Fox RC, Naylor BG (1986) A new species of *Didelphodon* Marsh (Marsupialia) from the Upper Cretaceous of Alberta, Canada: paleobiology and phylogeny. N Jb Geol Paläont, Abh 172:357–380

Frampton EK (2006) Taphonomy and palaeoecology of mixed invertebrate-vertebrate fossil assemblage in the Foremost Formation (Cretaceous, Campanian). MSc thesis. University of Calgary, Calgary

Frost DR (2013) Amphibian species of the world: an online reference. Version 5.6 (9 January 2013). Available at: http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York. Accessed15 May 2013

Gao K, Fox RC (1996) Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. Bull Carnegie Mus Nat Hist 33:1–107

Gao K-Q, Shubin NH (2012) A late Jurassic salamandroid from western Liaoning, China. Proc Natl Acad Sci USA 109:5767–5772

Gao K-Q, Chen J, Jia J (2013) Taxonomic diversity, stratigraphic range, and exceptional preservation of Juro-Cretaceous salamanders from northern China. Can J Earth Sci 50:255–267

Gangloff RA, Fiorillo AR (2010) Taphonomy and paleoecology of a bonebed from the Prince Creek Formation, North Slope, Alaska. Palaios 25:299–317

Gardner JD (1994) Amphibians from the Lower Cretaceous (Albian) Cedar Mountain Formation, Emery County, Utah. J Vertebr Paleontol 14[Suppl 3]:31A

Gardner JD (1995) Lower Cretaceous anurans from Texas and Utah. J Vertebr Paleontol 15[Suppl 3]:31A

Gardner JD (1999a) The amphibian *Albanerpeton arthridion* and the Aptian–Albian biogeography of albanerpetontids. Palaeontol 42:529–544

Gardner JD (1999b) New albanerpetontid amphibians from the Albian to Coniacian of Utah, USA—bridging the gap. J Vertebr Paleontol 19:632–638

Gardner JD (2000a) Albanerpetontid amphibians from the Upper Cretaceous (Campanian and Maastrichtian) of North America. Geodiversitas 22:349–388

Gardner JD (2000b) Systematics of albanerpetontids and other lissamphibians from the Late Cretaceous of western North America. PhD dissertation. University of Alberta, Edmonton

Gardner JD (2000c) Revised taxonomy of albanerpetontid amphibians. Acta Palaeontol Pol 45:55–70

Gardner JD (2002) Monophyly and intra-generic relationships of Albanerpeton (Lissamphibia; Albanerpetontidae). J Vertebr Paleontol 22:12–22

Gardner JD (2003a) Revision of Habrosaurus Gilmore (Caudata; Sirenidae) and relationships among sirenid salamanders. Palaeontol 46:1089–1122

Gardner JD (2003b) The fossil salamander Proamphiuma cretacea Estes (Caudata; Amphiumidae) and relationships within the Amphiumidae. J Vertebr Paleontol 23:769–782

Gardner JD (2005) Lissamphibians. In: Currie PC, Koppelhus EB (eds) Dinosaur Provincial Park: A spectacular ancient ecosystem revealed. Indiana University Press, Bloomington, pp 186–201

Gardner JD (2008) New information on frogs (Lissamphibia: Anura) from the Lance Formation (late Maastrichtian) and Bug Creek Anthills (late Maastrichtian and early Paleocene), Hell Creek Formation, USA. In: Sankey JT, Baszio S (eds) Vertebrate microfossil assemblages: Their role in paleoecology and paleobiogeography. Indiana University Press, Bloomington, pp 219–249

Gardner JD (2012) Revision of Piceoerpeton Meszoely (Caudata: Scapherpetontidae) and description of a new species from the Late Maastrichtian and ?early Paleocene of western North America. Bull Soc Géol France 183:611–620

Gardner JD, Böhme M (2008) Review of the Albanerpetontidae (Lissamphibia) with comments on the paleoecological preferences of European Tertiary albanerpetontids. In: Sankey JT, Baszio S (eds) Vertebrate microfossil assemblages: Their role in paleoecology and paleobiogeography. Indiana University Press, Bloomington, pp 178–218

Gardner JD, Brinkman DB (in press) A new frog (Lissamphibia, Anura) from the Upper Cretaceous (middle and late Campanian) Oldman and Dinosaur Park formations, of Alberta, Canada. Volume title to-be-determined (Festschrift volume for Anthony P. Russell)

Gardner JD, Roček Z, Přikryl T, Eaton JG, Blob RW, Sankey J (2010) Comparative morphology of the ilium of anurans and urodeles (Lissamphibia) and a re-assessment of the anuran affinities of Nezpercius dodsoni Blob et al. 2001. J Vertebr Paleontol 30:1684–1696

Gardner JD, Eaton JG, Cifelli RL (2013) Preliminary report on salamanders (Lissamphibia; Caudata) from the Late Cretaceous (late Cenomanian–late Campanian) of southern Utah, U.S.A. In: Titus AL, Lowen MA (eds) At the top of the grand staircase: The Late Cretaceous of southern Utah. Indiana University Press, Bloomington, pp 237–272

