TRIASSIC VERTEBRATE COPROLITE ICHNOFAUNAS

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Abstract—There is an abundant record of vertebrate coprolites in the Triassic. The Early Triassic record is quite limited and occurs only in Europe, Australia and South Africa. The distribution of coprolites in the Middle Triassic is worldwide, with occurrences in the USA, South Africa, Russia, Kazakhstan, Argentina, Brazil, India, Poland, Slovenia, Germany, England, France, Switzerland, Italy and China. The Late Triassic sample size is the largest, with records in the USA, Greenland, England, Netherlands, Switzerland, Germany, Madagascar, India, Brazil, Morocco and South Africa. The majority of Late Triassic coprolites are from the Chinde Group and Newark Supergroup in North America and the Rhaetic bonebeds in Europe. Santamaria coprolites may represent the basal Lias, but which is now recognized as the Rhaetian Westbury Formation of the Penarth Group (Duffin, 1979; Swift and Duffin, 1999). They noted “thin beds of a greenish siliceous grit, highly charged with mica, and loaded with the scales, teeth, palates and bones of fishes, and the bones of many gigantic reptiles. These siliceous strata, from the abundance of their organic remains, are known by the name of the Bone-beds’’ (Buckland and Conybeare, 1822, p. 301). “There occur also many irregular bodies, varying much in form and substance, which are usually, however, cylindrical with rounded ends, some having a black and glossy surface and fracture, others being of dull-brown colour. They are probably rolled palates, or rolled fragments of very solid bone” (Buckland and Conybeare, 1822, p. 302). Buckland (1829b, 1835) would later recognize these specimens as coprolites.

Sometime prior to 1829, Buckland became aware that the “fossils, locally called Bezoar-stones, which abound at Lyme [Regis, southwestern England], in the same beds of lias [sic] with the bones of Ichthyosaurus [sic], are the faeces of that animal [actually fish]” (Buckland, 1829a, p. 97). Mary Anning was the pre-eminent collector of fossils from the Lias, and she supplied Buckland with specimens such as the holotype of Santamaria elongatia, the first known ichnogen and ichnosp. nov. and Rhynchoceros soturi ichnogen et ichnosp. are new ichnotaxa of coprolites of herbivores from the Late Triassic Santa Maria Formation of Brazil.

INTRODUCTION

There is a Phanerozoic acme for vertebrate coprolites in Permnian-Triassic redbeds (Hunt and Lucas, 2005b) and a worldwide distribution of occurrences (Fig. 1). The majority of Triassic vertebrate coprolites in museum collections and mentioned or described in the literature are from the Late Triassic. Hunt et al. (2007) provided an initial summary of Triassic vertebrate coprolites. The purpose of this paper is to provide an updated review of the fossil record of Triassic coprolites and to illustrate a wide range of specimens.


WILLIAM BUCKLAND AND THE FIRST RECOGNITION OF TRIASSIC COPROLITES

William Buckland (1784-1856) was the first to identify fossil feces, and he coined the term coprolite (Buckland, 1829b: Duffin, 2006, 2009, 2012; Pemberton, 2012). He was also the first to recognize Triassic coprolites (Buckland, 1829b). Buckland first recognized Pleistocene coprolites in museum collections and mentioned or described in the literature are from the Late Triassic. Hunt et al. (2007) provided an initial summary of Triassic vertebrate coprolites. The purpose of this paper is to provide an updated review of the fossil record of Triassic coprolites and to illustrate a wide range of specimens.

In December 1821, William Buckland visited Kirkdale Cave in Yorkshire, England (Duffin, 2009). This cave contains numerous Pleistocene mammal bones (Boylan, 1981), including those of hyenas and “many small balls of the solid calcareous excrement of an animal that had fed on bones” (Buckland, 1822, p. 186). Clearly these specimens were similar to Recent mammal feces and occurred in association with multiple bones, so it was not conceptually difficult to interpret them as coprolites. Buckland (1822, 1824) identified these coprolites as pertaining to hyenas (Hyena coprolitus of Hunt et al., 2012a).

