

REVISION OF THE NEARCTIC *LEPIDURUS* (NOTOSTRACA)

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A B S T R A C T

Limited understanding of the morphological variation and genetics of the genus *Lepidurus* have caused confusion for workers attempting to determine North American species of this genus. In addition, preliminary culturing data suggests that food quality affects the form of structures previously used as specific characters. Morphological comparisons between *Lepidurus packardi* Simon, 1886, and the type material of *L. couesii* Packard, 1877, demonstrate that populations of *Lepidurus* occurring in the Sierra Nevada, the Cascade Mountains, and the Great Basin regions of north-eastern California and south central Oregon, previously reported as *L. couesii*, “*L. couesii*-1”, or as the “Modoc Plateau Tadpole Shrimp”, conform to the *L. packardi* morphotype. The results of my work and King and Hanner’s (1998) genetic data demonstrate the presence of a cryptic species within the *L. packardi* morphotype, described here as *Lepidurus cryptus* n. sp. Specific diagnoses and a key to North American *Lepidurus* are presented.

Lepidurus packardi Simon, 1886, has been reported as endemic to the Central Valley of California (Federal Register, 1994; King *et al.*, 1996; King, 1996; Helm, 1998; King and Hanner, 1998). However, Linder (1952) and Lynch (1972) both reported and identified *L. packardi* from outside of this region. The purpose of this paper is to correct confusion surrounding the identification and range of *L. packardi* and a taxon referred to as “*L. couesii*-1” by King and Hanner (1998), and provide a usable key and diagnoses to the North American *Lepidurus* to help prevent future identification errors.

Lepidurus packardi was originally described from “California” U.S.A. The types are apparently lost. Linder (1952) reported *L. packardi* from the California Central Valley one mile north of Davis, Yolo County and from the eastern side of the southern end of the Cascade Mountains in Lassen County. He also identified collections deposited at the U.S. National Museum of Natural History from the California Great Basin near Canby, Modoc County as *L. packardi* (NMNH 82029, 82030, 9377). Longhurst (1955) synonymized both *L. packardi* and *L. couesii* with the Eurasian *L. apus* (Linnaeus, 1756). Lynch (1972) redescribed *L. couesii* and produced a list of specific morphological characters for the genus *Lepidurus* in North America, emphasizing that both *L. packardi* and *L. couesii* are taxa distinct from each other and from

L. apus. Lynch deposited specimens at the U.S. National Museum of Natural History identified as *L. packardi* from the Great Basin Regions of south central Oregon (NMNH 138891).

In 1994 the United States Fish and Wildlife Service gave *L. packardi* protection as an endangered species (Federal Register, 1994). The U.S. Federal Register reported that *L. packardi* was known only from 18 populations in the Central Valley of California but did not mention the Linder nor the Lynch references or material.

Helm (1998) reported *L. couesii* from the east side of the Cascade Mountain ranges in Lassen County, California, and *Lepidurus* n. sp., the “Modoc Plateau Tadpole Shrimp” from two locations in Modoc County, California, citing King personal communication as his source for the shrimp’s identification. King and Hanner (1998) performed 12S rDNA and allozyme analysis of *Lepidurus* populations throughout western North America, reporting a taxon they referred to as “*L. couesii*-1” from Klamath County, Oregon, and the east side of the Cascade Mountains in Shasta and Lassen counties, California. In addition, they mentioned Linder’s Lassen County *L. packardi* material but did not comment on its implications. King and Hanner concluded that *L. couesii* populations from Manitoba, Canada, may represent a separate species from “*L. couesii*-1” in the Sierra

Nevada, the Cascade Mountains and the Great Basin regions of north eastern California and south central Oregon. Furthermore, King and Hanner (1998: 33) stated: "Because our Oregon locality ... seems to be the same as one of the sites from which Linder (1952) examined material (i.e., near Klamath Falls, OR) we suggest that the California/Oregon clade should retain the name '*L. couesii*'." However, as shown below, the specimens from King and Hanner's "*L. couesii*-1" localities are morphologically distinct from the type specimens of *L. couesii* (USNM 11605) from Montana, and thus their suggestion that the specific name *couesii* be applied to the taxon they call "*L. couesii*-1" cannot be accepted.

Lepidurus couesii has also been reported from the Mediterranean basin (Thiéry, 1996), eastern Europe, from the subarctic steppe zone to eastern Romania (Brtek and Thiéry, 1995), and Mongolia (Brtek *et al.*, 1984).

MATERIALS AND METHODS

I examined 830 *Lepidurus* specimens from 81 locations in North America, Denmark, and Morocco. Efforts were made to examine the same material, or material from the same locations, used by previous researchers. Material was obtained from the U.S. National Museum of Natural History, the California Academy of Sciences, the Bohart Museum of Entomology, Sacramento State University, Los Angeles County Museum of Natural History, the collections of Jamie King, the collections of Denton Belk, other researchers and field biologists, or was field collected. Field collections were made either using a dip net to capture adults or by collecting quantities of dry soil containing resting cysts (eggs) for rearing in the laboratory.

Examinations of preserved material focused on structures used by Longhurst (1952) and Lynch (1972) to separate North American *Lepidurus* species. These features include: comparison of the number of leg pairs and body rings, nuchal organ placement, the form of the fifth and sixth endites of the second trunk appendage, the pulvilli of the males, the ratio of the length of the carapace to the length of the caudal lamina, the form of the caudal lamina, the arrangement of the spines of the sulcus, and carinal armature. The ratio of the length of the carapace to the length of the caudal lamina was determined by measuring to the nearest millimeter the length of each structure (anterior to posterior). Then the length of the caudal lamina was divided by the length of the carapace to give the values reported below.

In addition, the following specimens were studied: *L. apus*, *L. packardi* (identified by F. Linder, J. Lynch, and me), *L. couesii* (type material, as well as material identified by D. Belk, A. Thiéry, J. Lynch, and me), *L. lemmoni* (collected by me from the type locality and locations where Lynch gathered material for his 1966 redescription), *L. bilobatus* (topotype material collected by Saunders and used in his 1980 redescription), and *L. arcticus* (identified by me). Lynch's (1966, 1972) redescriptions of *L. lemmoni* and *L. couesii* and Saunders' (1980) redescription of *L. bilobatus* were also consulted. The

morphological terminology predominantly follows Lynch (1972). Representative material from my collections has been deposited at the Bohart Museum of Entomology at the University of California at Davis, the U.S. National Museum of Natural History, and the California Academy of Sciences.

Three cultures of *Lepidurus* from Poison Lake, Lassen County, California, were fed different diets and compared to determine the effects of food quality on growth. Culture A was reared on dry commercial bulk fish food; culture B was reared on live copepods, cladocerans (to be specified), and the anostracan *Linderiella occidentalis* (Dodds, 1923) nauplii and immatures; and culture C was reared on the anostracan *Artemia franciscana* Kellogg, 1906, nauplii and immatures. The *Lepidurus* were compared at 30 days of age.

After performing the above comparisons, I removed the caudal lamina from one specimen, endites from the second thoracic segment from a second specimen, and the margin of the sulcus from a third specimen from culture B to observe the effects of regeneration on structures historically used for identification.

Material from Poison Lake, Lassen County; Tamarack Lake, Fall River and Millville Plains, Shasta County; and Hog Lake, Tehama County, from California, U.S.A. were sent to Florida State University for electrophoretic evaluation, using the same methods used by King and Hanner (1998). The 12S rDNA of these specimens were compared to King and Hanner's (1998) evaluation. The Poison Lake and Fall River sites were selected because *Lepidurus* populations from these locations were used in King and Hanner's study.