Garrison JR Jr, Brinkman D, Nichols DJ, Layer P, Burge D, Thayn D (2007) A multidisciplinary study of the Lower Cretaceous Cedar Mountain Formation, Mussentuchit Wash, Utah: a determination of the paleoenvironment and paleoecology of the Eolambia caroljonesa dinosaur quarry. Cret Res 28:461–494

Gates T, Makovicky P, Rieppel O (2010) Microvertebrate fauna from the Maastrichtian (Late Cretaceous) "Sue" quarry: implications for microsite origination and fine-scaled Hell Creek Formation biodiversity. J Vertebr Paleontol 30[Suppl 3]:94A

Gilmore CW (1928a) Fossil footprints from the Fort Union (Paleocene) of Montana. Proc US Natl Mus 74(2750):1–4

Gilmore CW (1928b) Fossil lizards of North America. Mem Natl Acad Sci 22:1–201

Gingerich PD (1987) Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming. Univ Michigan Contribs Mus Paleontol 27:275–320

Gohn GS (1992) Revised nomenclature, definitions, and correlations for the Cretaceous formations in USGS-Clubhouse Crossroads #1, Dorchester County, South Carolina. U S Geol Surv Prof Pap 1518:1–39

Goin CJ, Auffenberg W (1958) New salamanders of the family Sirenidae from the Cretaceous of North America. Fieldiana Geol 10:449–459

Greenwald MT (1971) The lower vertebrates of the Hell Creek Formation, Harding County. MSc thesis. South Dakota School of Mines and Technology, Rapid City

Harries PJ, Kauffman EG, Hansen TA (1996) Models for biotic survival following mass extinction. In: Hart MB (ed) Biotic recovery from mass extinction events. Geol Soc Special Publ 102:41–60

Harris JD, Johnson KR, Hicks J, Tauxe L (1996) Four-toed theropod footprints and a paleomagnetic age from the Whetstone Falls Member of the Harebell Formation (Upper Cretaceous: Maastrichtian), northwestern Wyoming. Cret Res 17:381–401

Hartman JE (1986) Paleontology and biostratigraphy of lower part of Polecat Bench Formation, southern Bighorn Basin, Wyoming. Univ Wyoming Contrib Geol 24:11–63

Hecht MK (1960) A new frog from an Eocene oil-well core in Nevada. Am Mus Novitates 2006:1–14

Hecht MK (1963) A reevaluation of the early history of the frogs. Part II. Syst Zool 12:20–35

Hecht MK, Estes R (1960) Fossil amphibians from Quarry Nine. Postilla 46:1–19

Heckert AB, Lucas SG, Krzyzanowski SE (2003) Vertebrate fauna of the late Campanian (Judithian) Fort Crittenden Formation, and the age of Cretaceous vertebrate faunas of southeastern Arizona (U.S.A.). N Jb Geol Paläont, Abh 227:343–364

Heckert AB, Mitchell JS, Schneider VP, Olsen PE (2012) Diverse new microvertebrate assemblage from the Upper Triassic Cumnock Formation, Sanford subbasin, North Carolina. USA J Paleontol 86:368–390

Henrici AC (1998a) New anurans from the Rainbow Park Microsite, Dinosaur National Monument, Utah. Modern Geol 23:1–16

Henrici AC (1998b) A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. J Vert Paleontol 18:321–332

Hoganson JW, Erickson JM, Holland FD Jr (2007) Amphibian, reptile, and avian remains from the Fox Hills Formation (Maastrichtian): shoreline and estuarine deposits of the Pierre Sea in south-central North Dakota. Geol Soc Am Spec Paper 427:239–256

Holman JA (2003) Fossil frogs and toads of North America. Indiana University Press, Bloomington

Holman JA (2006) Fossil salamanders of North America. Indiana University Press, Bloomington

Hunt AP, Lucas SG (1993) Cretaceous vertebrates of New Mexico. New Mexico Mus Nat Hist Sci Bull 2:77–81

Hunter JP, Heinrich RE, Weishampel DB (2010) Mammals from the St. Mary River Formation (Upper Cretaceous), Montana. J Vertebr Paleontol 30:885–898

Ivachnenko MF (1978) Urodelans from the Triassic and Jurassic of Soviet Central Asia. Palaeontol Zhur 1978:84–89 (in Russian) and Paleontol J 1978:362–368 (in English)

Jacobs LL, Winkler DA, Murry PA (1991) On the age and correlation of Trinity mammals, Early Cretaceous of Texas, USA. Newsl Stratigr 24:35–43

Janis CM, Scott KM, Jacobs LL (1998) Evolution of Tertiary mammals of North America. Volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge University Press, New York

Jenkins FA Jr, Shubin NH (1998) *Prosalirus bitis* and the anuran caudopelvic mechanisms. J Vert Paleontol 18:495–510

Jenkins FA Jr, Walsh DM (1993) An Early Jurassic caecilian with limbs. Nature 365:246–250

Jenkins FA Jr, Walsh DM, Carroll RL (2007) Anatomy of *Eocaecilia micropodia*, a limbed caecilian from the Early Jurassic. Bull Mus Comp Zool 158:285–366

Johnson KR (1986) Paleocene bird and amphibian tracks from the Fort Union Formation, Bighorn Basin, Wyoming. Univ Wyoming Contribs Geol 24:1–10