During the same time period, Buckland and Conybeare (1822) published a detailed study of “Observations on the South Western Coal District of England” in which they discussed what they considered to represent the basal Lias, but which is now recognized as the Rhaetian Westbury Formation of the Penarth Group (Duffin, 1979; Swift and Duffin, 1999). They noted “thin beds of a greenish siliceous grit, highly charged with mica, and loaded with the scales, teeth, palates and bones of fishes, and the bones of many gigantic reptiles. These siliceous strata, from the abundance of their organic remains, are known by the name of ‘the Bone-beds’” (Buckland and Conybeare, 1822, p. 301). “There occur also many irregular bodies, varying much in form and substance, which are usually, however, cylindrical with rounded ends, some having a black and glossy surface and fracture, others being of dull-brown colour. They are probably rolled palates, or rolled fragments of very solid bone” (Buckland and Conybeare, 1822, p. 302). Buckland (1829b, 1835) would later recognize these specimens as coprolites.

Sometime prior to 1829, Buckland became aware that the “fossils, locally called Bezoar-stones, which abound at Lyme [Regis, southwestern England], in the same beds of lias [sic] with the bones of Ichthyosaurus [sic], are the faeces of that animal [actually fish]” (Buckland, 1829a, p. 97). Mary Anning was the pre-eminent collector of fossils from the Lias, and she supplied Buckland with specimens such as the holotype of Santamaria elongatia, the first known ichnogen and ichnosp. nov. and Rhynchoceros soturi ichnogen et ichnosp. are new ichnotaxa of coprolites of herbivores from the Late Triassic Santa Maria Formation of Brazil.
and having a polished surface, which occur mixt [sic] with bones in the lowest strata of the lias [sic] on the banks of the Severn, near Bristol, are of faecal origin: - they appear to be co-extensive with this bone bed, and occur at many and distant localities. ... The author proposes the name of Nigrum Graecum for all these black varieties of fossil faeces. They may have been derived from the molluscous [sic] inhabitants of fossil nautiloid ammonites, and belemnites” (Buckland, 1829b, p. 142: Fig. 12B-O). These coprolites from the Rhaetian Westbury Formation of the Penarth Group are the least like Recent feces of all the specimens that Buckland had assigned to this type of ichnofossil. However, they do occur with specimens that are spiral or/and cylindrical and which thus are similar to the coprolites recognized from the Lias (e.g., Hunt et al., 2012a, fig. 4A-D; Hunt et al., 2012b, fig. 2F).

**TRIASSIC VERTEBRATE BIOCHRONOLOGY**

Lucas and co-authors (Lucas and Hunt, 1993; Lucas, 1997, 1998, 1999, 2010; Lucas and Hancox, 2001; Lucas and Huber, 2003; Hunt et al., 2005) have developed a global biochronological scheme for Triassic nonmarine tetrapods that we utilize here for nonmarine coprofaunas. This scheme involves the definition of eight land-vertebrate faunachrons (lvfs) to encompass Triassic time, with boundaries defined by the first appearance datums (FADs) of tetrapod genera or species (Lucas, 2010): (1) Lootsbergian (uppermost Changshingian, Induan and possibly earliest Olenekian); (2) Nonesian (majority of the Olenekian); (3) Perovkan (majority of the Anisian); (4) Berdyankian (latest Anisian? and Ladinian); (5) Otischalkian (early to late Carnian); (7) Adamanian (majority of the late Carnian); Revuelitan (early–middle Norian); and (8) Apachean (late Norian–Rhaetian). We use this nonmarine tetrapod biochronology to assign ages to Triassic coprolites from nonmarine facies. Several vertebrate coprolite localities are in marine strata, and we correlate these with the standard chronostratigraphic timescale (Lucas, 2010a).

**TRIASSIC VERTEBRATE COPROLITE RECORD**

**Early Triassic**

**Australia**

Northwood (1997, 2005) studied coprolites from the Arcadia Formation (Lootsbergian lvf) in Queensland, northeastern Australia (Fig. 2A-N). Northwood (2005) recognized three main forms of coprolites: (1) amphipolar coprolites assignable to *Hyronocopros amphipola* (Hunt et al., 2005c, 2007); (2) longitudinally-striated coprolites representing *Alococopros triassicus* (Hunt et al., 2007: Fig. 2I-N); and (3) *Eucoprus* sp. and indeterminate coprolites (Fig. 2A-H).

**France**

Coprolites occur in the “Grès à Voltzia” Formation (Anisian) of the upper Buntsandstein in eastern France (Gall, 1971; Gall and Grauvogel-Stamm, 1993).

