ABSTRACT—The 31 crania of the agriochoerid oreodont from the Hancock Mammal Quarry (HMQ) possess character states unique among described agriochoerid species. Characters unique to the HMQ agriochoerid include a triangular P2; a P3 with a posterolingual cone and heart-shaped occlusal outline; a P4 with separate anterolabial and posterolabial cones, but without a posterolingual conule; upper molars with large styles and lacking paraconules; lower molars without lingual cingulids, but possessing small metastylids and parastylids; and a mandibular symphysis that is perpendicular to the tooth row without ventral displacement of the pl. We subjected previous size comparisons to an F-test and Welch’s t-test and found that the tooth row lengths of the HMQ agriochoerid have significantly different variance and means from Agriochoerus matthewi crassus (P = .005), a taxon to which this population has previously been assigned. Taken together, these characters are diagnostic of a new species, which we describe here as Diplobunops kardoula. The HMQ specimens show that some of the diagnostic dental characters of agriochoerids currently in use change with wear and may be biased by taphonomy. Furthermore, characters diagnostic of both Agriochoerus and Diplobunops are present in the HMQ agriochoerid, and many of the species-level diagnostic characters of agriochoerids are continuously variable or polymorphic within the HMQ population.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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A. m. crassus. In an unpublished M.S. thesis, Ludtke (2008) suggested the resurrection of the genus *Diplobunops* on the basis of a rostral constriction at P2, a large C1–P1 diastema, and several tooth characteristics that link the genus with *Protoreodon* but separate it from *Agriochoerus*. Ludtke (2008) assigned the HMQ specimens to *D. crassus*, a species he separated from *Agriochoerus* by the rostral constriction at P2 and several other tooth characteristics, and characterized it as larger than *D. matthewi*. Here we reevaluate that assignment based on a reexamination of the sample.

### METHODS

All measurements were taken using Mitutoyo Absolute Digital digital calipers. All measurements were taken to produce the maximum value. To quantify intraoperator variability, five UOMNH specimens were remeasured three times each, with an hour between measurements. In addition to the use of original drawings and descriptions, we examined photographs of specimens of *D. crassus* and *D. matthewi* for potential new diagnostic characters.

### Terminology and Abbreviations

Our dental nomenclature follows Bärmann and Rössner (2011), save for ‘paraconule,’ ‘posterolingual conule,’ and ‘pre-entostylid,’ which describe features not discussed in that paper (Fig. 1). The posterolingual conule (hypoconule of Ludtke, 2008 and Lander and Hanson, 2006) describes an accessory cusp on the posterior side of the lingual cone of the fourth premolar. Pre-entostylid is used here to describe the stylid on the anterior of the entoconid, which is separated from the metastylid.

‘Oreodont’ is used here as a general term for any member of superfamiley Merycoidontidae, whereas ‘agriochoerid oreodont’ specifies a member of the family Agriochoeridae. Our specimens come from the University of Oregon’s Museum of Natural and Cultural History (UOMNH) and the University of California’s Museum of Paleontology (UCMP). For UCMP numbers, the locality number is attached and comes first, the catalog number second; for UOMNH numbers, the catalog number comes first and the locality number second.

### SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Superfamily MERYCOIDODONTOIDEA Hay, 1902
Family AGRIOCHOERIDAE Leidy, 1869
Genus *DIPLOBUNOPS* Peterson, 1919

**Type Species**—*Diplobunops matthewi* Peterson, 1919.

**Included Species**—*Diplobunops crassus* Scott, 1945; *Diplobunops kardoula* sp. nov.

**Emended Diagnosis**—Rostrum constricted at P2 and flared at the canines. No posterolingual conule on P4.

*DIPLOBUNOPS KARDOULA*, sp. nov. (Figs. 1-4)

*Diplobunops*, n. sp.: Hanson, 1996:233.
*Agriochoerinae*, new genus F, new species: Lander, 1998:409.
*Diplobunops* sp.: Retallack et al., 2000:81; Lucas et al., 2004:92.
*Agriochoerus matthewi* crassus (in part): Lander and Hanson, 2006:24, fig 3.