RESULTS

Morphology

The characters used most extensively here and in the literature are discussed below according to body region.

Pairs of Legs.—There are no fixed number of leg pairs. *Lepidurus lemmoni* Holmes, 1894, and *L. bilobatus* Packard, 1833, bear anywhere from 56 to 78 pairs of legs, while the remaining species have from 30 to 45 leg pairs.

Body Rings.—There are no fixed number of body rings. Linder (1952) defines the first 11 rings as the thorax, with the remainder constituting the abdomen. The body rings may be incomplete, may coil about the trunk more than once, and can bear multiple pairs of appendages. Each species has a "range" of body rings. *Lepidurus lemmoni* may have from 30 to 33 body rings, while *L. couesii* has 24 to 27. Males tend to have more body rings than females (Longhurst, 1952).

Nuchal Organ.—The nuchal organ (dorsal organ of Lynch, 1972) is a stout, light-sensitive tubercle positioned posterior to the eyes and is formed of the naupliar eye. In *L. lemmoni*, the nuchal organ would sit behind a line

Table 1. Comparison of structural features of 30-day-old *Lepidurus* sp. reared from Poison Lake, Lassen County, California, on bulk dry fish food (culture A), and mixed live crustaceans (culture B). SD = standard deviation.

Culture/ specimen	Characters					
	Number of leg pairs	Number of body rings	Length of body ring spines to length of body ring	Length of caudal lamina to carapace	Number of large spines on the caudal lamina	Number of small spines on the caudal lamina
Culture A/1	32	25	0.2	0.1	4	3
Culture A/2	33	27	0.3	0.1	3	2
Culture A/3	33	27	0.2	0.1	6	2
Culture B/1	37	27	0.6	0.3	8	6
Culture B/2	36	28	0.6	0.3	7	5
Culture B/3	37	27	0.6	0.3	8	7
Culture B/4	35	27	0.6	0.2	6	5

drawn between the posterior apices of the eyes, whereas in other North American species the nuchal organ would be intersected by a line drawn between the posterior apices of eyes.

Endites of the Second Trunk Appendage.—The third, fourth, and fifth endites are of some use in differentiating species; however, I frequently encounter material where the final segments of the endites are missing. I have observed predaceous diving beetles and salamanders bite off protruding endites from *L. packardi* and *L. cryptus* n. sp. With the exception of *L. arcticus*, the fourth and fifth endites, when undamaged, extend well beyond the carapace.

The endites of male *Lepidurus* bear pulvilli that may aid the male in grasping the female during mating.

Sulcus.—The sulcus (or posterior margins of the carapace in Linder, 1952) may be armed with various arrangements of spines. Lynch (1972) correctly argued that the armature of the sulcus presented a useful specific character. The spines may be rounded or triangulate, longer than broad, and may have smaller spines interspersed between the larger spines. The sulcus spines of immature *L. bilobatus* and *L. packardi* are similar to those of *L. lemmoni*.

Caudal Lamina.—The presence of the caudal lamina (supra-anal plate in Linder, 1952) is the defining characteristic of the genus *Lepidurus*. The relative length of the caudal lamina to that of the carapace can be a useful character. I have observed bilobation of the caudal lamina in some individuals of *L. bilobatus*, *L. packardi*, *L. cryptus* n. sp., and *L. lemmoni*; therefore, bilobation of the caudal lamina is not a valid character to distinguish

L. bilobatus from the other species. Arrangement of the spines on the dorsal surface of the caudal lamina is also variable within species. Lynch (1972) stated that the large caudal lamina of *L. couesii* set that species apart from all other North American *Lepidurus*. However, the caudal lamina of immature *L. couesii* is indistinguishable from that of all other North American species. Furthermore, one large, mature *L. couesii* (carapace length 16 mm) in the type series bears a caudal lamina 0.3 times the length of the carapace, whereas, in the remaining specimens, it is 0.7 times the length of the carapace.

Comparison of Cultures.—I reared three *Lepidurus* to maturity on bulk fish food (culture A) and four on mixed Crustacea (culture B). Two immature *Lepidurus* grew to 6 mm in length on *Artemia* nauplii before dying. The specific results of the comparison between cultures A and B are given in Table 1.

DIAGNOSES

Characters separating the North American *Lepidurus* species are listed in Table 2. The specific results are presented in Tables 3 through 7.

Morphological diagnoses for all recognized North American *Lepidurus* species are presented below.

Lepidurus arcticus (Pallas, 1793)

Monoculus arcticus Pallas, 1793.

Lepidurus glacialis Packard, 1883.

Lepidurus spitzbergensis Bernard, 1882.

Apus productus var. *glacialis* Braem, 1893.

Lepidurus ussuriensis Sidorov, 1927.

Lepidurus arcticus (Pallas) in Longhurst, 1952.

Diagnosis.—Nuchal organ intersected by line drawn between posterior apices of eyes; 24 to 27 body rings, 33 to 45 pairs of legs; cau-

Table 2. Specific characters separating mature specimens of North American *Lepidurus*.

Species	Characters				
	Number of leg pairs	Number of body rings	Nuchal organ placement	Length of caudal lamina to carapace	Sulcus spines
<i>L. lemmoni</i>	>50	>30	behind eyes	≤0.3	Acute, 1.3–1.5 times as long as broad, 2–5 small spines separating the larger spines
<i>L. bilobatus</i>	>50	>30	between eyes	<0.3	Triangular, generally as long as broad, of various sizes
<i>L. arcticus</i>	40–45	<30	between eyes	<0.3	Acute, 1.5–2.5 times as long as broad, separated by at least twice their width
<i>L. couesii</i>	<40	<30	between eyes	>0.4	Rounded, 1–1.3 times as long as broad, with occasional single, small, subacute spines in between the larger spines
<i>L. packardi</i> / <i>L. cryptus</i>	<40	<30	between eyes	<0.3	Triangular, as long as broad, separated by at least twice their width, with numerous small spines of varying shapes, sometimes in double rows, separating the larger spines

dal lamina short, 0.1 to 0.3 times length of carapace; sulcus spines acute, 1.5 to 2.5 times as long as broad, separated by at least twice their widths, without small spines in between; endites 3, 4, and 5 of second thoracic appendages just reaching carapace margin; carapace with long apical carinal spine. Adult length: 10–35 mm from anterior margin of carapace to tip of caudal lamina.

Distribution.—Circumpolar in areas of continuous permafrost in the Arctic and subarctic regions (Fig. 1).

Material Examined.—(Table 3) USA:ALASKA: Kotzebue, Cape Krusenstern, 67°07'02"N, 163°42'04"W, 23 June 1977, 2 individuals, W. P. Connors/J. T. Carlton, California Academy of Sciences 22098. Point Barrow, 1952, 25 individuals, J. Mohr, Los Angeles County Museum, LACM CR 19520811.

Lepidurus bilobatus Packard, 1883

Lepidurus bilobatus Packard, 1883.

Lepidurus bilobatus Packard in Linder, 1952.

Lepidurus bilobatus Packard in Longhurst, 1952.

Lepidurus bilobatus Packard in Saunders, 1980.

Lepidurus bilobatus Packard in Saunders, 1980.

Lepidurus bilobatus Packard in King and Hanner, 1998.