**Germany**

Vertebrate coprolites are present in the Buntsandstein but are essentially undescribed (e.g., Dachroth, 1985).

**South Africa**

Numerous coprolites, including some containing nonmarine bivalves, occur in the Burgersdorp Formation (Olenekian) of the “Kestrosaurus assemblage zone” (Bender and Hancox, 2004; Yates et al., 2012). Elsewhere vertebrate coprolites occur rarely throughout the Beaufort Group (Smith and Botha-Brink, 2011).
Kazakhstan

Smith and Botha-Brink (2011) noted that vertebrate coprolites occur rarely throughout the Upper Permian to Middle Triassic Beaufort Group of the main Karoo Basin but that they are relatively more common in the Early/Middle Triassic Cynognathus Assemblage Zone.

Russia

Ochev (1974) described coprolites from three Middle Triassic (Perovkan and Berdyanskian) localities: (1) Karagachka; (2) Donguz I; and (3) Bukobay V. These coprolites represent Alococopros triassicus and possibly Heteropolacopros texaniensis and Dicynodontocopros maximus (Hunt et al., 2007).

Kazakhstan

Ochev (1974) described three morphologies of coprolites from the Mollo-Khara-Bala-Kantemir locality (Perovkan). Alococopros triassicus and possibly Heteropolacopros texaniensis and Dicynodontocopros maximus are present in the coprofauna (Hunt et al., 2007).

Argentina

Abundant vertebrate coprolites occur in the Berdyanskian (?) Potrerillos, Cacheuta and Río Blanco formations of the Cuyana Basin. Large samples dominated by spiral morphologies were initially described by Rusconi (1947, 1949) and more recently by Mancuso et al. (2004). Hunt et al. (2007) suggested that Liassocopros, Hyronocopros and Dicynodontocopros are represented in the coprofauna. Some of the fosiliferous volcanicogenic concretions in the Ladinañ Chañares Formation of Argentina yield fusiform coprolites (Rogers et al., 2001).

Brazil

Souto (2001) first described samples of the abundant coprolites that occur in the Santa Maria Formation (Berdyanskian) of the Paraná basin. He analyzed a sample of 50 coprolites in 22 specimens (since many were agglomerated) and recognized two morphotypes based on shape and measurements. Both forms are rounded and are calcareous and not phosphatic (Souto, 2001, table 2). One morphotype is ovoid (e.g., Souto, 1991, fig. 5 lower) with a width that is half or more of the length (Souto, 1991, table 1). The other morphotype is more elongate (e.g., Souto, 1991, fig. 4 upper left) with a width of less than half the length (Souto, 2001, table 1).

We have examined a much larger collection of approximately 150 coprolites in the PUCRS collection from 56 localities from the Dinodontosaurus level of the Santa Maria Formation and we recognize the same two morphotypes which we name in the Appendix as Rhynchocopros soutoi ichnogen et ichnosp. nov. for the more rounded form and Santamariacopros elongatus ichnogen et ichnosp. nov. for the more cylindrical form (Figs. 3-4; Table 1). Rhynchocopros soutoi ichnogen et ichnosp. nov. (Fig. 3C-H, Fig. 4A-F, I-J) are much more common than Santamariacopros elongatus ichnogen et ichnosp. nov. (Fig. 3A-B, 4G-H). Individual coprolites range from 25 to 125 mm in length, with the majority in the lower half of the range.

We consider both these ichnotaxa to have been produced by herbivores because: (1) they are calcareous rather than phosphatic in composition (Souto, 2001, table 2); (2) they do not include any animal inclusions; and (3) their pellet-like structure is more common in herbivores than carnivores (e.g., Hunt and Lucas, 2012, table 1). Based on their frequency and association with osteological remains we believe it likely that Rhynchocopros soutoi ichnogen et ichnosp. nov. was produced by a rynchosaurs and thus Santamariacopros elongatus ichnogen et ichnosp. nov. may be the product of a dicynodont.

India

The Yerrapilli Formation (early Middle Triassic) yields spherical, ovoid and elliptical coprolites (Chatterjee, 1967; Jain, 1983). These specimens are covered by desiccation cracks and differ in morphology from those from the Late Triassic of India (Jain, 1983).