**Etymology**—from the Greek καρδούλα, meaning ‘little heart,’ in reference to the heart-shaped occlusal outline of the P3.

**Holotype**—UOMNH F-30334/UO 2473, skull with premolar row and associated canines.

**Paratype**—UCMP V75203/218678, skull with C1–M3 and partial, deformed basioccipitum. UCMP V75203/154600, right dentary with p1–m3.

**Referred Specimens**—UCMP V75203/154593, badly distorted skull with LP3–M3, and fractured RM1–M2; UCMP V75203/154596, partial maxilla with P1–P2; UCMP V75203/154597, right dentary with p3–m3; UCMP V75203/154601, left dentary fragment with m2 and m3; UCMP V75203/154604, right dentary with m2, m3, and some of the ramus; UCMP V75203/154605, right dentary with p4–m4; UCMP V75203/154606, cast of UWC 56943, right M1 and M2; UCMP V75203/154602, fractured left dentary with partial molar fragments; UCMP V75203/196318, well-preserved right dentary with p3–m3; UOMNH F-20430/UO 2473, left dentary fragment with m2 and m3; UOMNH F-20496/UO 2473, left dentary fragment with fragmented p4–m3; UOMNH F-20483/UO 2473, Lp1; UOMNH F-20925/UO 2473, upper canine; UOMNH F-21397/UO 2473, right maxilla section with fragmented M1–M3; UOMNH F-21427/UO 2473, left dentary section with p3–m3; UOMNH F-27687/UO 2473, laterally compressed skull with LP3–M3, and RP2–M3; UOMNH F-27688/UO 2473, frontal portion of a badly distorted skull, with an edentulous premaxilla, and fragmented LM1 and M2 and RM2 and M3; UOMNH F-27689/UO 2473, partial skull with fragmented LP4 and left molars, and nothing preserved posterior to the orbit; UOMNH F-27690/UO 2473, skull with RP3–M1, LP2, and molar fragments; UOMNH F-27691/UO 2473, left partial maxilla with P2–M1; UOMNH F-27697/UO 2473, skull with LC1–P4, and partial LM1, RP1–P4, and fragmented RM1 and M2; UOMNH F-28320/UO 2473, left maxilla with fragmented P2–M3; UOMNH F-28326/UO 2473, left dentary fragment with molar fragments; UOMNH F-28342/UO 2473, isolated LM3; UOMNH F-28324/UO 2473, right partial maxilla with M2 and M3; UOMNH F-29549/UO 2473, right partial maxilla with M2 and M3; UOMNH F-36419/UO 2473, isolated M3, broken off behind the orbit; UOMNH F-56848/UO 2473, posterior part of skull with sagittal crest and basisphenoid. The minimum number of individuals found in the quarry is 14, calculated from the number of the most common independent skeletal element: crania and independent maxilla fragments.

**Comparative Material**—We compared our material with photographs of other *Diplobunops* species from the Carnegie Museum of Natural History. *D. crassus*: CM 2967 (holotype), CM 11799; *D. matthewi*: CM 2929, CM 2974 (holotype), CM 3394, CM 6497, CM 8927, CM 9559, CM 11769, CM 11801A. We also examined plates of *D. vanhouteni* (pls. 8 and 9) from Gazin (1955).

**Occurrence**—Hancock Mammal Quarry (JDNM-13, UCMP V75203, UO 2473, UO 10775), a locality in the uppermost Clarno Formation near Fossil, Oregon; late Uintan ((Bestland et al., 1999; Lucas et al., 2004) or early Duchesnean (Hanson, 1996; Lander and Hanson, 2006), middle Eocene.