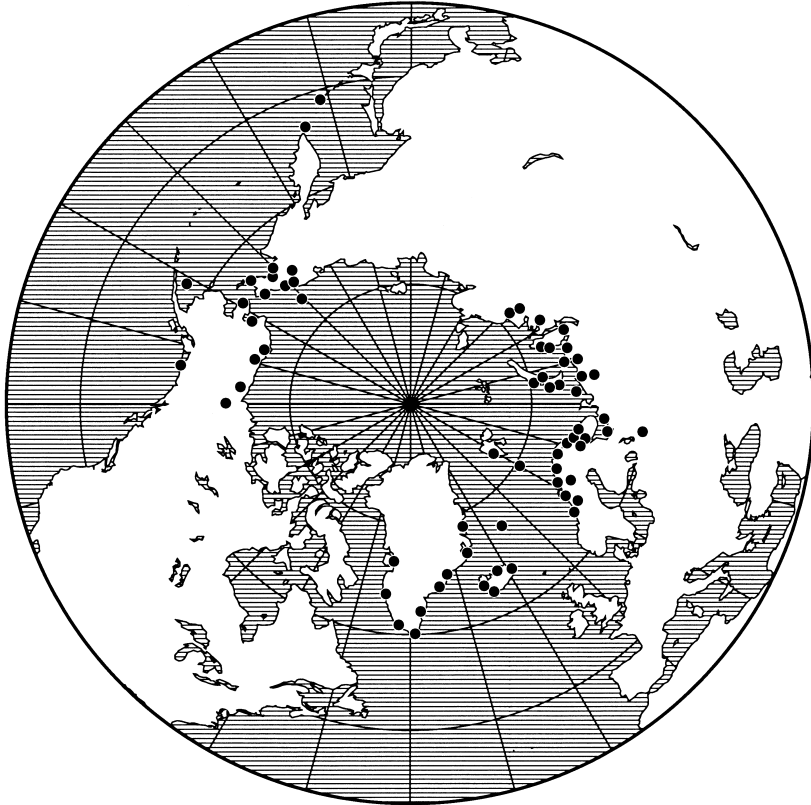
Diagnosis.—Nuchal organ intersected by line drawn between posterior apices of eyes; 32 to 34 body rings, 56 to 65 pairs of legs; caudal lamina may be constricted at base, subquadrate in very mature specimens, 0.2 to 0.3 times length of carapace; sulcus spines triangular, generally as long as broad, of various sizes; endites 4 and 5 of second thoracic appendages projecting beyond carapace margin. Adult length: 15–70 mm from anterior margin of carapace to tip of caudal lamina.

Distribution.—Colorado, Montana, Idaho, Nevada, and Wyoming. State-level record only for Utah. (Arizona, Oregon?) (Fig. 2).

Material Examined.—(Table 4) USA: COLORADO, Moffet County: (Topotypes) Pond at north end of Irish Canyon, T10N, R101W, 2 June 1979, 35 individuals, J. F. Saunders. IDAHO, Camas County: Macon Flat Pond #3, T. 1S, R.16E, S. 35, 2 individuals, L. Suzann Henrikson, 29 April 1998. NEVADA, Mineral County: Jack Springs Creek Drainage, Toiyabe National Forest, R. Holland, 13 May 1995. Storey County: Globe Road Pool, NW

Table 3. Variable characters observed in *Lepidurus arcticus*. SD = standard deviation.

Location	n	Characters								
		Number of leg pairs			Number of body rings			Length of caudal lamina to carapace		
		Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
1 Kotzebue, Alaska	2	44	44–45	0.7	27	27	0	0.2	0.2	0
2 Pt. Barrow, Alaska	25	41	40–43	0.9	26	24–29	1.2	0.1	0.1–0.2	0.04



● = *Lepidurus arcticus*

Fig. 1. Locations of *Lepidurus arcticus* reported from the literature and this study.

of Virginia City, 3 individuals, D. C. Rogers, E. C. Rogers, 4 April 2000.

Lepidurus couesii Packard, 1875

- Lepidurus couesii* Packard, 1875.
- Lepidurus couesii* Packard in Linder, 1952.
- Lepidurus apus* (Linnaeus) in Longhurst, 1952.
- Lepidurus couesii* Packard in Lynch, 1972.
- Lepidurus couesii* Packard in Hartland-Rowe, 1965.
- Lepidurus* "couessi-2" King and Hanner, 1998.

Diagnosis.—Nuchal organ intersected by line drawn between posterior apices of eyes; 24 to 27 body rings, 33 to 40 pairs of legs; mature specimens with caudal lamina long, ovate, 0.4 to 0.7 times length of carapace, small specimens with caudal lamina 0.1 to 0.3 times length of carapace; sulcus spines rounded, 1 to 1.3 times as long as broad, separated by at least twice their width, with occasional single,

Table 4. Variable characters observed in *Lepidurus bilobatus*. SD = standard deviation.

Location	n	Characters								
		Number of leg pairs			Number of body rings			Length of caudal lamina to carapace		
		Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
1 Irish Canyon, Moffet Co., Colorado Topotypes	35	64	60–77	4.5	34	31–36	1.6	0.3	0.2–0.4	0.05
2 Macon Flat Pond, Camas Co., Idaho	2	58	58	0	29	29	0	0.2	0.2	0
3 Jak Springs Creek Drainage, Mineral Co., Nevada	3	58	55–61	3.1	33	30–35	1.6	0.1	0.1	0
4 Globe Road Pool, Storey Co., Nevada	3	57	54–60	3.1	31	29–35	3.2	0.1	0.1–0.2	0.06



Fig. 2. Locations of *Lepidurus bilobatus* and *Lepidurus packardii* reported from the literature and this study.

small, subacute spine separating larger spines; endites 3, 4, and 5 of second thoracic appendages projecting beyond carapace margin. Adult length: 10–70 mm from anterior margin of carapace to tip of caudal lamina.

Distribution.—Idaho and North Dakota, U.S.A., and Saskatchewan, Manitoba, and Alberta, Canada (Fig. 3). State-level records only (Lynch, 1972) for Montana, Oregon, Utah, and Minnesota.

Table 5. Variable characters observed in *Lepidurus couesii*. SD = standard deviation.

Location	n	Characters								
		Number of leg pairs			Number of body rings			Length of caudal lamina to carapace		
		Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
1 Trans-Canada Highway, Manitoba, Canada	10	37	35–38	0.9	26	25–27	0.7	0.6	0.5–0.7	0.04
2 Lake, Idaho	1	36	36	0	27	27	0	0.6	0.6	0
3 Ashton, Idaho	8	38	36–38	0.7	25	25–27	0.7	0.6	0.4–0.7	0.1
4 Montana Types	3	36	36–37	0.6	25	25	0	0.6	0.6–0.7	0.06