Johnson KA, Culver SJ, Kamola DL (2005) Marginal marine foraminifera of the Blackhawk Formation (Late Cretaceous, Utah). J Foram Res 35:50–64

Johnston PA (1980) The first record of Mesozoic mammals from Saskatchewan. Can J Earth Sci 17:512–519

Johnston PA, Fox RC (1984) Paleocene and Late Cretaceous mammals from Saskatchewan, Canada. Palaeontographica Abt A 186:163–222, +15 plates

Kaye FT, Padian K (1994) Microvertebrates from the Placerias Quarry: a window on Late Triassic vertebrate diversity in the American Southwest. In: Sues H-D, Fraser NC (eds) In the shadow of the dinosaurs: Early Mesozoic tetrapods. Cambridge University Press, Cambridge, pp 171–196

Kielan-Jaworowska Z, Cifelli RL, Luo Z-X (2004) Mammals from the Age of Dinosaurs: Origins, evolution, and structure. Columbia University Press, New York

Kranz PM (1998) Mostly dinosaurs: a review of the vertebrates of the Potomac Group (Aptian Arundel Formation), USA. New Mexico Mus Nat Hist Sci Bull 14:235–238

Krause DW (1980) Early Tertiary amphibians from the Bighorn Basin, Wyoming. In: Gingerich PD (ed) Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ Michigan Pap Paleontol 24:69–71

Krumenacker LJ (2005) Preliminary report on new vertebrates from the upper Gannett Group (Aptian) and Wayan Formation (Albian) of east Idaho. Paludicola 5:55–64

Kuhn O (1967) Amphibien und Reptilien: Katalog der Subfamilien und höheren Taxa mit Nachweis des ersten Auftretens. Gustav Fischer Verlag, Stuttgart

Lambe LM (1902) New genera and species from the Belly River Series (Mid-Cretaceous). Contrib Can Paleontol 3:23–81 + 21 plates

Langston W Jr (1975) Ceratopsian dinosaurs and associated lower vertebrates from the St. Mary River Formation (Maestrichtian) at Scabby Butte, southern Alberta. Can J Earth Sci 12:1576–1608

Langston W Jr (1976) A Late Cretaceous vertebrate fauna from the St. Mary River Formation in western Canada. In: Churcher CS (ed) Athlon: Essays on palaeontology in honour of Loris Shano Russell. Royal Ontario Museum, Life Sciences, Miscellaneous Publications. Royal Ontario Museum, Toronto. pp 114–133

Langston W Jr, Standhardt B, Stevens M (1989) Fossil vertebrate collecting in the Big Bend—history and retrospective. In: Busbey AB III, Lehman TM (eds) Vertebrate paleontology, biostratigraphy and depositional environments, Latest Cretaceous and Tertiary, Big Bend Area, Texas. Society of Vertebrate Paleontology, 49th Annual Meeting, 31 October–1 November 1986, Austin, Texas, Guidebook, Field Trip Numbers 1A, B, and C. pp 11–21

Larson DW, Brinkman DB, Bell PR (2010) Faunal assemblages from the upper Horseshoe Canyon Formation, an early Maastrichtian cool-climate assemblage from Alberta, with special reference to the *Albertosaurus sarcophagus* bonebed. Can J Earth Sci 47:1159–1181

Leahy GD, Lerbekmo JF (1995) Macrofossil magnetostratigraphy for the upper Santonian–lower Campanian interval in the Western Interior of North America: comparisons with European stage boundaries and planktonic foraminiferal zonal boundaries. Can J Earth Sci 32:247–260

Lee Y-N (1997) The Archosauria from the Woodbine Formation (Cenomanian) in Texas. J Paleontol 71:1147–1156

Levinton J (1988) Genetics, Paleontology and Macroevolution. Cambridge University Press, Cambridge

Lewis C, Heckert AB, Forys M (2006) Paleoecology of the aqueous paleoenvironments of the Late Cretaceous (early Campanian) Allison Member of the Menefee Formation in northwestern New Mexico. New Mexico Geological Survey 2006 Meetings Program and Abstracts. Available at: http://geoinfo.nmt.edu/nmgs/meeting/2006/NMGS_2006_meeting_program-abstracts.pdf. Accessed 10 Nov 2006

Lewis C, Heckert AB, Lucas S, Williamson T (2007) A diverse new microvertebrate fauna from the Upper Cretaceous (late Santonian-early Campanian) Menefee Formation of New Mexico. J Vertebr Paleontol 27[Suppl 3]:105A

Lewis C, Heckert AB, Lucas S (2008) A mixed marine/non-marine and terrestrial microvertebrate assemblage from the Late Cretaceous (late Santonian-early Campanian) Menefee Formation of New Mexico: fauna, biostratigraphy, and paleoecology. J Vertebr Paleontol 28[Suppl 3]:105A

Lillegraven JA (1972) Preliminary report on Late Cretaceous mammals from the "El Gallo Formation", Baja California del Norte, Mexico. Nat Hist Mus, Los Angeles County Contrib Sci 232:1–11

Lillegraven JA (1976) A new genus of therian mammal from the Late Cretaceous "El Gallo Formation", Baja California, Mexico. J Paleontol 50:437–443