**Revised Diagnosis**—The rostrum is constricted at P2, as in all species of *Diplobunops* but unlike *Agriochoerus*. The P3 differs from *D. crassus* and *D. matthewi* in having a mesiolingual cone that is adjusted posteriorly and in possessing strongly pronounced anterior and posterior styles that give it a heart-shaped appearance. The P4 differs from *D. matthewi* and *D. crassus* in having fully separated anterolabial and posterolabial conules, but differs from *Agriochoerus* in lacking a posterolingual conule. The upper molars differ from other
species of *Diplobunops* and *Protoreodon* in lacking paracoonules. The upper molars differ from *D. crassus* and *D. matthewi* in possessing very large, rounded meso- and metastyles. Unlike in *D. crassus*, the symphysis of the mandible does not jut anteriorly, and the p1 crown is not bent to labial. The lower molars differ from those of other species of *Diplobunops* in lacking lingual cingulids and having small metastylids and parastylids.

**Description**

Non-dental characteristics are distorted or lost in many specimens, but the basisphenoid is marginally raised and not
flattened, and the dome of the skull is heavily arched. Specimens UOMNH F-27697 and UCMP 218678 preserve auditory bullae that are oval in outline, rounded, and dorsoventrally small (Supplementary Data, Table S1). All specimens with parietals possess clear sagittal crests. On UOMNH F-56848 and UOMNH F-27690, these crests flare out into an occipital shield. The posterior edge of the occipital shield is fragmented in both specimens, leaving its extent unknown. Specimen UOMNH F-27688 has ‘D’-shaped palatine foramina that are 17.40 mm long anteroposteriorly and 10.62 mm wide mediolaterally. The flat sides of the foramina are arranged lingually.

No specimens have teeth or premaxillae anterior to C1, precluding description of incisors. The zygomatic arches and postorbital bar were not preserved in any specimens.

The canines are enlarged and ‘D’-shaped in occlusal view, with a flat mesial surface. Their height is highly variable, possibly indicative of sexual dimorphism. The rostrum is expanded at the canines and constricted again at P2.

The P1 is bladelike and shaped like an equilateral triangle in mesial view in specimens without wear. It is oval in occlusal view, and the anterior end is bent to labial, putting it out of alignment with the tooth row but maintaining alignment with the constricted muzzle. Although a small diastema between P1 and P2 is typical in our sample, one adult specimen (UOMNH F-27967) lacks this diastema, demonstrating some variability in this character. The P2 possesses a weak mesolingual cone, giving it a triangular shape unlike the rectangular P2 of D. crassus (Scott, 1945; Ludtke, 2008). The P3 has strong anterior and posterior styles and is heart-shaped in occlusal view. There are no crests connecting the mesolabial cone to the mesolingual cone on P3. The P3 mesolingual cone is posterior to the centerline of the tooth.

The P4 has separate antero- and posterolabial cones but lacks a posterolabial conule (Figs. 1A, B and 2A). The anterolabial and posterolabial cones of P4 are close together, so that greater tooth wear gives them the appearance of a partial, rather than full split. This difference can be seen in UOMNH F-27697 (Fig. 1) or UCMP V75203/218678 (Fig. S1) specimens with demonstrable P4 wear, compared with UOMNH F-30334, which displays two less worn cones (Fig. 2). The P4 is an isosceles triangle in outline when viewed from the occlusal surface, with the mesolingual cone lying almost directly on or slightly anterior to the centerline of the anterolabial and posterolabial cones. The P4 has an accessory crest on the mesolingual cone that becomes more prominent with wear.

As in all oreodonts, the molars are incompletely selenodont, the postprotoconid (posterolabial cone of Ludtke, 2008) and premetaconid crista (the anterior arm of the metacrista of Ludtke, 2008) do not form a loph (Ludtke, 2008; Thorpe, 1937). Paraconules are not present. A cingulum of variable strength is present on the anterior side of the protocone. A cingulum of comparable size is also present on the metaconule of some individuals (Table 1). A cingulum on the anterior face of the protocone of the molars is always present, although not always strongly expressed. Additionally, cingula on the posterior edge of the metaconule and protocone and on the anterior edge of the metacone are sometimes present. No cingula were found on the labial edge of the upper molars.