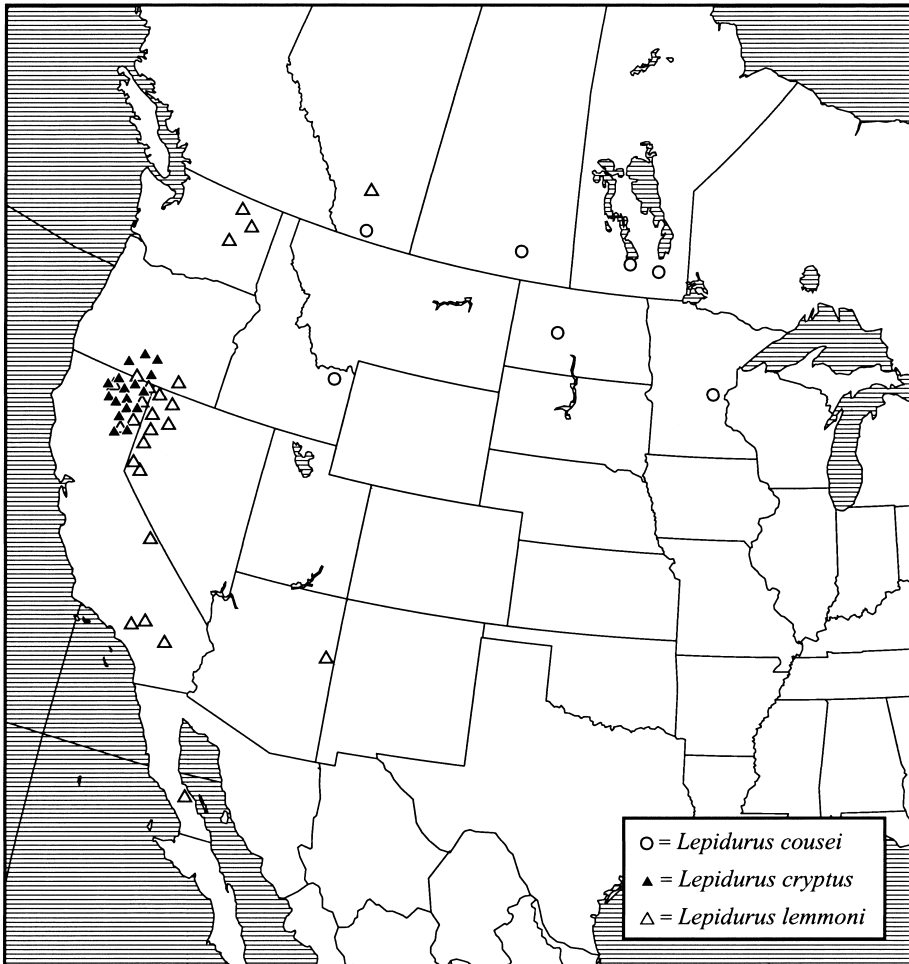


Fig. 3. Locations of *Lepidurus couesii*, *Lepidurus cryptus*, and *Lepidurus lemmoni* reported from the literature and this study.

Material Examined.—(Table 5) CANADA: MANITOBA. Flooded grassy roadside ditch on the Trans-Canada Highway just west of Spruce Siding (west of the Whitemouth River) about 80 km from the western boundary of Ontario, K. A. L. Reading, 12 May 1998. U.S.A.: IDAHO: "Lake," 1 individual, det. F. Linder, 1946, USNM 50569. Fremont County: Alkali pool 25 miles N of Ashton, M. M. & M. D. Ellis; USNM 68363. MONTANA: (Types) "Montana" A. S. Packard, 3 individuals, USNM 11605.

Lepidurus cryptus, new species

Lepidurus packardi: Linder, 1952.

Lepidurus packardi: Lynch, 1972.

Lepidurus "couesii"-1" King and Hanner, 1998.

Diagnosis.—Nuchal organ intersected by line drawn between the posterior apices of eyes; 24 to 29 body rings, 30 to 35 pairs of legs; caudal lamina truncate, 0.3 to 0.1 times length of carapace; mature specimens with sulcus

spines triangular, as long as broad, separated by at least twice their width, with numerous small spines of varying shapes, sometimes in double rows, separating larger spines, small specimens with large spines acute, 1.2 to 1.5 times as long as broad, old specimens may have large sulcus spines rounded: endites 3, 4, and 5 of second thoracic appendages projecting beyond carapace margin (see Fig. 5C). Adult length: 15–60 mm from anterior margin of carapace to tip of caudal lamina.

Types.—Holotype female: CALIFORNIA, Lassen County: Poison Lake, temporary lake, 17 March 1998, D. C. Rogers, deposited: Bohart Museum of Entomology, University of California, Davis, U.S.A. Type no. 1646. Paratypes females: same data as holotype, de-

Table 6. Variable characters observed in specimens conforming to the *Lepidurus packardii*-*L. cryptus* morphotype. SD = standard deviation. (* = material or location from which material was collected and used by King and Hanner, 1998).

Location	n	Characters								
		Number of leg pairs			Number of body rings			Length of caudal lamina to carapace		
		Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
1 Williams, Colusa Co., California	8	37	37	0	26	26	0	0.2	0.2	0
2 Sacramento Wildlife Refuge, Glenn Co., California	10	32	32-33	0.6	28	27-29	0.6	0.1	0.1	0
3 Lassen Co., California	2	36	36	0	29	28-29	0.7	0.3	0.2-0.3	0.07
4 Poison Lake, Lassen Co., California	7	37	36-38	1.0	26	25-27	0.6	0.3	0.3	0
5 McCoy Flat, Lassen Co., California*	2	37	35-39	2.8	27	25-29	2.8	0.3	0.3	0
6 Pittville Road, Lassen Co., California*	11	36	34-37	0.8	29	27-29	0.7	0.3	0.1-0.3	0.08
7 Long Lake, Lassen Co., California*	18	35	34-38	1.2	28	27-29	0.7	0.3	0.2-0.3	0.05
8 Grass Valley Lake, Lassen Co., California	1	34	34	0	28	28	0	0.1	0.1	0
9 Pine Creek Valley, Lassen Co., California	3	38	37-38	0.6	28	28	0	0.1	0.1	0
10 Madeline Plains, Lassen Co., California	1	38	38	0	29	29	0	0.1	0.1	0
11 Sloat Ranch, Lassen Co., California	23	34	32-36	0.8	24	23-26	0.7	0.2	0.1-0.3	0.06
12 Eagle Lake, Lassen Co., California	8	39	37-39	0.9	27	25-28	0.9	0.2	0.2	0
13 Flying "M" Ranch, Merced Co., California	2	35	35	0	25	25	0	0.1	0.1	0
14 Canby, Modoc Co., California	5	37	35-39	1.5	30	29-30	0.5	0.2	0.1-0.3	0.09
15 Clear Lake Reservoir Road, Modoc Co., California	4	37	37	0	28	25-29	1.7	0.2	0.2	0
16 Harvey Buttes Road, Modoc Co., California	14	36	32-37	1.2	29	28-29	0.4	0.1	0.1-0.3	0.06
17 Harvey Buttes Road, Modoc Co., California	7	37	34-38	1.1	28	24-28	1.5	0.1	0.1-0.3	0.08
18 Harvey Buttes Road, Modoc Co., California	1	34	34	0	28	28	0	0.3	0.3	0
19 Tucker Buttes Road, Modoc Co., California	6	36	31-39	2.8	27	24-29	1.7	0.3	0.3	0
20 Tionesta Road, Modoc Co., California	3	31	32-30	1.0	28	28	0	0.3	0.3	0
21 Big Sage Reservoir, Modoc Co., California	2	38	38	0	24	24	0	0.2	0.2	0
22 Lost Chance Creek Road, Plumas Co., California	7	38	37-39	0.6	25	24-27	1.0	0.2	0.1-0.3	0.07
23 Mather AFB, Sacramento Co., California	3	32	32-33	0.6	25	25-26	0.6	0.3	0.3	0
24 Galt, Sacramento Co., California	8	35	32-38	1.9	27	24-29	1.5	0.3	0.1-0.3	0.07
25 Rancho Seco, Sacramento Co., California	64	35	32-38	1.3	27	24-29	0.9	0.3	0.1-0.3	0.05
26 Lodi, San Joaquin Co., California	1	36	36	0	28	28	0	0.3	0.3	0
27 Hartnell Road, Shasta Co., California	10	35	32-35	1.0	29	28-29	0.3	0.2	0.2	0
28 Beatty Lane, Shasta Co., California	6	33	32-36	1.6	27	27-29	0.8	0.3	0.2-0.3	0.05
29 Millville Way, Shasta Co., California	1	33	33	0	27	27	0	0.3	0.3	0

Table 6. Continued.