Lillegraven JA (1987) Stratigraphic and evolutionary implications of a new species of *Meniscoessus* (Multituberculata, Mammalia) from the Upper Cretaceous Williams Fork Formation, Moffat County, Colorado. In: Martin JE, Ostrander GE (eds) Papers in vertebrate paleontology in Honor of Morton Green. Dakoterra, Spec. Paper 3: 46–56

Lillegraven JA, Eberle JJ (1999) Vertebrate faunal changes through Lancian and Puercan time in southern Wyoming. J Paleontol 73: 691–710

Lillegraven JA, McKenna MC (1986) Fossil mammals from the "Mesaverde" Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River basins, Wyoming, with definitions of Late Cretaceous North American Land Mammal "ages". Am Mus Novit 2840:1–68

Lipka TR (1998) The affinities of the enigmatic theropods of the Arundel Clay facies (Aptian), Potomac Formation, Atlantic Coastal Plain of Maryland. New Mexico Mus Nat Hist Sci Bull 14:229–234

Lipka TR, Therrien F, Weishampel DB, Jamniczky HA, Joyce WG, Colbert MW, Brinkman DB (2006) A new turtle from the Arundel Clay facies (Potomac Formation, Early Cretaceous) of Maryland, U.S.A. J Vertebr Paleontol 26:300–307

Lofgren DL (1995) The Bug Creek problem and the Cretaceous–Tertiary transition at McGuire Creek, Montana. Univ Calif Publ Geol Sci 140:1–185

Lofgren DL, Lillegraven JA, Clemens WA, Gingerich PD, Williamson TE (2004) Paleocene biochronology: the Puercan through Clarkforkian Land Mammal Ages. In: Woodburne MO (ed) Late Cretaceous and Cenozoic mammals of North America: Biostratigraphy and geochronology. Columbia University Press, New York, pp 43–105

Love JD (1973) Harebell Formation (Upper Cretaceous) and Pinyon Conglomerate (uppermost Cretaceous and Paleocene), northwestern Wyoming. US Geol Surv Prof Paper 734-A:1–54

Lucas SG, Heckert AB (2005) Distribution, age and correlation of Cretaceous fossil vertebrates from Arizona. New Mexico Mus Nat Hist Sci Bull 29:105–110

Lupton C, Gabriel D, West RM (1980) Paleobiology and depositional setting of a Late Cretaceous vertebrate locality, Hell Creek Formation, McCone County, Montana. Univ Wyoming Contrib Geol 18:117–126

Lynch JD (1971) Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. Univ Kansas Mus Nat Hist Misc Publ 53:1–238

MacLeod N, Rawson PF, Forey PL, Banner FT, Boudagher-Fadel MK, Bown PR, Burnett JA, Chambers P, Culver S, Evans SE, Jeffery C, Kaminski MA, Lord AR, Milner AC, Milner AR, Morris N, Owen E, Rosen BR, Smith AB, Taylor PD, Urquhart E, Young JR (1997) The Cretaceous–Tertiary biotic transition. J Geol Soc, Lond 154:265–292

Maddin HC, Jenkins FA Jr, Anderson JS (2012) The braincase of *Eocaecilia micropodia* (Lissamphibia, Gymnophiona) and the origin of caecilians. PLoS ONE 7(12):e50743. doi:10.1371/journal.pone.0050743

Marsh OC (1887) American Jurassic Mammals. Am J Sci Ser 33:327–348

McCord R, McCullough G, Tegowski BJ, Hodnett JP, Scarborough R (2001) Ongoing research in the Late Cretaceous Fort Crittenden Formation, southeastern Arizona: the non-dinosaurian vertebrate fauna. Mesa Southwest Mus Bull 8:65–71

McGowan GJ, Evans SE (1995) Albanerpetontid amphibians from the Cretaceous of Spain. Nature 373:143–145

McKenna MC (1962) Collecting small fossils by washing and screening. Curator 5:221–235

McKenna MC (1980) Late Cretaceous and early Tertiary vertebrate paleontological reconnaissance, Togwotee Pass area, northwestern Wyoming. In: Jacobs LL (ed) Aspects of vertebrate history: Essays in honor of Edwin Harris Colbert. Museum of Northern Arizona Press, Flagstaff, pp 321–343

Meszoely CAM (1967) A new cryptobranchid salamander from the Early Eocene of Wyoming. Copeia 1967:346–349

Middleton MD, Dewar EW (2004) New mammals from the early Paleocene Littleton fauna (Denver Formation, Colorado). In: Lucas SG, Zeigler KE, Kondrashov PE (eds) Paleogene mammals. New Mexico Mus Nat Hist Sci Bull 26:59–80

Milner AR (1994) Late Triassic and Jurassic amphibians: fossil record and phylogeny. In: Sues H-D, Fraser NC (eds) In the shadow of the dinosaurs: Early Mesozoic tetrapods. Cambridge University Press, Cambridge, pp 5–22

Milner AR (2000) Mesozoic and Tertiary Caudata and Albanerpetontidae. In: Heatwole H, Carroll RL (eds) Amphibian biology, vol 4. Palaeontology. Surrey Beatty & Sons, Chipping Norton, pp 1412–1444