The M1 is distinctly smaller than M2 and M3 in both width and length, whereas M2 is only slightly smaller than M3 (Table 2; Fig. 1A, B). The M1 and M2 have large, well-rounded para- and mesostyles, but the metastyle slopes lingually and mesially. The M3 has large, well-rounded para-, meso-, and metastyles, but no prominent labial cingulum overlapping the external fossettes as seen in D. crassus (Scott, 1945). On all three molars, the para- and mesostyles protrude so much that we took no labiolingual measurements on specimens without them to prevent underestimation.

Observations of the cingulum on the anterior side (A) of the protocone, and of the cingulum dam between the protocone and metacone, or of the posterior (P) side of the protocone in P4 were recorded. 0, not visible; 1, visible but not prominent; 2, prominent, but not shelf-like; 3, shelf-like and very prominent.

Emery et al.—Reassessment of the HMQ agriochoerid (e1041970-4)
TABLE 2. Measurements of the upper teeth (in millimeters).

| Collection | Specimen no. | Tooth | Ap | L  | H  |
|------------|--------------|-------|----|----|----|
| UCMP       | 154593       | LM1   | 13.08 |    |    |
| UCMP       | 154593       | LM2   | 15.96 |    |    |
| UCMP       | 154593       | LM3   | 17.98 |    |    |
| UCMP       | 154593       | LP3   | 11.29 | 9.54 |    |
| UCMP       | 154593       | LP4   | 9.62  | 12.44 |    |
| UCMP       | 154593       | RM1   | 13.49 |    |    |
| UCMP       | 154593       | RM2   | 14.7  |    |    |
| UCMP       | 154593       | RM3   | 15.59 |    |    |
| UCMP       | 154594       | LM3   | 15.29 |    |    |
| UCMP       | 154594       | RM1   | 12.34 |    |    |
| UCMP       | 154594       | RM2   | 13.8  |    |    |
| UCMP       | 154594       | RM3   | 15.35 | 18.12 |    |
| UCMP       | 154594       | RP2   | 9.39  | 3.83 |    |
| UCMP       | 154594       | RP3   | 10.69 | 8.43 |    |
| UCMP       | 154594       | RP4   | 9.84  |    |    |
| UCMP       | 154596       | LP1   | 10.21 | 5.22 |    |
| UCMP       | 154596       | LP2   | 10.5  | 5.69 |    |
| UOMNH      | F-28320      | LP4   | 9.81  | 12.09 |    |
| UOMNH      | F-28320      | LP3   | 9.37  | 10.11 |    |
| UOMNH      | F-28320      | LM2   | 12.91 | 15.81 |    |
| UOMNH      | F-28320      | LM1   | 11.08 |    |    |
| UOMNH      | F-27697      | LP4   | 12.79 | 10.93 |    |
| UOMNH      | F-27697      | LP3   | 10.31 | 8.97 |    |
| UOMNH      | F-27697      | LM3   | 16.53 | 19.73 |    |
| UOMNH      | F-27697      | LM2   | 15.63 | 17.55 |    |
| UOMNH      | F-27697      | RM3   | 15.35 | 17.55 |    |
| UOMNH      | F-27697      | RM2   | 15.13 | 17.98 |    |
| UOMNH      | F-27697      | RM1   | 14.7  | 17.32 |    |
| UOMNH      | F-27687      | RC1   | 12.56 | 13.23 | 38.04 |
| UOMNH      | F-27687      | LM3   | 15.32 |    |    |
| UOMNH      | F-27687      | LM2   | 15.23 |    |    |
| UOMNH      | F-27687      | LM1   | 12.78 |    |    |
| UOMNH      | F-27687      | LM3   | 15.32 |    |    |
| UOMNH      | F-27687      | LP4   | 10.13 |    |    |
| UOMNH      | F-27687      | RP3   | 10.65 | 10.13 |    |
| UOMNH      | F-28320      | LM1   | 11.08 |    |    |
| UOMNH      | F-28320      | LM2   | 12.91 | 15.81 |    |
| UOMNH      | F-28320      | LP3   | 9.37  | 10.11 |    |
| UOMNH      | F-28320      | RP3   | 10.65 | 10.13 |    |
| UOMNH      | F-28342      | RM3   | 16.89 | 20.38 |    |
| UOMNH      | F-29549      | RM2   | 15.13 | 17.98 |    |
| UOMNH      | F-29549      | RM1   | 14.7  | 17.32 |    |
| UMC        | 65943        | RM1   | 12.27 |    |    |
| UMC        | 65943        | RM2   | 15.07 | 17.24 |    |
| UMC        | 65943        | RM3   | 9.34  | 9.8  |    |
| UMC        | 65943        | RP4   | 9.72  |    |    |