Poland

Chrzastek (2008, fig. 6E-I) described coprolites from two horizons in the Lower Muschelkalk, and Kowal-Linka and Bodzioch (2012) noted other specimens. Salamon et al. (2012) described bromalites of durophagous vertebrates from the Middle Triassic Gogolin Formation, of Upper Silesia, that they interpret to be regurgitalites. These unusual specimens are principally composed of angular bivalve shell fragments and broken crinoid ossicles.

Slovenia

Abundant vertebrate coprolites occur in the Lower-Middle(?) Anisian of the Kamnik-Savinja Alps (Hitij et al., 2010).

France

The Muschelkalk (Anisian to Ladinian) of France yields coprolites (e.g., Carter, 1888; Milner et al., 1990).

Switzerland/Italy

Coprolites are common in localities of the Upper Ladinian Monte San Giorgio Formation (e.g., Etter, 2002).

United States

Arizona: A large sample of coprolites occurs in the Holbrook Member of the Moenkopi Formation (early Anisian: Perovkan) at Radar Mesa in northern Arizona (Benz, 1980; Morales, 1987). Coprolites are present at other Moenkopi localities in the northeastern part of the state, but they have not been described (Hunt et al., 2007). There is an unstudied coprolite collection from the Holbrook Member collection at MNA.

New Mexico: The Anton Chico Formation of the Moenkopi Group is also of early Anisian age, and it yields many coprolites from localities in northeastern New Mexico (Boy et al., 2001; Schoch et al., 2010; Fig. 2O-V, HH-KK) including Heteropolacopros texaniensis (Fig. 2Q-V).

China

Two of the four types of coprolites from the Lupong Lagerstätte (Anisian) were produced by fish (Hu et al., 2010).

Late Triassic

Western United States

Vertebrate coprolites are common and locally abundant in strata of the Upper Triassic Chinle Group in the western United States (Hunt and Lucas, 1989, 1993a, b; Murry, 1989; Murry and Long, 1989; Heckert
TABLE 1. Measurements of selected coprolites from the Middle Triassic Santa Maria Formation in the PUCRS collection.

<table>
<thead>
<tr>
<th>Specimen number</th>
<th>Length of coprolite (mm)</th>
<th>Width of coprolite (mm)</th>
<th>Ichnotaxon</th>
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<td>37</td>
<td>25</td>
<td><em>Rhynchocopros soutoi</em></td>
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<td></td>
<td>42</td>
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<td></td>
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<td><em>Rhynchocopros soutoi</em></td>
</tr>
</tbody>
</table>
et al., 2005; Hunt et al., 1998, 2005c). The oldest, Otischalkian, specimens are restricted to West Texas and Wyoming. Adamanian samples are the most abundant followed by Revueltian. Apachean coprolites are only abundant in eastern New Mexico.

**Arizona:** Vertebrate coprolites are common in Adamanian localities in northeastern Arizona. Heckert et al. (2002) described coprolites from the Shinarump Formation or lowermost Cameron Formation near Cameron. Coprolites, including multiple specimens of *Dicynodontocopros maximus*, are abundant in the Bluewater Creek Formation at the Placerias quarry near St. Johns (e.g., Camp and Welles, 1956; Kaye and Padian, 1994; Hunt et al., 1998). Coprolites, including *Dicynodontocopros maximus*, occur in the Blue Mesa Member of the Petrified Forest in the Blue Hills, also near St. Johns (e.g., Norman et al., 2009: Fig. 7N-Q).

Adamanian coprolites are common at Petrified Forest National Park in the Blue Mesa Member of the Petrified Forest Formation (Murry and Long, 1989; Hunt and Santucci, 1994; Hunt et al., 1998; Wahl et al., 1998; Heckert, 2001, 2004; Hunt et al., 2012d). A notable locality is the “Dying Grounds,” which is a fossiliferous horizon high in the Blue Mesa Member near Blue Mesa (e.g., Murry and Long, 1989; Heckert, 2001, 2004). Hunt et al. (1998) noted that *Heteropolacopros texaniensis* occurs in the Blue Mesa Member at the Park Hunt et al. (2012d, fig. 2A) described *Falcocopros ooxidens* from an unknown Blue Mesa locality. The USNM collection includes *Heteropolacopros* and indeterminate coprolites from a sample collected near Petrified Forest National Park, presumably from the Blue Mesa Member (Hunt et al., 2012b).