Moodie RL (1912) An American Jurassic frog. Am J Sci Ser 34:286–288

Moodie RL (1914) The fossil frogs of North America. Am J Sci Ser 38:531–536

Murie OJ (1974) A field guide to animal tracks. The Peterson field guide series, 2nd edn. Houghton Mifflin, Boston

Naylor BG (1978a) The systematics of fossil and recent salamanders (Amphibia: Caudata), with special reference to the vertebral column and trunk musculature. PhD dissertation. University of Alberta, Edmonton

Naylor BG (1978b) The earliest known *Necturus* (Amphibia, Urodela), from the Paleocene Ravenscrag Formation of Saskatchewan. J Herpetol 12:565–569

Naylor BG (1979) The Cretaceous salamander *Prodesmodon* (Amphibia: Caudata). Herpetologica 35:11–20

Naylor BG (1981a) A new salamander of the family Batrachosauroididae from the late Miocene of North America, with notes on other batrachosauroidids. PaleoBios 39:1–14

Naylor BG (1981b) Cryptobranchid salamanders from the Paleocene and Miocene of Saskatchewan. Copeia 1981(1):76–86

Naylor BG (1983) New salamander (Amphibia: Caudata) atlantes from the Upper Cretaceous of North America. J Paleontol 57:48–52

Naylor BG, Fox RC (1993) A new ambystomatid salamander, *Dicamptodon antiquus* n.sp., from the Paleocene of Alberta, Canada. Can J Earth Sci 30:814–818

Naylor BG, Krause DW (1981) *Piceoerpeton*, a giant Early Tertiary salamander from western North America. J Paleontol 55:507–523

Nessov L (1992) New salamanders from the Upper Jurassic Morrison Fm. of Dinosaur National Monument. In: Santucci VL (ed) National Park Service Paleontological Research Abstract Volume, 3rd Fossil Resources Conference, September 1992, Fossil Butte National Monument, Wyoming, p 30

Nevo E, Estes R (1969) *Ramonellus longispinus*, an Early Cretaceous salamander from Israel. Copeia 1969:540–547

Newbrey MG, Bozek MA (2000) A new species of *Joffrichthys* (Teleostei: Osteoglossidae) of the Sentinel Butte Formation (Paleocene), of North Dakota, USA. J Vertebr Paleontol 20:6–14

Nydam RL, Caldwell MW, Fanti F (2010) Borioteiioidean lizard skulls from Kleskun Hill (Wapiti Formation; Upper Campanian), west-central Alberta, Canada. J Vertebr Paleontol 30:1090–1099

Oreska MPJ, Carrano MT, Dzikiewicz KM (2013) Vertebrate paleontology of the Cloverly Formation (Lower Cretaceous), 1: Faunal composition, biogeographic relationships, and sampling. J Vertebr Paleontol 33:264–292

Ostrom JH (1970) Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana 35:1–234+27 plates

Payenberg THD, Braman DR, Davis DW, Miall AD (2002) Litho- and chronostratigraphic relationships of the Santonian–Campanian Milk River Formation in southern Alberta and Eagle formation in Montana utilizing stratigraphy, U-Pb geochronology, and palynology. Can J Earth Sci 39:1553–1577

Peabody FE (1954) Trackways of an ambystomid salamander from the Paleocene of Montana. J Paleontol 28:79–83

Peabody FE (1959) Trackways of living and fossil salamanders. Univ Calif Publ Zool 63:1–71

Pearson DA, Schaefer T, Johnson KR, Nichols DJ, Hunter JP (2002) Vertebrate biostratigraphy of the Hell Creek Formation in southwestern North Dakota and northwestern South Dakota. In: Hartman JH, Johnson KR, Nichols DJ (eds) The Hell Creek Formation and the Cretaceous–Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous. Geol Soc Am Spec Paper, 361:145–167

Peng J, Brinkman DB, Russell AP (1995) A paleoecological study of vertebrate microfossil assemblages from the lower Judith River Group (Campanian) of southeastern Alberta, Canada. In: Sun A, Wang Y (eds) Sixth symposium on Mesozoic terrestrial ecosystems and biota. Short papers. China Ocean Press, Beijing, pp 185–187

Peng J, Russell AP, Brinkman DB (2001) Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide. Prov Mus Alberta Nat Hist Occ Pap 25:1–54

Polcyn MJ, Winkler DA, Jacobs LL, Newman K (2002) Fossil occurrences and structural disturbance in the Triassic Chinle Formation at North Stinking Springs Mountain near St. Johns, Arizona. New Mexico Mus Nat Hist Sci Bull 21:43–49

Prasad GVR, Rage J-C (2004) Fossil frogs (Amphibia: Anura) from the Upper Cretaceous intertrappean beds of Naskal, Andrhra Pradesh, India. Rev Paléobiol Genève 23:99–116

Prothero DR (1998) The chronological, climatic, and paleogeographic background to North American mammalian evolution. In: Janis CM, Scott KM, Jacobs LL (eds) Evolution of tertiary mammals of North America, vol 1. Terrestrial carnivores, ungulates, and ungulatelike mammals. Cambridge University Press, New York, pp 9–36

Ratkevich R, Duffek K (1996) Small macro- and larger micro-vertebrate faunas of the Fort Crittenden Formation, southeast Arizona. Proc Fossils Arizona Symp 4:115–120