Abbreviations: Ap, anterior-posterior (length); H, crown height; Lb, labiolingual (width); L, left; M, molar; P, premolar; R, right.

DISCUSSION

One of the key qualitative characters of the HMQ agriochorid is the split labial cone of the P4, often referred to as the level of ‘molarity’ (Lander, 1998; Lander and Hanson, 2006). Lander (2006) described the P4 labial cone of the HMQ agriochorid as minimally split. All of our specimens show two complete P4 labial cones. Theodor (1999) suggested that many of the apparently polymorphic states of Protoreodon species (including the splitting of the P4 labial cone) resulted from grouping species from different stratigraphic levels. Her examination of P. walshi showed no such variability (Theodor, 1999). It is likely that the previously recognized variability of this character in the HMQ agriochorid came from examining it together with specimens from other localities. Similarly, our examination of the material revealed no paracune with any of the molars of the HMQ agriochorid. We suspect that the detection of the paracune in Lander and Hanson (2006) was also a consequence of combining specimens from more than one locality into a single species, misinterpreting what we regard as between-species variability in this character.

Lander and Hanson (2006) previously grouped the HMQ agriochorid with two specimens of A. m. crassus (Carnegie Museum of Natural History specimen 2967 and Texas Memorial Museum specimen 42554-6), providing estimated measurements of the P1–M3 and P2–M3 tooth row of the HMQ specimens as additional support for subspecies status. We subjected the
measurements provided in Lander and Hanson (2006) to an F-test and found the difference in variances between the HMQ agriochoerid and other A. m. crassus specimens to be significant at $\alpha = 0.05$. Consequently, unable to pool the variances in the two groups, we used Welch’s approximate t-test for differences between the distribution of tooth row lengths of HMQ specimens and the other individuals of A. m. crassus (Welch, 1947). We found a significant difference between their means as well, allowing us to reject the null hypothesis of a single source population ($P < 0.005$ for both P1–M3 and P2–M3 tooth row comparisons). Although not conclusive evidence for two species, this significant difference means that size alone indicates that these two samples are substantially different. This quantitative difference is particularly important when placed in the context of the additional morphological differences between the HMQ samples and other specimens assigned to A. m. crassus discussed in the Systematic Paleontology section of this paper.

**Trait Variability**

Lander and Hanson (2006) noted medial displacement of the P1 in the HMQ specimens (Fig. 3B). This P1 displacement results from the P1–P2 constriction of the muzzle, which is a diagnostic character of Diplobunops. Consequently, these two characters cannot be considered independent and should not be coded separately in future phylogenetic analyses. Additionally, rotation of teeth, particularly the premolars, is a well-documented defect among modern artiodactyl species and is typically identical on both sides (Miles et al., 1990). Because of both the character linkage with muzzle constriction and the polymorphism of this character in modern artiodactyls, we reject the use of P1 displacement for diagnosing any agriochoerid taxa.