Location	n	Characters								
		Number of leg pairs			Number of body rings			Length of caudal lamina to carapace		
		Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
30 Stillwater Gun Club Road, Shasta Co., California	1	38	38	0	28	27	0	0.3	0.3	0
31 Millville Plains Road, Shasta Co., California	1	38	38	0	26	26	0	0.2	0.2	0
32 Fig Tree Lane, Shasta Co., California	1	33	33	0	27	27	0	0.2	0.2	0
33 Fall River Valley, Shasta Co., California*	2	35	35	0	26	26	0	0.3	0.3	0
34 Tamarak Lake, Shasta Co., California	22	38	36–38	0.7	27	24–28	0.7	0.3	0.3	0
35 Green Place, Shasta Co., California*	2	34	34	0	26	26	0	0.2	0.2	0
36 White Deer Lake, Siskiyou Co., California	2	34	34	0	26	25–26	0.7	0.3	0.3	0
37 Butte Valley Airport, Siskiyou Co., California	1	35	35	0	27	27	0	0.3	0.3	0
38 Pondosa, Siskiyou Co., California*	2	36	36	0	28	28	0	0.3	0.3	0
39 Olcott Lake, Solano Co., California	35	34	32–36	0.7	27	25–29	0.7	0.3	0.2–0.3	0.02
40 Hickman Pool, Stanislaus Co., California	4	35	34–36	0.8	28	28	0	0.3	0.3	0
41 Vina Plains, Tehama Co., California	10	35	34–36	0.6	24	24–25	0.4	0.3	0.1–0.3	0.07
42 Spring Branch Road, Pool 1, Tehama Co., California	17	36	34–36	0.6	24	24–26	0.6	0.3	0.2–0.3	0.04
43 Spring Branch Road, Pool 2, Tehama Co., California	26	37	35–37	0.4	24	25–26	0.6	0.3	0.3	0
44 Lassen View Road, Tehama Co., California	23	33	33–37	1.0	27	26–27	0.3	0.3	0.2–0.3	0.04
45 North of Davis, Yolo Co., California	2	37	37	0	29	29	0	0.3	0.3	0
46 Western Aggregates, Yuba Co., California.	7	35	33–36	0.9	25	24–25	0.6	0.3	0.2–0.3	0.04
47 Beale AFB, Yuba Co., California	28	33	33–36	0.6	29	28–29	0.4	0.3	0.2–0.3	0.04
48 Wagontire, Harney Co., Oregon	9	33	33	0	27	25–29	1.0	0.3	0.3	0
49 Dry Lake North, Klamath Co., Oregon	5	37	35–37	0.9	28	26–29	1.3	0.2	0.2–0.3	0.04
50 Lakeview, Lake Co., Oregon	7	37	35–37	0.9	28	25–29	1.6	0.3	0.3	0

posited: Bohart Museum of Entomology, University of California, Davis, U.S.A. (same catalog number as holotype). Paratypes females: same data as holotype, deposited: California Academy of Sciences, San Francisco, U.S.A.; CASIZ 146044. Paratypes females: same data as holotype, deposited: National Museum of Natural History, Washington D.C., U.S.A.; USNM 310300. Paratypes females: same data as holotype, deposited: Centro de Investigaciones Biológicas del

Noroeste, La Paz, México. Paratypes females: same data as holotype, deposited: DCR collection, deposited: collection of Richard Hill.

Type Locality.—Poison Lake, a temporary winter lake northwest of Susanville on Highway 44, Lassen County, California, U.S.A. The area lies east of Lassen Park and north of the community of Chester. This pool is at an altitude of 1,530 m in a sage flat, ringed with conifers. The pool is approximately 200

ha in size, generally inundating in November and drying in August. From the end of November through March the pool is frozen and under a few feet of snow. The pool has a grassy bottom dominated by *Eleocharis*, with wetland sage species. The surrounding uplands are dominated by *Artemisia* sp., annual grasses, pines, and cedar. Other crustacean species collected from Poison Lake include: *Streptocephalus sealii* Ryder, 1879, *Eubranchipus serratus* Forbes, 1876, and *Branchinecta coloradensis* Packard, 1874 (Anostraca); *Lynceus brachyurus* Müller, 1776 (Conchostraca); and unidentified Cladocera, Copepoda and Ostracoda.

This site was selected as the type locality because material used by King and Hanner (1998) in their electrophoretic and 12S rDNA analysis came from this site.

Etymology.—The species name is from the Latin word for hidden “*cryptus*,” and refers to the fact that this species cannot be separated from *Lepidurus packardi* based on morphology alone.

Remarks.—I will accept for the purposes of this paper that King and Hanner’s (1998) *Lepidurus “couesii-2”* is in fact *L. couesii*, as none of their specimens were available for examination. *Lepidurus cryptus* is separated from *L. couesii* by the presence of numerous small spines, occasionally in double rows, between the larger spines of the sulcus.

Lepidurus cryptus has fewer than 30 body rings, whereas *L. lemmoni* and *L. bilobatus* have more than 30 body rings. *Lepidurus cryptus* has fewer than 40 pairs of legs where *L. arcticus* has between 40 and 45.

Lepidurus cryptus is inseparable morphologically from *L. packardi*. Analysis of 12S rDNA and allozyme data, performed by King and Hanner (1998), demonstrates that it is genetically distinct from *L. packardi* (see their Tables 2, 3, and 4, and Fig. 3A and 3C, as well as the discussion section in King and Hanner, 1998). Within the 12S rDNA bases *L. cryptus*, at positions 11, 148, 160, 168, 229 and 263 has guanine, whereas *L. packardi* and *L. couesii* have adenine. At position 93, *L. cryptus* has guanine, whereas *L. packardi*, *L. lemmoni*, *L. bilobatus*, and *L. couesii* have adenine. At position 161, *L. cryptus* has cytosine, whereas *L. packardi*, *L. lemmoni*, *L. bilobatus* and *L. couesii* have thymine. At po-

sition 209, *L. cryptus* has adenine, whereas *L. packardi*, *L. lemmoni*, *L. bilobatus*, and *L. couesii* have guanine. At position 305, *L. cryptus* has cytosine, whereas *L. packardi*, *L. lemmoni*, *L. bilobatus*, and *L. couesii* have thymine.

Distribution.—Great Basin and intermountain regions of northern California, and south and eastern Oregon (Fig. 3). The boundary between *L. cryptus* and *L. packardi* was verified electrophoretically. The 12S rDNA from material from Poison Lake, Lassen County; Tamarack Lake, and Fall River, Shasta County, California, U.S.A. were evaluated electrophoretically, following King and Hanner (1998), and were compared to King and Hanner’s (1998) results. No *L. cryptus* were found inside California’s Great Central Valley.