Renne PR, Deino AL, Hilgen FJ, Kuiper KF, Mark DF, Mitchell WS III, Morgan LE, Mundil R, Smit J (2013) Time scales of critical events around the Cretaceous–Paleogene boundary. Science 339:684–687

Reynoso V-H (2006) Research on fossil amphibians and reptiles in Mexico, from 1869 to early 2004 (including marine forms but excluding pterosaurs, dinosaurs, and obviously birds). In: Vega F, Nyborg TG, Perrilliat MDC, Montellano-Ballesteros M, Cevallos-Ferriz SRS, Quiroz-Barroso SA (eds) Studies on Mexican paleontology. Topics in Geobiology 24. Springer, Dordrecht, pp 209–231

Roberts EM, Deino AL, Chan MA (2005) ^{40}Ar/^{39}Ar age of the Kaiparowits Formation, southern Utah, and correlation of contemporaneous Campanian strata and vertebrate faunas along the margin of the Western Interior Basin. Cret Res 26:307–318

Robison SF (1991) Bird and frog tracks from the Late Cretaceous Blackhawk Formation in East-Central Utah. In: Chidsey TC Jr (ed) Geology of east-central Utah. Utah Geol Assoc Publ 19:325–334

Roček Z (2000) Mesozoic anurans. In: Heatwole H, Carroll RL (eds) Amphibian biology, vol 4. Palaeontology. Surrey Beatty & Sons, Chipping Norton, pp 1295–1331

Roček Z (2013) Mesozoic and Tertiary Anura of Laurasia. In: Gardner JD, Nydam RL (eds) Mesozoic and Cenozoic lissamphibian and squamate assemblages of Laurasia. Palaeobio Palaeoenv 93(4). doi: 10.1007/s12549-013-0131-y

Roček Z, Nessov LA (1993) Cretaceous anurans from Central Asia. Palaeontogr Abt A 266:1–54

Roček Z, Rage J-C (2000) Tertiary Anura of Europe, Africa, Asia, North America, and Australia. In: Heatwole H, Carroll RL (eds) Amphibian biology, vol 4. Palaeontology. Surrey Beatty & Sons, Chipping Norton, pp 1332–1387

Roček Z, Eaton JG, Gardner JD, Přikryl T (2010) Evolution of anuran assemblages in the Late Cretaceous of Utah, USA. Palaeobio Palaeoenv 90:341–394

Roček Z, Gardner JD, Eaton JG, Přikryl T (2012) Similarities and differences in the ilia of Late Cretaceous anurans and urodeles. Bull Soc Géol France 183:529–535

Roček Z, Gardner JD, Eaton JG, Přikryl T (2013) Anuran ilia from the Upper Cretaceous of Utah—diversity and stratigraphic patterns. In: Titus AL, Lowen MA (eds) At the top of the grand staircase: The Late Cretaceous of southern Utah. Indiana University Press, Bloomington, pp 273–294

Rogers RR (1995) Sequence stratigraphy and vertebrate taphonomy of the Upper Cretaceous Two Medicine and Judith River formations. PhD dissertation, University of Chicago, Chicago

Rogers RR, Brady ME (2010) Origins of microfossil bonebeds: insights from the Upper Cretaceous Judith River Formation of north-central Montana. Paleobiol 36:80–112

Rose KD (2006) The beginning of the Age of mammals. Johns Hopkins University Press, Baltimore

Rowe T, Cifelli RL, Lehman TM, Weil A (1992) The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos Texas. J Vertebr Paleontol 12:472–493

Russell LS (1929) Paleocene vertebrates from Alberta. Am J Sci Ser 17:162–178

Russell LS (1964) Cretaceous non-marine faunas of northwestern North America. Roy Ontario Mus Life Sci Contrib 61:1–24

Russell LS (1975) Mammalian faunal succession in the Cretaceous System of western North America. In: Caldwell WGE (ed) The Cretaceous System in the Western Interior of North America: Geol Assoc Can Spec Paper 13:137–161

Sahni A (1972) The vertebrate fauna of the Judith River Formation, Montana. Bull Am Mus Nat Hist 147:321–412

Sanchiz B (1998) Salientia. In: Wellnhofer P (ed) Encyclopedia of paleoherpetology, part 4. Verlag Dr. Friedrich Pfeil, Munich, pp 1–275

Sankey JT (1998) Vertebrate paleontology and magnetostratigraphy of the upper Aguja Formation (late Campanian), Talley Mountain area, Big Bend National Park. PhD dissertation. Louisiana State University and Agricultural and Mechanical College, Baton Rouge

Sankey JT (2008) Vertebrate paleoecology from microsites, Talley Mountain, Aguja Formation (Late Cretaceous), Big Bend National park, Texas, USA. In: Sankey JT, Baszio S (eds) Vertebrate microfossil assemblages: Their role in paleoecology and paleobiogeography. Indiana University Press, Bloomington, pp 61–77

Scott CS (2003) Late Torrejonian (middle Paleocene) mammals from south central Alberta, Canada. J Paleontol 77:745–768