Cingula and cingulids are frequently referred to in descriptions and occasionally used for formal diagnosis within both families of oreodonts (Lander, 1998; Ludtke, 2006, 2008). The lingual cingulids of the lower molars described and figured in Scott’s (1945) description of D. crassus were not present in our specimens, so we examined other cingula on upper premolars and molars for their potential as diagnostic characters. Within the small HMQ sample present at the UOMNH, we found that the cingula of the upper molars were variably expressed, their prominence ranging between large enough to form a small shelf to only faintly visible (Fig. 4; Table 1). Specimen UOMNH F-27687 possessed all three of these cingula and had the strongest relative expression of all our specimens, implying that there may be a single developmental regulatory mechanism for the cingula in the upper molars. In anthracotheres, the cingula and the styles of the teeth show greater morphological variability than other aspects of the tooth (Ducrocq et al., 1995). The variability in the HMQ agriochoerid sample suggests that relative strength of cingula or cingulid expression should not be used for diagnosis in oreodonts, but presence or absence of certain cingula may be consistent enough for future taxonomic use.

**Genus Assignment**

The diagnosis of genera within the Agriochoeridae has been heavily debated, and specimens (and species) are regularly reassigned between the three named genera (Agriochoerus, Diplobunops, and Protoreodon) and a variable number of unnamed genera (Lander, 1998; Lander and Hanson, 2006; Ludtke, 2008). Our specimens display characters previously considered diagnostic of two of the three named genera, Diplobunops and Agriochoerus, as summarized in Table 3. Of 12 characters commonly used to diagnose agriochoerid genera, the HMQ specimens share seven with Diplobunops, five with Agriochoerus, and one with both (as the P1–P2 diastema is variably expressed in this sample). The only truly discrete morphologies between these two genera that are clearly presented in our specimens are the expanded rostrum and the split P4 labial cone without a P4 postero-lingual conule—both characteristics that place the HMQ...
TABLE 3. Character matrix for genus-level characters of *Diplobunops* and *Agriochoerus*, as described in Ludtke (2008), Lander and Hanson (2006), and Theodor (1999).

| Character                        | Protoreodon | Agriochoerus | Diplobunops | HMQ agriochoere |
|----------------------------------|-------------|--------------|-------------|-----------------|
| Comparatively small P4 AP        | 1/0         | 0            | 1           | 1               |
| P4 posterolingual cone            | 0           | 1            | 0           | 0               |
| Expanded rostrum                 | 0           | 0            | 0           | 0               |
| Weak P3 lingual cone             | 0           | 0            | 0           | 0               |
| Similarly sized M2 and M3        | 1/0         | 1            | 1           | 1               |
| Inflated molar styles            | 0           | 0            | 0           | 0               |
| Rounded meta- and parastylies    | 0           | 1            | 0           | 0               |
| Large P1–P2 diastema             | 1           | 0            | 1           | 1/0             |
| Distinct p4 entocodon            | 0           | 1            | 0           | 0               |
| Paraconules                      | 0           | 0            | 1           | 0               |
| Split P4 labial cone             | 1/0         | 1            | 0           | 0               |
| Strong External Ribs             | 1           | 0            | 0           | 0               |
| Circular p3 cristid connection    | 0           | 1            | 1           | 1               |

1, character is present; 0, character is absent; 1/0, character is variably absent or present.

specimens with *Diplobunops*, even as the continuous characters suggest *Agriochoerus*.

*Diplobunops* is known from the late Uintan to the early Duchesnean, whereas *Agriochoerus* is known from the middle Duchesnean to late early Arikareean (Lucas et al., 2004; Ludtke, 2008). Lander (1998), Lander and Hanson (2006), and Ludtke (2008) have proposed that *Diplobunops* represents an early grade phylogenetically below *Agriochoerus*, a hypothesis supported by the affinities of the HMQ sample with both genera. *Protoreodon* also shares many genus-level diagnostic characteristics with both *Agriochoerus* and *Diplobunops*, leaving it unclear whether the HMQ specimens represent an evolutionary transition or taxonomic confusion between *Agriochoerus* and *Diplobunops*.

