

A NEW FOSSIL FROG FROM THE UPPER CRETACEOUS JUDITH RIVER FORMATION OF MONTANA

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Fossil microvertebrate localities from the Judith River Formation of western North America have been examined extensively over the past quarter-century. Early taxonomic studies by Sahni (1972) and Case (1978) have been followed by analyses focusing on broad paleoecological issues, such as preservational biases (Eberth, 1990; Fiorillo, 1991; Rogers, 1995; Blob and Fiorillo, 1996; Blob, 1997) and patterns of taxonomic change (Dodson, 1983, 1987; Fiorillo, 1989; Brinkman, 1990). To date, most accounts of the Judith River fauna have concentrated on the taxonomy and diversity of dinosaurs (e.g., Dodson, 1986; Fiorillo, 1987; Currie et al., 1990; Fiorillo and Currie, 1994; Brinkman et al., 1998; Ryan and Currie, 1998), mammals (e.g., Sahni, 1972; Montellano, 1992; Carrano et al., 1995, 1997), or fishes (e.g., Case, 1978; Brinkman, 1990; Eberth and Brinkman, 1997). In contrast, the smaller herpetofauna of the Judith River Formation has received little detailed attention since Sahni's (1972) initial study of the type area.

Over two recent field seasons, intensive resampling of the vertebrate microfauna from the Judith River Formation type area by crews from the University of Chicago and the Field Museum of Natural History has yielded thousands of herpetofaunal fossils. This new sample reflects a diverse community of abundant small amphibians and reptiles. Among the herpetofaunal specimens are three unusual anuran ilia, recovered from two separate localities, that we describe in this report and refer to a new genus and species.

Fossil frogs have been reported from numerous North American Cretaceous localities (e.g., Estes, 1964; Brinkman, 1990), but relatively few distinct taxa have been recognized formally (Estes, 1969; Fox, 1976; Estes and Sanchíz, 1982). This is due, in part, to the fragmentary and disarticulated nature of most specimens from microvertebrate collections. Sahni (1972), for instance, declined to formally designate new taxa for any of the three morphotypes of isolated anuran ilia that he collected from the Judith River Formation type area. However, in spite of potential difficulties associated with taxonomic characters derived from anuran ilia (Asher, 1995), the specimens that we describe warrant recognition as a new taxon, as they are clearly distinguishable from other known anurans and possess at least one autapomorphy.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; UC, University of Chicago.

GEOLOGIC SETTING

The Upper Cretaceous (Campanian) Judith River Formation appears throughout much of Montana, Alberta, and northern Wyoming. The type area is located in the Missouri Breaks along the Missouri River in north-central Montana. In the type area, the ~180 m thick Judith River section comprises the distal reaches of a single eastward-thinning clastic tongue of alluvial, coastal plain, and shallow marine sediments that accumulated during regression of the Claggett Sea and subsequent transgression of the Bearpaw Sea. The formation consists of silty claystones, siltstones, and fine- to medium-grained sandstones of fluvial, tidal, and shallow marine origin (Rogers, 1995, 1998).

The anuran ilia described here were collected from two separate lo-

calities, UC-913 and UC-8303 (Fig. 1; see Rogers, 1995 for further locality data). The UC-8303 assemblage is preserved in carbonaceous lacustrine facies that accumulated within a few kilometers of the western paleoshoreline of the Cretaceous Interior Sea during the Bearpaw transgression (Rogers, 1994, 1995, 1998). The UC-913 assemblage is preserved in a channel-lag deposit, but its stratigraphic position with respect to transgressive and regressive deposits is uncertain (Rogers, 1995).

SYSTEMATIC PALEONTOLOGY

SALIENTA Laurenti, 1768

ANURA Rafinesque, 1815

NEZPERCIUS DODSONI, gen. et sp. nov.

(Figs. 2, 3)

Holotype—FMNH PR 2078 (Fig. 2): small, well-preserved right ilium with shaft broken anteriorly, most of subacetabular expansion missing, and small fragments missing from the lateral and medial aspects of the ilioischial junction.

Referred Specimens—FMNH PR 2079 (Fig. 3A): large right ilium missing almost entire shaft; FMNH PR 2080 (Fig. 3B): left ilium with shaft broken anteriorly.