Shirk A, Bonde J, Druschke P, Hilton R (2009) Two distinct frog death assemblages from the Sheep Pass Formation (Maastrichtian-Eocene), east-central Nevada. Geological Society of America, 60th Annual Meeting, Northeastern Section, 18–21 October 2009, Portland, Maine, Abstracts with Programs 41(7), p. 103

Shubin NH, Jenkins FA Jr (1995) An Early Jurassic jumping frog. Nature 377:49–52

Skutschas PP (2007) New specimens of albanerpetontid amphibians from the Upper Cretaceous of Uzbekistan. Acta Palaeontol Pol 52:819–821

Skutschas PP (2013) Mesozoic salamanders and albanerpetontids of Middle Asia, Kazakhstan and Siberia. In: Gardner JD, Nydam RL (eds) Mesozoic and Cenozoic lissamphibian and squamate assemblages of Laurasia. Palaeobio Palaeoenv 93(4). doi:10.1007/s12549-013-0126-8

Skutschas PP, Martin T (2011) Cranial anatomy of the stem salamander Kokartus honorarius (Amphibia: Caudata) from the Middle Jurassic of Kyrgyzstan. Zool J Linn Soc 161:816–838

Sloan RE, Russell LS (1974) Mammals from the St. Mary River Formation (Cretaceous) of southwestern Alberta. Roy Ontario Mus Life Sci Contrib 95:1–21

Sloan RE, Van Valen L (1965) Cretaceous mammals from Montana. Science 148:220–227

Špinar ZV (1972) Tertiary frogs from Central Europe. Dr. W. Junk N.V, The Hague

Standhardt BR (1986) Vertebrate paleontology of the Cretaceous/Tertiary Transition of Big Bend National Park. PhD dissertation. Louisiana State University and Agricultural and Mechanical College, Baton Rouge

Sternberg CM (1924) Notes on the Lance Formation of southern Saskatchewan. Can Field-Naturalist 38(4):66–70

Storer JE (1991) The mammals of the Gryde Local Fauna, Frenchman Formation (Maastrichtian: Lancian), Saskatchewan. J Vertebr Paleontol 11:350–369

Storer JE (1993) Additions to the mammalian palaeofauna of Saskatchewan. Modern Geol 18:475–487

Sues H-D, Fraser NC (2010) Triassic life on land: The great transition. Columbia University Press, New York

Sues H-D, Olsen PE (1990) Triassic vertebrates of Gondwanan aspect from the Richmond Basin of Virgina. Science 249:1020–1023

Sues H-D, Clark JM, Jenkins FA Jr (1994a) A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest. In: Sues H-D, Fraser NC (eds) In the shadow of the dinosaurs: Early Mesozoic tetrapods. Cambridge University Press, Cambridge, pp 284–294

Sues H-D, Olsen PE, Kroehler PA (1994b) Small tetrapods from the Upper Triassic of the Richmond basin (Newark Supergroup), Virginia. In: Sues H-D, Fraser NC (eds) In the shadow of the dinosaurs: Early Mesozoic tetrapods. Cambridge University Press, Cambridge, pp 161–170

Sullivan RM (1980) Lower vertebrates from Swain Quarry "Fort Union Formation", middle Paleocene (Torrejonian), Carbon County. Michigan State University, East Lansing

Sullivan RM (1991) Paleocene Caudata and Squamata from Gidley and Silberling Quarries, Montana. J Vertebr Paleontol 11:293–301

Sullivan RM, Lucas SG (1986) Annotated list of lower vertebrates from the Paleocene Nacimiento Formation (Puercan-Torrejonian), San Juan Basin, New Mexico. J Herpetol 20:202–209

Szentesi Z, Gardner JD, Venczel M (2013) Albanerpetontid amphibians from the Late Cretaceous (Santonian) of Iharkút, Hungary, with remarks on regional differences in Late Cretaceous Laurasian amphibian assemblages. Can J Earth Sci 50:268–281

Sweetman SC, Gardner JD (2013) A new albanerpetontid amphibian from the Barremian (Early Cretaceous) Wessex Formation of the Isle of Wight, southern England. Acta Palaeontol Pol 58:295–324

Tanke DH (2004) The 2003 Royal Tyrrell Museum of Palaeontology expedition to the Grande Prairie region (northwestern Alberta, Canada). Alberta Palaeontol Soc Bull 19:3–31

Tokaryk TT (1988) Preliminary vertebrate faunal list of the Oldman Formation, Saskatchewan. J Vertebr Paleontol 30[Suppl 3]:28A

Tokaryk TT (1997) Preliminary review of the non-mammalian vertebrates from the Frenchman Formation (late Maastichtian [sic]) of Saskatchewan. In: McAnally LM (ed) Upper Cretaceous and Tertiary stratigraphy and paleontology of Southern Saskatchewan Canadian Paleontology Conference, 27–29 September 1997, Saskatoon, Saskatchewan, Field Trip Guidebook, vol. 6. pp 34–44

Tokaryk TT, Bryant HN (2004) The fauna from the *Tyrannosaurus rex* excavation, Frenchman Formation (Late Maastrichtian), Saskatchewan. Summary of Investigations 2004, vol. 1. Saskatchewan Geological Survey, Saskatchewan Industry Resources, Misc. Rep. 2004–4.1 Paper A-18, pp. 1–12