Significant accumulations of coprolites occur in the lower part of the Revueltian Painted Desert Member at Petrified Forest National Park at localities that include Dinosaur Hill (Hunt and Lucas, 1993c). Coprolites are also common in the Revueltian Owl Rock Formation at Ward Terrace (Kirby, 1989). Lipman and McLees (1940) described a new species of fossil bacteria from a coprolite from an unknown locality in Arizona.

**New Mexico:** Ash (1978a, b) described a large number of coprolites from a lacustrine mudstone unit in the Adamanian Bluewater Creek Formation of western New Mexico (Figs. 5U-Z, 6, 7A-M, 8A-C). The sample includes *Dicynodontocopros maximus* (Figs. 7A-C, J-M, 8A-C), *Heteropolacopros texaniensis* (Figs. 6R-S, T-U, V-Y, 7G-I) and *Alococopros triassicus* (Fig. 6O-Q). Weber and Lawler (1978) analyzed the lipid content of a sample of these coprolites. Other localities in the Bluewater Creek Formation yield abundant coprolites, including specimens of *Dicynodontocopros maximus* (Heckert and Lucas, 2003; Fig. 8D-M).

Adamanian coprolites occur in several other stratigraphic units, including the Los Esteros Member of the Santa Rosa Formation, Garita Creek Formation, lower Petrified Forest Formation and Salitral Formation (Hunt and Lucas, 1988, 1990, 1993; Hunt et al., 1989).

The Revueltian Bull Canyon Formation of east-central New Mexico yields large coprofaunas (Lucas et al., 1985; Hunt, 1994, 2001; Figs. 8N-T, 10A-H*). Lucas et al. (1985) described three morphologies of coprolites: (1) longitudinally furrowed specimens that represent *Alococopros triassicus* (Lucas et al., 1985, fig. 7M-R); (2) small specimens with a rod-like to oval morphology (> 90% of sample) (Lucas et al., 1985, fig. 7A-L); and (3) large, irregularly shaped forms with numerous inclusions (fish scales, bone fragments) (Lucas et al., 1985, fig. 7S-U). The largest coprolite locality is in Revuelto Creek (NMMNH locality 1) and yields *Eucoprus cylindratus* (Fig. 10A-I, *Alococopros triassicus* (Fig. 10Y-JJ), heteropolar form similar to *Heteropolacopros* (Fig. 10M-X), coiled coprolites (Fig. 10KK-VV) and comma-shaped specimens (Fig. 10WW-H*). NMMNH P-16204 from NMMNH locality 447 is a complex specimen that consists of small *Alococopros* specimens en-cased in a sheath of coprolite material (Fig. 8N-Q). It is 35 mm long and ovoid in cross section (20 by 17 mm). The outer 1.9 mm-thick outer layer surrounds small striated lunate coprolites. This specimen could represent an evisceralite or section of the gastrointestinal tracts preserved outside the body cavity (Hunt and Lucas, 2012).

Coprolites are also present at other Revueltian localities in New Mexico, including the upper Petrified Forest Formation in the San Ysidro area (Hunt and Lucas, 1990) and Chama Basin (Hunt and Lucas, 1993), and the Trujillo Formation (Hunt, 1991) and Correoso Sandstone Member of the Petrified Forest Formation at Mesa Gigante and the Hagan Basin (Hunt and Lucas, 1993b).

The Apachean Redonda Formation of east-central New Mexico yields numerous coprolites. The largest concentration is at the Gregory quarry (NMMNH locality 485) in Apache Canyon (Figs. 8U-KK, 11). This large sample includes the holotype and other specimens of *Eucoprus cylindratus* (Hunt and Lucas, 2012, fig. 4: Figs. 8U-X, 11O-Z), *Alococopros* sp. (Figs. 8CC-GG, 11M-N) as well as *Heteropolacopros texaniensis* (Fig. 8HH-KK) and other heteropolar forms (Fig. 11A-L).

Coprolites occur associated with skeletons of *Coelophysis* in the Apachean Rock Point Formation at Ghost Ranch (Rinehart et al., 2005a, b, 2009).

**Texas:** Vertebrate coprolites are common in the Upper Triassic strata of West Texas. Otischalkian coprolites occur in the Colorado City Formation near Midland (Elder, 1978, 1987; Figs. 2AA-GG, LL-MM, 5A-I) and are particularly abundant at Otis Chalk quarries 1 and 2. These samples include *Heteropolacopros texaniensis* (Elder, 1978, pl. 14, fig. 1a; 2AA-GG, LL-MM), *Alococopros triassicus* (Elder, 1978, pl. 14, fig. 1b: Fig. 5I-K) and *Dicynodontocopros maximus* (Fig. 5A-G).