Locality and Horizon—Holotype and FMNH PR 2079 from locality UC-913; FMNH PR 2080 from UC-8303 (Rogers, 1995). Judith River Formation (type area). North-central Montana, USA, T23N, R22E (Baker Monument Quadrangle).

Age—Late Cretaceous (Campanian).

Etymology—Genus name honors the Nez Percé tribe. The type locality for the genus is within sight of Cow Island, where the Nez Percé crossed the Missouri River as they were pursued toward Canada in 1877. Species name honors Peter Dodson for his contributions to paleoecological research in the Judith River Formation.

Diagnosis—A frog that differs from all other anurans in possessing a pronounced, anteroposteriorly elongate tuberosity on the ventrolateral aspect of the ilial shaft, just anterior to the preacetabular zone, that does not contact the dorsal margin of the ilial shaft but contacts or nearly contacts the ventral margin of the shaft. Relative to other frogs of Judithian age from western North America, it differs from *Palaebatrachus* in possessing a semi-circular (rather than "bell-shaped") acetabulum, possessing a subacetabular expansion, and lacking interiliac synchondrosis. It differs from *Eopelobates* in possessing a large tuberosity on the ilial shaft and in lacking a spiral groove at the base of the ilial shaft.

Description—Unless otherwise noted, description is made with primary reference to the holotype. The holotype and FMNH PR 2080 are from considerably smaller individuals than FMNH PR 2079 and might represent juveniles or subadults: FMNH PR 2078 measures under 1.5 mm along the posterior margin of the acetabular region, whereas FMNH PR 2080 and FMNH PR 2079 measure 2.5 mm and 3.5 mm, respectively, along the same length. Based on a regression equation reported by Esteban et al. (1995) relating the posterior width of the acetabulum to body mass in the frog *Rana temporaria*, these specimens would have belonged to animals with body masses of 1 g (FMNH PR 2078), 15 g (FMNH PR 2080), and 29 g (FMNH PR 2079). This regression may introduce error into mass estimates for non-ranid species; however, such

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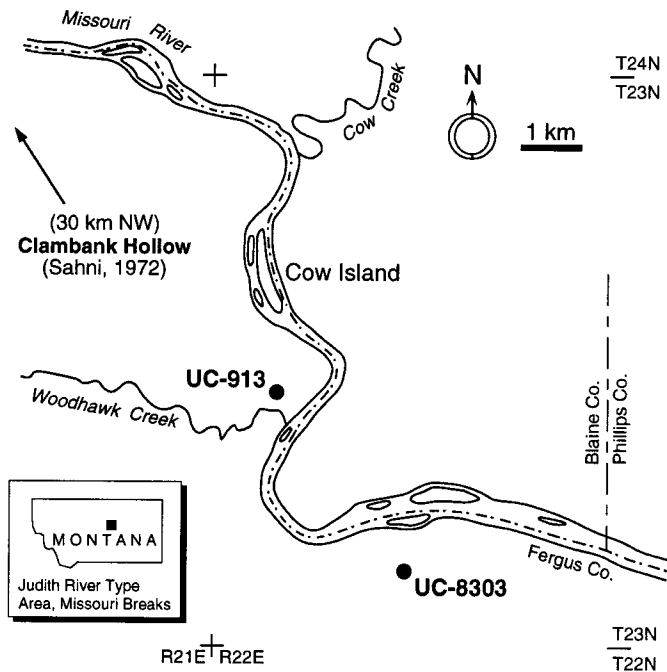


FIGURE 1. Map of the Missouri Breaks, Montana (USA), indicating locations of the quarries from which specimens of *Nezpercius dodsoni* were collected.

a range of postmetamorphic growth is not unusual among extant frogs (e.g., Durham and Bennett, 1963; Espinoza, 2000), suggesting that it is reasonable for specimens of these sizes to belong to a single species.