Van Valen L, Sloan RE (1965) The earliest primates. Science 150:743–745

Varricchio DJ (2002) A new bird from the Upper Cretaceous Two Medicine Formation of Montana. Can J Earth Sci 39:19–26

Venczel M, Gardner JD (2005) The geologically youngest albanerpetontid amphibian, from the lower Pliocene of Hungary. Palaeontology 48:1273–1300

Wake TA, Wake MH, Lesure RG (1999) First Quaternary record of caecilians from a Mexican archaeological site. Quat Res 52:138–140

Walker JD, Geissmann JW (2009) 2009 GSA Geologic Time Scale. GSA Today 19:60–61

Walker JD, Geissmann JW, Bowring SA, Babcock LE (2013) The Geological Society of America Time Scale. Geol Soc Am Bull 125:259–272

Wang Y (2004) Taxonomy and stratigraphy of Late Mesozoic anurans and urodeles from China. Acta Geol Sinica 78:1169–1178

Weishampel DB, Dodson P, Osmólska H (2004) The Dinosauria, 2nd edn. University of California Press, Berkeley

Weems RE, Bachman JM (1997) Cretaceous anuran and dinosaur footprints from the Patuxent Formation of Virginia. Proc Biol Soc Washington 100:1–17

Weil A (1999) Multituberculate phylogeny and mammalian biogeography in the Late Cretaceous and earliest Paleocene Western Interior of North America. PhD disertation. University of California, Berkeley

Whitmore JL, Martin JE (1986) Vertebrate fossils from the Greasewood Creek locality in the Late Cretaceous Lance Formation of Niobrara County, Wyoming. Proc North Dakota Acad Sci 65:33–50

Wilf P, Beard KC, Davies-Vollum KS, Korejko JW (1998) Portrait of a late Paleocene (early Clarkforkian) terrestrial ecosystem: Big Multi Quarry and associated strata, Washakie Basin, southwestern Wyoming. Palaeois 13:514–532

Williamson TE, Lucas SG (1993) Paleocene vertebrate paleontology of the San Juan Basin, New Mexico. In: Lucas SG, Zidek J (eds) Vertebrate paleontology in New Mexico. New Mexico Mus Natl Hist Sci Bull 2, pp 105–136

Wilson GP (2014) Mammalian extinction, survival, and recovery dynamics across the Cretaceous-Paleogene boundary in northeastern Montana, U.S.A. In: Wilson GP, Clemens WA, Horner JA, Hartman JH (eds) Through the end of the Cretaceous in the type locality of the Hell Creek Formation in Montana and adjacent areas. Geol Soc Am Spec Pap 503. doi:10.1130/2014.250315

Wilson GP, Dechesne ME, Anderson IR (2010) New latest Cretaceous mammals from northeastern Colorado with biochronologic and biogeographic implications. J Vertebr Paleontol 30:499–520

Wilson GP, Evans AR, Corfe IJ, Smits PD, Fortelius M, Jernvall J (2012) Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483:457–460

Wilson GP, DeMar DG, Jr, Carter G (2014) Extinction and survival of salamander and salamander-like amphibians across the Cretaceous-Paleogene boundary in northeastern Montana, U.S.A. In: Wilson GP, Clemens WA, Horner JR, Hartman JH (eds) Through the End of the Cretaceous in the Type Locality of the Hell Creek Formation in Montana and Adjacent Areas. Geol Soc Am Spec Pap 503. doi:10.1130/2014.2503(10)

Wilson LE (2008) Comparative taphonomy and paleoecological reconstruction of two microvertebrate accumulations from the Late Cretaceous Hell Creek Formation (Maastrichtian), eastern Montana. Palaios 23:289–297

Wilson MVH (1980) Oldest known *Esox* (Pisces: Esocidae), part of a new Paleocene teleost fauna from western Canada. Can J Earth Sci 17:307–312

Winkler DA, Jacobs LL (2002) Cenomanian vertebrate faunas of the Woodbine Formation, Texas. J Vertebr Paleontol 22[Suppl 3]:120A

Winkler DA, Murry PA, Jacobs LL (1989) Vertebrate paleontology of the Trinity Group, Lower Cretaceous of central Texas. In: Winkler DA, Murry PA, Jacobs LL (eds) Field guide to the vertebrate paleontology of the Trinity Group, Lower Cretaceous of Central Texas. Institute for the Study of Earth and Man. Southern Methodist University, Dallas, pp 1–22

Winkler DA, Murry PA, Jacobs LL (1990) Early Cretaceous (Comanchean) vertebrates of central Texas. J Vertebr Paleontol 10:95–116

Wuttke M, Přikryl T, Ratnikov VY, Dvořák Z, Roček Z (2012) Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura). Palaeobio Palaeoenv 92:367–395

Wroblewski AF-J (1997) Non-mammalian paleontology of latest Cretaceous-early Paleocene Ferris Formation, western Hanna Basin. MSc thesis. University of Wyoming, Laramie

Zangerl R, Denison RH (1950) Discovery of Early Cretaceous mammals and frogs in Texas. Science 112:61

Zetter R, Farabee MJ, Pigg KB, Manchester SR, DeVore ML, Nowak MD (2011) Palynoflora of the late Paleocene silicified shale at Almont, North Dakota, USA. Palynology 35:179–211