**Possible Sexual Dimorphism**

Specimen UOMNH F-27967 displays several characters unique among the HMQ agriochoerid specimens: it lacks a P1–P2 diastema and has a canine that is wider labiolingually but shorter in height than other canines measured (Table 2). The distance between the canine and the first premolar (13.77 mm) is within 2 standard deviations of the mean of the HMQ sample (12.28 [mean] ± 0.88 [SD] mm), whereas the size of each individual tooth is within 1 standard deviation. Sexual dimorphism of the diastema and canine has been previously hypothesized in other oreodonts (Schultz and Falkenbach, 1968; Stevens and Stevens, 1996). Cranial sutures are not preserved well in any of the HMQ specimens, leaving only tooth eruption and wear for ontogenetic age estimates. The molars in UOMNH F-27967 are fully erupted but show very little wear, indicating that this specimen is a young adult. Without a larger sample size, it is impossible to tell whether the reduced size of these characters in UOMNH F-27967 are expressions of sexual dimorphism or individual variability.

**CONCLUSIONS**

The distinct characters we recognize as diagnostic of a new HMQ species were either overlooked or considered polymorphic traits by previous workers. When examined as a unique population, the diagnostic characters of the HMQ agriochoerid are monomorphic, numerous in type, and together show no overlap with known species of agriochoerids. Therefore, we recognize the HMQ agriochoerid as a new species of *Diplobunops*, characterized by fully split labial cones of the P4 without posterolingual conule, triangular P2, heart-shaped P3 with a posterolingual cone, large, rounded styles on the molars, no paraconules, a mandibular symphysis nearly perpendicular to the tooth row, and no lingual cingulids on the lower molars.

Many of the characters used in the past to diagnose agriochoerid taxa are variable within the HMQ agriochoerid, including molar ribs and the P1–P2 diastema. The variation and continuous nature of these characters makes them difficult to use effectively and consistently between workers. Character variability is an important consideration when assigning specimens to taxa at any level. Oreodont taxonomy has historically been plagued by extensive reassignment of specimens between and among subspecies-, species-, genus-, and family-level designations, with different researchers lumping, splitting, or reassigning depending on which characters they found important (Cope, 1884; Thorpe, 1937; Schultz and Falkenbach, 1968; Stevens and Stevens, 1996; Lander, 1998; Ludtke, 2008). Because the HMQ sample is dominated by cranial material and established diagnostic characters for agriochoerids are predominantly cranial, we have not described associated postcranial material here. However, postcranial material could be an important reservoir for additional phylogenetic characters (Klein et al., 2010; Louys et al., 2012), so their study at the HMQ and other oreodont-rich sites should be a priority for future work.

Oreodonts have no modern descendants but are commonly considered analogous to pigs, sheep, or camels (Peterson, 1919; Thorpe, 1937; Scott, 1945; Schultz and Falkenbach, 1968; Stevens and Stevens, 1996; Lander, 1998; Ludtke, 2008). To truly understand the appropriate range of character variability within an oreodont species, greater consideration needs to be paid to modern analogues and how they inform our character choice. Empirical evaluation of agriochoerid taxonomic characters, combined with a thorough examination of analogous and homologous characters in modern artiodactyls, will clarify the use of these characters in taxon diagnosis.

We found that many of the characters previously used to diagnose genera of agriochoerids were not unique to a particular genus, indicating a need to reevaluate the distribution of characters among agriochoerid genera. The only currently available phylogeny of agriochoerids (Ludtke, 2008) found that Agriochoeridae was not monophyletic when *Protoreodon* and *Diplobunops* were included, further supporting a needed revision of diagnostic characters in this clade. *Diplobunops kardoula* could represent an evolutionarily transitional form between *Agriochoerus* and *Diplobunops*, although more work on its evolutionary affinities will be required to test this hypothesis. A reassessment of the phylogenetic relationships of agriochoerid oreodonts is outside of the scope of this paper, but remains a necessity before the evolutionary place of the HMQ specimens will be fully understood.

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