The ilial shaft is tubular and nearly circular in cross-section, lacking a dorsal crest (Figs. 2A–D, 3B). The unique feature of these specimens, the ventrolateral tuberosity, occurs at the base of the shaft near the acetabulum but is distinctly separated from the anterior acetabular margin (Figs. 2A, B, D, 3; see Appendix 1 for list of comparative material examined). In lateral view (Figs. 2A, 3), the dorsal margin of the tuberosity is situated approximately midway between the dorsal and ventral edges of the shaft. It is anteroposteriorly elongate, forming a smooth, ovoid bump approximately twice as long anteroposteriorly as dorsoventrally. The anteroposterior length of the tuberosity is just greater than one half of the anteroposterior length of the acetabulum (measured from the juncture with the other pelvic elements to the anterior apex of the acetabular margin). The tuberosity is more strongly developed closer to the acetabulum, gradually sloping away distally until it merges into the shaft.

Supra- and subacetabular expansions are subequal in size and small relative to the acetabular fossa (Fig. 3). Dorsal and ventral flaring of these expansions are negligible. The acetabulum projects strongly from the surface of the surrounding region, but this feature becomes less pronounced posteriorly (Fig. 2B, D). The acetabular fossa fills most of the acetabular region of the ilium and is slightly shorter anteroposteriorly than dorsoventrally (Figs. 2A, 3). The fossa is somewhat rugose in all the specimens, suggesting a cartilaginous component to the surface. The dorsal prominence is roughened and slightly raised (Figs. 2A, 3). There is no distinct tubercle on the dorsal aspect of the shaft (Figs. 2A, B, D, 3B). The sutural surface of the posterior ilium is strongly concave and rugose, indicating a cartilaginous attachment to the other pelvic elements (Fig. 2E). The medial aspect of the acetabular region is flat and essentially featureless (Fig. 2C).

DISCUSSION

The presence of a unique, discrete, and easily identifiable feature on multiple fossil specimens from two Judithian localities suggests that the designation of a new taxon is warranted for the anuran ilia described in this report. Although frogs are common components of Judithian faunas, their diversity has not been well documented. In a census of 25 microvertebrate sites from the Judith River Formation of Dinosaur Pro-