Case (1922) recognized three coprolite forms from the Adamanian Tecomav Formation that include the holotype and referred specimens of *Heteropolacopros texaniensis* (Case, 1922, fig. 33A-B; Hunt et al., 1998, fig. 2C-L: Figs. 2NN-PP, 5J-O). Other specimens from the Tecomav include the holotype of *Dicynodontocopros maximus* (Hunt et al., 1998, fig. 2A-B) and specimens of *Alococopros triassicus* Case (1922, fig. 33C-D; Hunt et al., 2007: Fig. 5L-P).

Localities in the badlands north of Amarillo include the extremely fossiliferous Rotten Hill bonebed. This locality is in the Tecomav Formation and has yielded a large sample of coprolites (Fig. 9). Like most Adamanian coprolite faunas in the Chinle this collection includes *Heteropolacopros* (Fig. 9L-M, GG ) and *Alococopros* (Fig. 9K-K, CCFF) as well as *Eucoprus* (Fig. 9O-Q, U-CC, GG-UU). *Heteropolacopros texaniensis* was initially described from the Adamanian of Texas and Arizona.

**Colorado:** Specimens of *Heteropolacopros* and *Alococopros triassicus* from the Purgatoire River Valley probably derive from the Revueltian Cobert Canyon Sandstone Bed of the Baldy Hill Formation (Hunt et al., 2012b). The largest broken specimen is 89 mm long and is the largest known nonmarine Triassic coprolite (Hunt et al., 2012b, fig. 2A). Coprolites also occur in fish beds of the Apachian Rock Point Formation in the southwestern part of the state.

**Utah:** Parrish (1999) reported abundant coprolites from the Adamanian Monitor Butte Formation in southern Utah. DeBaiseux et al. (2006, figs. 9A-C) illustrated numerous coprolites from the Petrified Forest Formation of Zion National Park in southern Utah that may be either Adamanian or Revueltian in age. Coprolites are common in a laterally extensive interval in the upper Apachian Bell Springs Formation at Dinosaur National Monument (Hunt et al., 1993). Coprolites occur on the main track bed at the Shay Canyon tracksite (Rock Point Formation) in southeastern Utah (Lockley, 1986; Lockley and Hunt, 1995, fig. 3.8).

**Wyoming:** Coprolites are locally common in the Popo Agie Formation (e.g., High et al., 1969; Hunt et al., 1998: Fig. 5Q-T).

**Eastern United States**

The Newark Supergroup ranges in age from Middle Triassic to Early Jurassic. However, there are very few references to Newark coprolites, but it seems that they are most common in the Carnian and Jurassic strata (e.g., Olsen, 1988; Olsen et al., 1989, 2003, 2005a,b; Olsen and Flynn, 1989; Olsen and Huber, 1997, 1998; Olsen and Rainforth, 2002; Gillilian and Olsen, 2000; Hunt et al., 2007). Gillilian and Olsen (2000) noted that coprolites are the most common trace fossils in the fish-

bearing lacustrine units of the Newark and that large specimens probably derive from coelacanths.

Olsen (1988) noted abundant Carnian coprolites in the Cumnock Formation, and the Lockatong Formation also yields coprolites from several localities (Olsen et al., 1989; Olsen and Flynn, 1989; Olsen and Rainforth, 2002; Jenkins in Hantschel et al., 1968; YPM PU specimens). Other Carnian localities include the Pekin Formation in North Carolina (Olsen and Huber, 1998, table 1) and the Falling Creek Formation of Virginia (Weems, 1980).

Argentina

Hollocher et al. (2005) described the chemistry and mineralogy of a small sample of coprolites from the Ischigualasto Formation (see also Contreras, 1995).

Greenland

Milàn et al. (2012) provided a preliminary description of an extensive coprolite fauna from the basal Rhaetian part of the Kap Stewart Formation of Jameson Land. They recognized three morphologies: (1) elongated cylindrical masses, composed of irregularly wrapped layers; (2) elongated cylindrical masses with constriction marks; and (3) spirally-coiled specimens.