Other Material Examined.—(Table 6) (* = indicates material or location from which material was collected and used by King and Hanner, 1998) USA: CALIFORNIA, Lassen County: “Lassen County” 1 June 1884, 2 individuals, USNM 9377, det. F. Linder, 1946. Poison Lake, 5 July 1989, 7 individuals, D. C. Rogers*. McCoy Flat Reservoir, 5 July 1989, 2 individuals, D. C. Rogers*. Pool east of Poison Lake on Pittville Road and railroad track at Highway 44, 23 April 1992, 10 individuals, King, Gluesenkamp, and Tritt*. Pool east of Poison Lake on Pittville Road and railroad track at Highway 44, 5 April 1990, 11 individuals, D. C. Rogers*. Long Lake, Highway 44, 18 May 1994, 18 individuals, D. C. Rogers*. Grass Valley Lake, 18 May 1994, 2 individuals, D. C. Rogers*. Vernal Pool in Pine Creek Valley, 18 May 1994, 1 individual, D. C. Rogers. Madeline Plains, 13 May 1994, 1 individual, S. Myers. Vernal pools southeast east of corner of Road 402 and Kauffenberg Road, Sloat Ranch, 19 February 1997, 23 individuals, D. C. Rogers. Wet meadow north of Eagle Lake on dirt road, 18 April 1995, 8 individuals, D. C. Rogers. Modoc County: 10 miles north of Canby, 1 June 1897, 5 individuals, V. Bailey, USNM 82029, det. F. Linder, 1946. Railroad bed pool, Clear Lake Reservoir Road, 26 March 1998, 4 individuals, D. C. Rogers. Mud-flow temporary pool along Harvey Buttes Road, 1,800-m elevation, 17 March 1998, 14 individuals, D. C. Rogers. Volcanic mud-flow vernal pool, Harvey Buttes Road, 1,800-m elevation 3 miles west of Harvey Lake, 17 March 1998, 7 individuals, D. C. Rogers. Volcanic mud-flow vernal pool, Harvey Buttes Road, 2 miles east of Harvey Lake, 1,800-m elevation, 17 March 1998, 1 individual, D. C. Rogers. Volcanic mud-flow vernal pool, Tucker Buttes Road, 3 miles east of Harvey Lake, 1,800-m elevation, 17 March 1998, 5 individuals, D. C. Rogers. Volcanic mud-flow vernal pool, Tionesta Road, Perez 0.25 miles west of Highway 139, 1,750-m elevation, 17 March 1998, 3 individuals, D. C. Rogers. Volcanic mud-flow vernal pool, 2.5 miles north of Big Sage Reservoir, 1,750-m elevation, 17 March 1998, 2 individuals, D. C. Rogers. Plumas County: Pool on north-west side of Lake Almanor, Lost Chance Creek Road, 10 May 1995, 7 individuals, D. C. Rogers. Shasta County: Fall River Valley at intersection of Brown Road and Red

Table 7. Variable characters observed in *Lepidurus lemmoni*. SD = standard deviation.

Location	n	Characters								
		Number of leg pairs			Number of body rings			Length of caudal lamina to carapace		
		Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
1 No Data	1	69	69	0	32	32	0	0.2	0.2	0
2 Alberta, Canada	2	68	65–71	4.24	34	32–36	2.8	0.2	0.2	0
3 Springerville, Arizona	4	74	71–77	3.0	32	30–32	1.5	0.2	0.1–0.2	0.05
4 Horse Lake, Lassen Co., California	6	76	74–76	0.8	31	31–33	1.0	0.2	0.1–0.2	0.05
5 Honey Lake, Lassen Co., California (Topotypes)	15	74	73–76	0.8	33	33–35	0.6	0.2	0.2	0
6 Goose Lake, Modoc Co., California	1	77	77	0	32	32	0	0.2	0.2	0
7 Middle Alkali Lake, Modoc Co., California	7	71	70–72	0.6	34	32–34	0.8	0.2	0.1–0.2	0.04
8 Upper Alkali Lake, Modoc Co., California	9	68	62–72	2.8	34	31–36	1.4	0.2	0.1–0.2	0.05
9 Rogers Dry Lake, Kern Co., California	8	64	60–76	7.2	32	31–34	1.3	0.2	0.2	0
10 Iron Gate Reservoir, Siskiyou Co., California	6	66	60–77	6.4	35	34–36	0.6	0.1	0.1	0
11 White Lake, Washoe Co., Nevada	1	65	65	0	33	33	0	0.1	0.1	0
12 Grant Co., Washington	30	72	66–77	2.7	33	31–36	1.3	0.2	0.1–0.2	0.04

Mountain Road, 3 May 1992, 2 individuals, D. C. Rogers. "Fall River," 10 individuals, J. King, Glusenkamp, Tritt*. Tamarak Lake, east side of Tamarak Road, south of Burney, 25 May 1999, 22 individuals, D. C. Rogers. Tamarak Lake, east side of Tamarak Road, south of Burney, 13 April 2000, 26 individuals, D. C. Rogers. Summit Lake, on north side of Highway 44, 24 April 1993, 8 individuals, J. King, Glusenkamp, Tritt*. Green Place, 41°10'N, 121°23'W, 4 individuals, J. King*. Siskiyou County: Railroad toe drain, Highway 97, north of Butte Valley Airport, 3 April 1981, 1 individual, C. Atwood. White Deer Lake, White Deer Well, Shasta Trinity National Forest, McLoud Road, 2 individuals, 24 June 1999, R. Clementson. 3 miles northeast of Pondosa, 2 individuals, 14 July 1993, R. Callas*. OREGON, Harney County: 15 miles north of Wagentire, on Highway 395, 7 May 1958, 9 individuals, USNM 138891, J. Lynch. Klamath County: Dry Lake North, on west side of NFD road 9714 on cliff above Highway 97, approximately 10 miles north of the city of Klamath Falls, 20 May 1996, 5 individuals, R. Nauman. Dry Lake North, on the west side of NFD road 9714 on cliff above Highway 97, approximately 10 miles north of the city of Klamath Falls, 12 April 2000, 10 individuals, D. C. Rogers. Lake County: Roadside ditch, Highway 395, 10 miles north of Lakeview, 27 March 1995, 7 individuals, D. C. Rogers. Antelope Flat, roadside ditch, Bear Flat Road, 12 April 2000, 35 individuals, D. C. Rogers.

Lepidurus lemmoni Holmes, 1894

Lepidurus lemmoni Holmes, 1894.

Lepidurus lynchi Linder, 1952.

Lepidurus lynchi var. *echinatus* Linder, 1952.

Lepidurus lynchi Linder in Longhurst, 1952.

Lepidurus lemmoni Holmes in Lynch, 1966.

Lepidurus lemmoni Holmes in King and Hanner, 1998.

Diagnosis.—Nuchal organ behind line drawn between posterior apices of eyes; 30 to 35 body rings, 50 to 78 pairs of legs; caudal lamina subrectangular or truncate, 0.1 to 0.3 times length of carapace; sulcus spines acute, 1.3 to 1.5 times as long as broad, 2 to 5 small spines separating larger spines; endites 3, 4, and 5 of second thoracic appendages projecting beyond carapace margin; carapace carina may be armed with large triangular spines; living animals tend to be shining yellow or grayish silver to light green. Adult length: 15–70 mm from anterior margin of carapace to tip of caudal lamina.

Distribution.—Laguna Chapala, Baja California (Norte), México (Maeda-Martinez *et al.*, 1997); Alberta, Canada; Arizona, California, Oregon, Nevada, and Washington, U.S.A. (Fig. 3). State-level records (Lynch, 1966) for Wyoming and Montana.