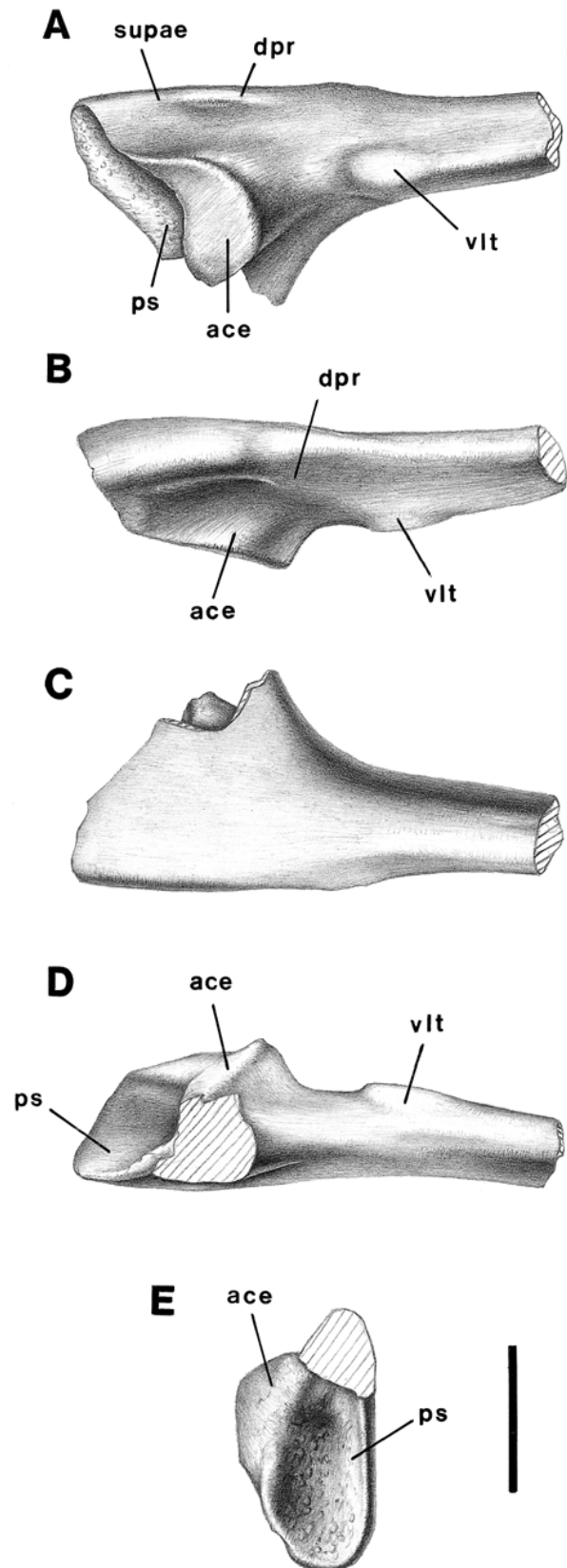


FIGURE 2. Holotype of *Nezpercius dodsoni*, FMNH PR 2078, right ilium. **A**, lateral view; **B**, dorsal view; **C**, medial view; **D**, ventral view; **E**, view of surface for articulation with ischium. **Abbreviations:** ace, acetabulum; dpr, dorsal prominence; ps, posterior surface; supae, supraacetabular expansion; vlt, ventrolateral tuberosity. Scale bar equals 1 mm.

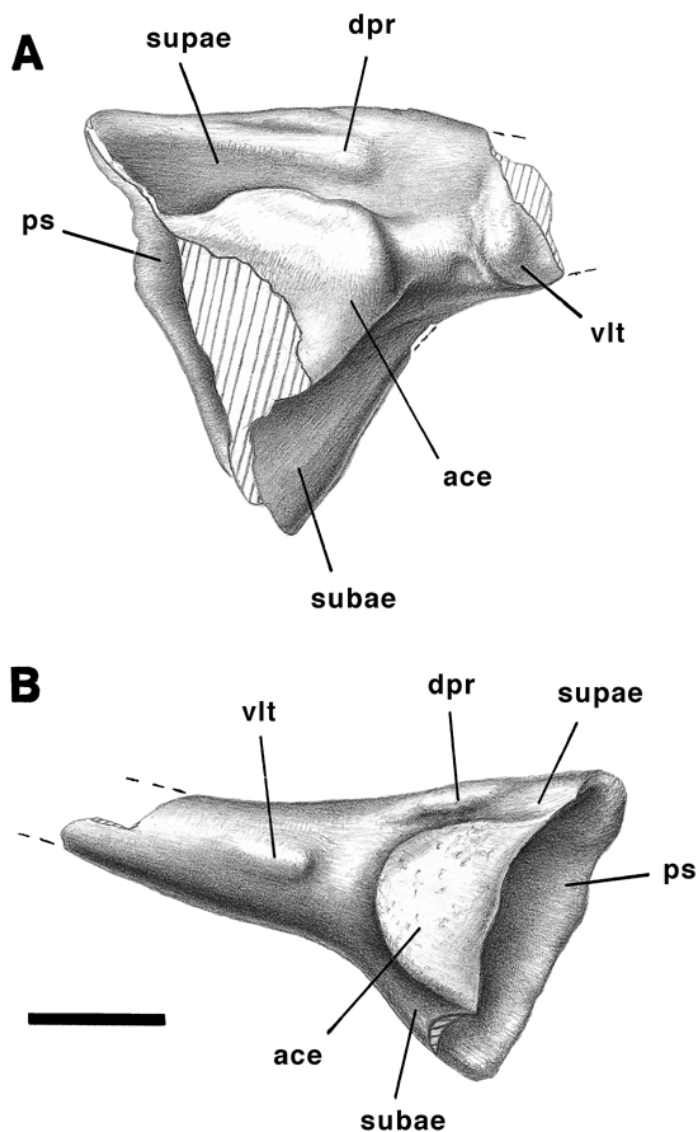


FIGURE 3. Referred specimens of *Nezipercius dodsoni*. **A**, lateral view of FMNH PR 2079, right ilium; **B**, lateral view of FMNH PR 2080, left ilium. **Abbreviations:** subae, subacetabular expansion; others as in Figure 2. Scale bar equals 1 mm.