England

Coprolites are very common in the bone beds of the Westbury Formation in southwestern England, and many specimens are preserved in museum collections (e.g., Buckland, 1829; Duffin, 1979; Storrs, 1994; Martill, 1999; Swift and Duffin, 1999; Gallois, 2007; Hunt et al., 2012a-

b: Fig. 12). There are more than half a dozen morphotypes in the Westbury coprofaunas including both spiral (amphipolar and heteropolar) and non-spiral forms, Liassocopros hawkinsi, Saurocopros bucklandi and Strabelocoprus pollardi (Duffin, 1979; Swift and Duffin, 1999; Hunt et al., 2007; Hunt et al., 2012a-c: Fig. 12).

Netherlands

Klompmaker et al. (2010) noted coprolites in Rhaetian shale.

South Africa

Anderson et al. (1998) noted that coprolites are very rare in the Molteno Formation.

Thailand

The Carnian-Norian Huai Hin Lat Formation at Huai Nam Aun in Chaiyaphum province has yielded abundant coprolites (Laojumpon et al., 2012). Laojumpon et al. (2012) recognize seven different morphotypes, including Liassocopros hawkinsi and Saurocopros bucklandi.

India

Coprolites were recognized in the Otischalkian-Adamanian Maleri Formation more than 150 years ago and are locally common (Oldham, 1859; King, 1881; Aiyengar, 1937; Matley, 1939; Sohn and Chatterjee, 1979; Jain, 1983; Vijaya et al., 2009). Most fossils, including coprolites, derive from the Otischalkian portion of the Maleri Formation (Hunt et
al., 2007). Coprolites include *Malericopros matleyi*, *Heteropolacopros texaniensis*, *Liassocopros hawkinsi* and probably *Saurocops bucklandi*, as well as amphipolar forms (Matley, 1939a; Jain, 1983; Hunt et al., 2007; Vijaya et al., 2009).

**Switzerland**

Coprolites are common in the Rhaetic bone beds (e.g., Fluckiger, 1861).

**Germany**

Fraas (1891) reported common spiral coprolites from the “Keuper,” which he attributed to sharks. The Stuttgart Formation (middle Carnian) includes coprolites (Schoch, 2012).

**Morocco**

Sebastian Voigt donated to NMMNH a specimen of *Heteropolacopros texaniensis* from the Trohalene Member of the Timezgaderine Formation (Otischalkian) at Aït Moussi, Argana Basin (Fig. 2W-Z).

**Madagascar**

Burmeister et al. (2006, fig. 6) described coprolites from the Isalo “Group” (Isalo II beds) of Madagascar. These coprolites range from 10-60 mm in length and are not spiral in form.

**Brazil**

Langer (2005) noted that coprolites were collected from the lower Caturrita Formation (Adamanian).

### TRIASSIC COPROLITE BIOSTRATIGRAPHY AND BIOCHRONOLOGY

Coprolites are potentially of biochronological utility (e.g., Hunt, 1992; Hunt et al., 1998, 2005a, 2007). Ichnotaxa almost always correspond to higher level taxonomic groups of body fossils. Thus, footprint ichnogenera are commonly only equivalent to the “family” level of body fossils (Lucas, 2007). Coprolites probably represent, in most cases, even higher level taxonomic levels (“order” or above) (Hunt et al., 2007).

However, coprolite ichnotaxa do have defined stratigraphic ranges that parallel the stratigraphic ranges of the producing animals and thus do have a utility in biostratigraphy and biochronology (Hunt and Lucas, 2005; Hunt et al., 2007).

*Alcococops triassicus* is abundant and characteristic of the Triassic, although there are rare occurrences from the Permian to the Cretaceous (Cantrell et al., 2012; Suazo et al., 2012).

*Hyronocops amphipolaris* is common in the Permian and apparently has its last occurrence in the Early Triassic. *Dicynodontocops maximus* is restricted to the Late Triassic (upper Carnian) and it occurs in some faunas as the only evidence of the presence of dicynodonts (e.g. Chinle Group of West Texas).

*Heteropolacopros texaniensis* first occurs in the Pennsylvanian and it does not appear to be present in strata younger than Carnian.

There appears to be a change in coprofaunas near the end of the Norian in nonmarine environments. Apachean (upper Norian/Rhaetian) and Rhaetian assemblages have few specimens of *Alcococops triassicus* or heteropolar coprolites. Further description of coprofaunas should allow refinement of the coprolite biochronology of the Triassic.