Material Examined.—(Table 7) 1 individual, no data, Los Angeles County Museum, LACM CR 15000111. CANADA: ALBERTA: Sullivan Lake, 20 June 1951, 2 individuals, J. E. Moore, Los Angeles County Museum, LACM CR 19510791. USA: ARIZONA, Apache County: Near Springerville, September 1929, 4 individuals, J. E. Lynch, Los Angeles County Museum, LACM CR 19290011. CALIFORNIA, Kern County: Rogers Dry Lake, 6 January 1983, 8 individuals, D. C. Rogers. Lassen County: Horse Lake, 17 May 1980, 6 individuals, J. Belman. Honey Lake, (topotypes) 15 March 1998, 15 indi-

viduals, D. C. Rogers. Modoc County: Goose Lake, April 1973, 1 female, California Academy of Sciences 78048. Middle Alkali Lake, 26 April 1993, 24 individuals, females, D. C. Rogers. Upper Alkali Lake, 26 April 1993, 9 individuals, D. C. Rogers. Middle Alkali Lake, 12 June 1995, 7 individuals, D. C. Rogers. Siskiyou County: Alkali pool on south side of Iron Gate Reservoir, 6 April 1983, 6 individuals, S. Cepello. NEVADA, Washoe County: White Lake, 28 March 1999, 1 individual, D. C. Rogers. WASHINGTON, Grant County: Seven miles north of Grand Coulee, 14 May 1937, 30 individuals, R. Coats, California Academy of Sciences 104292.

Lepidurus packardi Simon, 1886

Lepidurus packardi Simon, 1886.

Lepidurus packardi Simon in Linder, 1952.

Lepidurus apus packardi Simon in Longhurst, 1952.

Lepidurus packardi Simon in Lynch, 1972.

Lepidurus packardi Simon in King, 1996.

Lepidurus packardi Simon in King and Hanner, 1998.

Diagnosis.—Nuchal organ intersected by line drawn between posterior apices of eyes; 24 to 29 body rings, 30 to 35 pairs of legs; caudal lamina truncate, 0.3 to 0.1 times length of carapace; mature specimens with sulcus spines triangular, as long as broad, separated by at least twice their width, with numerous small spines of varying shapes, sometimes in double rows, separating larger spines, small specimens with large spines acute, 1.2 to 1.5 times as long as broad, old specimens may have large sulcus spines rounded; endites 3, 4, and 5 of second thoracic appendages projecting beyond carapace margin. Adult length: 15–86 mm from anterior margin of carapace to tip of caudal lamina.

Distribution.—The Great Central Valley, and the Sacramento River Delta to the east side of San Francisco Bay, California, U.S.A. (Fig. 2). The boundary between *L. cryptus* and *L. packardi* were verified electrophoretically. The 12S rDNA from material from Millville Plains, Shasta County and Hog Lake, Tehama County, from California, U.S.A. were evaluated electrophoretically, following King and Hanner (1998), and were compared to King and Hanner's (1998) results. No *L. packardi* were found north or east of California's Great Central Valley.

Material Examined.—(Table 6) (* = indicates material or location from which material was collected and used by King and Hanner, 1998) USA: CALIFORNIA, Colusa County: Roadside ditch, Williams, 21 February 1971, 8 individuals, Shasta College Collection, R. L. Blakeley. "Colusa" 40, 1 April 1992, J. King, Glusenkamp, Josephson*. Glenn County: Sacramento Wildlife Refuge, 8 km south of Willows, 100 m elevation, 14 February 1994, 10 individuals, J. Silveira. Merced County: Flying "M"

Ranch, 13 individuals, B. P. Helm*. Flying "M" Ranch, March 1993, J. King*. "Kesterson", 4 February 1993, 4 individuals, J. King*. Sacramento County: Mather Air Force Base, 12 February 1996, 3 individuals, D. C. Rogers. CCT Railroad, Galt, 21 February 1991, 8 individuals, D. C. Rogers. Rancho Seco, 18 January 1995, 64 individuals, D. C. Rogers. San Joaquin County: Lodi, 10 April 1990, 1 individual, A. Weil. Shasta County: Large vernal pool at east end of Hartenell Road, Redding, 3 February 1983, 10 individuals, D. C. Rogers. Vernal pools on Bureau of Land Management land west of Beatty Lane, Palo Cedro, 2 February 1988, 6 individuals, D. C. Rogers. Vernal pools along Millville Way, Palo Cedro, 3 March 1992, D. C. Rogers. Vernal pools along Stillwater Gun Club Road, south of Redding, 6 July 1993. Vernal pools along Millville Plains Road, Palo Cedro, 2 February 1994. Large pool between south end of Redding Airport and Fig Tree Lane, Redding, 18 March 1992, 1 individual, M. Seth and D. C. Rogers. Solano County: Olcott Lake, 35 individuals, 21 May 1994, D. C. Rogers. Stanislaus County: Hickman Pool, Hickman, 4 individuals, C. Eriksen. Hickman Pool, Hickman, 2 individuals, J. King and B. Goettle*. Tehama County: Vina Plains, 18 March 1989, 10 individuals, D. C. Rogers. Spring Branch Road Vernal Pool 1, 3 June 1991, 17 individuals, D. C. Rogers. Spring Branch Road Vernal Pool 2, 3 June 1991, 26 individuals, D. C. Rogers. Dale's Lake, Highway 36, 10 individuals, 24 March 1992, King, Glusenkamp, and Josephson*. Vernal pools along Lassen View Road, Vina Plains, 14 January 1993, 23 individuals, D. C. Rogers. Vina Plains, 2 February 1994, 10 individuals, D. C. Rogers. Vina Plains, 20 March 1992, 5 individuals, J. King and Glusenkamp*. Yolo County: 1 mile north of Davis, 26 February 1946, 2 individuals, and 19 April 1946, 1 individual, USNM 173262, L. S. Gordon, det. F. Linder, 1946. Davis, 2 February 1966, 1 individual, R. Meyer. Yuba County: Western Aggregates, 21 January 1995, 7 individuals, D. C. Rogers. Beale Air Force Base, 25 January–27 February 1996, 28 individuals, D. C. Rogers.

DISCUSSION

One of the most notable characteristics of the Notostraca is the extreme polymorphism exhibited by many species (Linder, 1952; Longhurst, 1952; Lynch, 1966). This polymorphism is the obvious cause of confusion between certain species. Characters used in previous treatments have been shown to be highly variable.

In the cultures, *Lepidurus* fed a varied diet developed more pairs of legs and body rings, as well as a larger body and more and larger caudal lamina spines. *Lepidurus* from culture B, from which I removed caudal lamina and the endites of the second thoracic segment, regenerated these structures within 20 days. The regenerated caudal lamina was smaller and bore fewer and smaller spines than the original structure (eight large spines *versus* five large spines). The *Lepidurus* that had the sulcus margin removed died after three hours.

Although this is preliminary data, it suggests that food quality and regeneration of injured body parts may affect the reliability of structures previously used for identification.

Most of the North American *Lepidurus* have specific characters that are monomorphic (e.g., sulcus spines) or fit within a range of variability (i.e., numbers of leg pairs or body rings), with little overlap. These characters are the basis for the key presented below. *Lepidurus cryptus* and *L. packardii* are the only two species without reliable morphologic characters to separate them from each other. *T*-test analyses of variability in number of leg pairs, body rings, and spine patterns between the two species did not yield any significant differences.

Lepidurus arcticus occurs in summer pools and lakes in continuous permafrost regions of North America, Greenland, Iceland, and Eurasia (Johansen, 1922; Vekhoff, 1993). *Lepidurus arcticus* has also been reported from the montane steppe zones of Russia (Vekhoff, 1993) and from the Kuril Archipelago (Sayenko and Minakawa, 1999). Weather data collected from Point Barrow, Alaska, give winter lowest average temperature in March as -34.4°C , summer highest average temperature at 7.2°C . All collections were made between July and October.