vincial Park in Alberta, Brinkman (1990) found that frogs averaged 3.1% of the fauna and accounted for as much as 9.5% in one locality (BB 98). However, Bryant (1989) reports that only two genera are known from Judithian age deposits: the rare palaeobatrachid *Palaeobatrachus* and the much more common pelobatid *Eopelobates*. In his examination of the type area microfauna, Sahni (1972) reported three anuran maxillary and three anuran humeral morphotypes (all six referred to discoglossids), as well as three ilial morphotypes (two referred to discoglossids, one to pelobatids). Sahni (1972) found no features on these elements sufficient to allow their diagnosis below the family level but, based on his family attributions, at least four distinct taxa (three discoglossids and one pelobatid) appear to be represented. However, the number of amphibian specimens in Sahni's collection is small; larger faunal samples from the Judith River Formation type area could recover many additional distinct anuran taxa. Even with the recognition of *Nezipercius*, the diversity of named anuran taxa remains lower in the Judithian of western North America (three species) than in the succeeding Lancian (five species: Fox, 1976; Estes and Sanchíz, 1982; Bryant, 1989), but it is difficult to ascribe significance to this difference considering how few species have been recognized. To a large extent, the low anuran diversity of the Judithian and Lancian might be an artifact

of the difficulties inherent in identifying diagnostic characters on the fragmentary material that represents the bulk of herpetofaunal specimens from these intervals. For instance, it is possible that an unnamed humerus or maxilla morphotype described by Sahni (1972) could belong to *Nezipercius*; however, typical modes of both fossil accumulation and collection at microvertebrate localities impede the association of isolated elements.

It is not clear whether the ventrolateral tuberosity on the ilium of *Nezipercius* corresponds to the dorsal tubercle found on the ilium of many other frog species. A second tubercle is not present on the dorsal margin of the ilium of *Nezipercius*. It is possible that the "dorsal tubercle" was lost (or never present) in *Nezipercius* and that the ventrolateral tuberosity represents a completely novel feature, but it is also possible that a formerly "dorsal" tubercle migrated to the ventrolateral aspect of the ilium in *Nezipercius*. Tyler (1976) and Estes and Sanchíz (1982) note considerable variation in the form and location of the dorsal tubercle among extant Australian frogs and extinct palaeobatrachid frogs, respectively, but the range of variation that these authors discuss does not encompass complete isolation of the tubercle from the dorsal aspect of the ilium. However, the low, dorsal excrescence on the ilial shaft of the Jurassic frog *Prosaliris bitis* reaches far ventrally and overlaps the area occupied by the ventrolateral tuberosity of *Nezipercius* (Shubin and Jenkins, 1995; Jenkins and Shubin, 1998). Thus, interpretation of the ventrolateral tuberosity of *Nezipercius* as a migrant "dorsal" tubercle may be justifiable. In living anurans, the dorsal tubercle is associated with the origin of the *M. glutaesus magnus*, a muscle that inserts on the cranial aspect of the proximal tibia and acts to protract the leg and extend the knee (Ritland, 1955; Dunlap, 1960; Tyler, 1976; Estes and Sanchíz, 1982; Duellman and Trueb, 1986). If the origin of *M. glutaesus magnus* was associated with the ventrolateral tuberosity in *Nezipercius*, the anterior displacement of its origin from the acetabulum would have provided a long moment arm (and increased mechanical advantage) for leg protraction relative to frogs with a tubercle in the usual posterodorsal location.

It is difficult to evaluate the relationships of *Nezipercius* to other frogs. Though the anuran ilium can be a valuable source of phylogenetic data (e.g., Cannatella, 1985), as an isolated element it is often insufficient to allow referral of a specimen to a particular clade. *Nezipercius* exhibits none of the derived ilial features described by Cannatella (1985) in his cladistic analysis of archaebatrachian frogs (sensu Ford and Cannatella, 1993). Furthermore, many ilial traits that have been used previously to assign fossil specimens to particular families might actually represent primitive character states. For instance, Rage (1974) and Evans and Milner (1993) note that pelobatoids can be characterized by ilia lacking both a dorsal tuberosity and a dorsal bony crest on the shaft. However, the dorsal tuberosity and bony crest are also absent in *Ascaphus*, *Leiopelma*, and the Bombinatoridae, the three outgroups to all other living frogs and three of the four outgroups to the clade containing pelobatoids (Cannatella, 1985; Ford and Cannatella, 1993; Green and Cannatella, 1993). They are also absent from the Jurassic frog *Notobatrachus* (Reig, 1957; Estes and Reig, 1973). Absences in these taxa suggest that the lack of these traits might not be diagnostic for pelobatoids, but rather retentions of ancestral conditions. Similarly, Asher (1995) noted that an enlarged supraacetabular process, supposedly diagnostic for discoglossids, can be observed in at least four other frog families.