### CONCLUSIONS

There is clearly a large abundant record of vertebrate coprolites in the Triassic (Fig. 1). It is equally apparent that all ichnofaunas are in need of significant study.

The Early Triassic record is quite small and occurs only in Europe, Australia and South Africa. The Buntsandstein and redbeds in South Africa and probably Russia offer opportunities for further collections. The distribution of coprolites in the Middle Triassic is worldwide and mirrors the record of the Permian (Hunt and Lucas, 2013). The Late Triassic sample size is the largest but it is skewed by the record from the Chinle Group and Newark Supergroup in North America and the Rhaetic bonebeds in Europe.

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APPENDIX

SYSTEMATIC ICHNOTAXONOMY

**Rhynchocopros, ichnogen. nov.**

*Type ichnospecies:* *Rhynchocopros soutoi* Hunt et al., 2013.

*Included ichnospecies:* Known only from the type ichnospecies.

*Etymology:* From the Greek *rhunkhos,* (beak) in allusion to the hypothesized producer being a rhynchosaur and *kopros* (dung).

*Distribution:* Middle Triassic.

*Diagnosis:* Coprolite that differs from other ichnogenera in having the shape of a well rounded ovoid with a length: width ratio of approximately 1:0.5, in being composed primarily of calcite and often occurring in masses of up to six.

*Discussion:* The prevalence of this ichnogenus in occurrence with rhynchosaur bones is a strong indication of the probable source animal.

**Rhynchocopros soutoi, ichnosp. nov.**

*Holotype:* PUCRS 891, six conjoined coprolites (Fig. 4A-B).

*Etymology:* For Paulo Roberto de Figueiredo Souto, who first described this morphology, for his contributions to the study of South American coprolites.

*Type locality:* Gal. Camara, Villa Melo, Brazil.

*Type horizon:* Santa Maria Formation (Ladinian).

*Distribution:* As for ichnogenus.

*Referred specimens:* PUCRS 100 (Fig. 4I-J), PUCRS 101 (Fig. 4C-D), PUCRS 105 (Fig. 3G-H), PUCRS 112 (Fig. 3E-F), PUCRS 1222 (Fig. 3C-D), PUCRS 3029g (Fig. 4E-F).

*Diagnosis:* As for ichnogenus.

*Description:* The holotype specimen (PUCRS 891) is a group of six coprolites (Fig. 4A-B). Individual coprolites range from a length of 42 mm and a width of 24 mm to a length of 30 mm and a width of 22 mm. Coprolites are well rounded and ovoid in general morphology. They are calcareous rather than apatitic in composition.

*Discussion:* This ichnogenus would be expected to be common in Middle Triassic ichnofaunas.

**Santamariacopros, ichnogen. nov.**

*Type ichnospecies:* *Santamariacopros elongatus* Hunt et al., 2013.

*Included ichnospecies:* Known only from the type ichnospecies.

*Etymology:* For the Santa Maria Formation from which the holotype derives. Distribution: Middle Triassic.

*Diagnosis:* Coprolite that differs from other ichnogenera in elongate, rounded cylinder with a length: width ratio of 1 : >0.5 which is composed principally of calcite and lacks inclusions and often occurs in masses of up to four.

*Discussion:* It is likely that this herbivore coprolite pertains to the dicynodonts in the Santa Maria fauna.

**Santamariacopros elongatus, ichnosp. nov.**

*Holotype:* PUCRS 821, two conjoined coprolites with a piece of a third (Fig. 3A-B).

*Etymology:* From the Latin *elongatus* (protracted) in allusion to the morphology of the coprolite.

*Type locality:* Gal. Camara, Villa Melo, Brazil.

*Type horizon:* Santa Maria Formation (Ladinian).

*Distribution:* As for ichnogenus.

*Referred specimens:* PUCRS 686 (Fig. 4G-H).

*Diagnosis:* As for ichnogenus.

*Description:* The holotype specimen (PUCRS 821) is two conjoined coprolites with a fragment of a third (Fig. 3A-B). The complete coprolites are 88 mm long and 43 mm wide and 90 mm long and 41 mm wide. The individual coprolites are well rounded. They are calcareous in composition.

*Discussion:* This ichnogenus occurs in smaller groupings than *Rhynchocopros.*