These examples underscore a more general problem: the lack of a cladistic appraisal of the evolution of the anuran pelvis that clarifies the distribution of character states and provides insight into which states represent diagnostic features of particular lineages. The ilium of *Nezipercius* does not possess features which unquestionably diagnose membership in a recognized clade of frogs, such as a lateral crest on the ilial shaft (Pipidae: Cannatella, 1985), a spiral groove at the base of the shaft (Pelobatoidea: Henrici, 1994), or ventral displacement of the acetabulum beyond the ventral margin of the subacetabular expansion (Palaeobatrachidae: Estes and Sanchíz, 1982). As a result, although *N. dodsoni* can be recognized as a species distinct from other anurans, formal assignment of *Nezipercius* to a specific anuran clade must await more complete materials and further analysis of morphologic evolution in the anuran pelvis.

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- numbers are FMNH specimens). None of the taxa listed below, examined firsthand or through literature illustrations and descriptions, exhibited the ventrolateral tuberosity on the ilium that diagnoses *Nezpercius*. Taxonomy follows that of Ford and Cannatella (1993).
- Ascaphidae: *Ascapthus truei*—166510; Leiopelmatidae: *Leiopelma hochstetteri*—51692; Bombinatoridae: Clarke (1987); Discoglossidae: Estes (1969), Estes and Sanchíz (1982), Evans et al. (1990); Pelobatoidae: *Megaphrys stejneri*—96159, *Pelobates fuscus*—1568, *Scaphiopus couchii*—6856, *Scaphiopus holbrookii*—4872, *Spea bombifrons*—216164, *Spea hammondii*, 26193, *Spea hurterii*—98016, *Scutigera mammatum*—22286; Pipoidae: *Pipa pipa*—196149, *Xenopus laevis*—22378; Bufonidae: *Atelopus zeteki*—51624, *Bufo alvarius*—26192, *Bufo americanus*—98096, *Bufo asper*—210103, *Bufo blombergi*—232740, *Bufo cognatus*—98094; Hylidae: *Hyla squirella*—196162, *Hyla versicolor*—98240, *Litoria infrafrenata*—22255, *Osteopilus septentrionalis*—229909, *Pseudacris clarkii*—27871, *Smilisca baudinii*—98170; Leptodactylidae: *Ceratophrys aurita*—51704, *Eleutheroedactylus bufoniformis*—13322, *Hylorina sylvatica*—9977, *Leptodactylus ocellatus*—9162, *Physalaemus pustulosus*—98041; Myobatrachidae: *Neobatrachus pictus*—97281; Dendrobatidae: *Dendrobates* sp.—212580; Hyperoliidae: *Cryptothylax greshoffi*—120147, *Leptopelis cinnamomeus*—80892; Microhylidae: *Gastrophryne olivacea*—104387, *Hypopachus varolosus*—99264; Ranidae: *Conraua goliath*—15980, *Limnonectes ingeri*—14316, *Pyxicephalus adspersus*—232743, *Rana blairi*—196215, *Rana pipiens*—3182; Rhacophoridae: *Polypedates leucomystax*—63745, *Rhacophorus robustus*—96729.

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APPENDIX 1

Comparisons of *Nezpercius* to extant anuran lineages were based on the following museum specimens and literature sources (all catalogue

In addition, the following anuran fossil specimens described by Sahni (1972) from the Judith River type area also were examined firsthand and found to lack a ventrolateral tuberosity on the ilium (all AMNH): 8452, 8453, 8456, 8457, 8458 (4 specimens catalogued under this number), and 8459.