Lepidurus lemmoni Holmes has long been known from large alkali playas in the Mojave Desert and Great Basin regions in California, Nevada, Oregon, and Washington (Lynch, 1966). I have collected *L. lemmoni* from small turbid alkaline pools in California and Oregon on rare occasions.

Lepidurus bilobatus was reported from Christmas Lake, Lake County, Oregon, and from near Virginia City, Storey County, Nevada, by King and Hanner (1998). I was unable to locate any material from Christmas Lake, and I could neither rear nor find any *Lepidurus* cysts (resting eggs) in any of the 15 gallons of surface soil I collected from that location. I was able to collect *L. bilobatus* from the Virginia City location, and I was able to review the topotype material that Saunders (1980) used in his redescription of *L. bilobatus*.

Characters that define *L. couesii* (*sensu* Lynch, 1972, and from the type specimens USNM 11605) were not observed in any of the California, Oregon, or Moroccan material reviewed in this study. King and Hanner

(1998) and Helm (1998) reported *L. couesii* from nine California and south central Oregon locations. Helm (1998) reported the "Modoc Plateau tadpole shrimp" from one location and commented on its similarity to *L. couesii* and *L. packardii*. Material I reviewed from these locations (locations 4 through 10, 33, and 35 in Table 7) and from 15 locations in the same vicinity as all of their California/Oregon *L. couesii* locations (locations 4, 3, 11, 14 through 21, 36, 37, 48, and 49 in Table 7) all conformed to the *L. packardii* morphotype. Lynch (1972) reported *L. couesii* from Idaho, Oregon, Utah, and Minnesota in the United States, and from Alberta and Saskatchewan, Canada. Unfortunately, Lynch provided no further location information, and I have been unable to find his Oregon *L. couesii* material. Other collections of *L. couesii* obtained from the U.S. National Museum of Natural History from Montana (USNM 11605), Idaho (50569, 55800), and North Dakota (67649), U.S.A.; and Alberta (54814) and Saskatchewan (49121), Canada, all conform to the *L. couesii* morphotype as defined here.

All the other material studied, including Lynch's and Linder's material, from northern California and south-central Oregon conformed morphologically to *L. packardii*. Therefore, I did not find *L. couesii* to occur in California.

Material I examined from Morocco (Daya Mertissiliouine, Atlas Mountains, Morocco, 3 June 1985, A. Thiéry) that was identified as *L. couesii* differs from *L. couesii* by having 25 to 30 body rings; 41 to 45 leg pairs; and the sulcus spines triangular, as long as broad, separated by 1–1.5 times the width of the spines. The caudal lamina is 0.4 to 0.5 times the length of the carapace, tapering proximally, and the endites of the second thoracic appendages just reach the carapace margin. This material is morphologically inconsistent with the *L. couesii* type material, Lynch's (1972) redescription, and other *L. couesii* material examined during this study. Unfortunately, no "*L. couesii*" material from Eurasia was available for study.

Three *Lepidurus* specimens from Denmark labeled "*L. apus*" that I examined at the Los Angeles County Museum (Dragor, Amager, Denmark, April 1927, collected and determined by Ad. S. Jensen, LACM CR 19270031), differed from most North Amer-



Fig. 4. Representative ocular tubercle and nuchal organ arrangement of (left) *Lepidurus lemmoni* (2.3-mm width) and (right) *Lepidurus bilobatus* (1.8-mm width).

ican *Lepidurus* in the arrangement of the sulcus spines, which are triangular, as long as broad, alternating large and small spines separated by the width of the large spines. The small spines are one half the size of the large spines. The number of leg pairs (38, 44, and 43) and body rings (30, 35, and 32 respectively), fit in the same range as *L. arcticus*.

Therefore, assuming that these specimens are in fact *L. apus*, I must agree with Lynch (1972) that *L. couesii* is a separate species from *L. apus*.

In the California Central Valley, *L. packardii* occurs from Merced County north to Shasta County, and the Sacramento/San Joaquin River Delta region to the east side

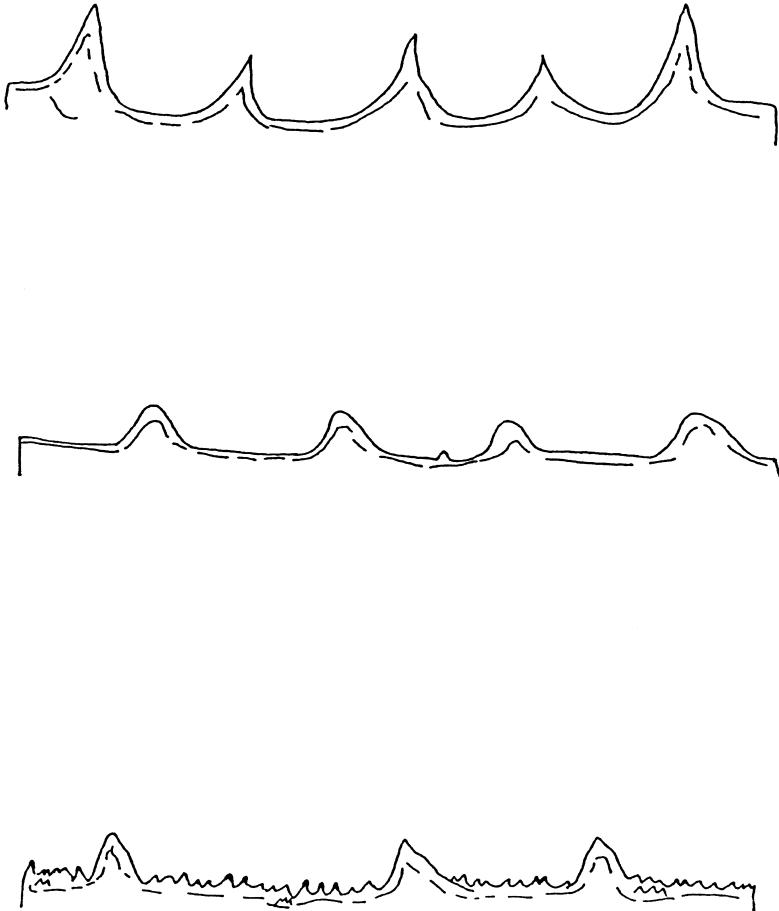


Fig. 5. Four-mm portion of sulcus margin of representative *Lepidurus* species: (top) *Lepidurus arcticus*, (middle) *Lepidurus couesii*, and (bottom) *Lepidurus cryptus* n. sp.

of San Francisco Bay. *Lepidurus packardii* can on occasion reach very large sizes; one specimen that I examined from Stanislaus County measured 86 mm from the anterior carapace margin to the apex of the caudal lamina.

Lepidurus cryptus occurs in California on the east side of the northern end of the Sierra Nevada Mountains in Plumas County, the east side of the Cascade/Siskiyou inter-mountain regions of Lassen, Shasta, and eastern Siskiyou counties, including the Fall River Valley, and the Great Basin Regions of Lassen and Modoc counties. In Oregon, *L. cryptus* occurs in the Great Basin regions of Lake, Harney, and Klamath counties. Similar habitat occurs in western Washoe County, Nevada, but as yet I have no material from that state. However, I do have specimens from within one half mile of the California/Nevada border northeast of Honey Lake, suggesting that *L. cryptus* could be found in western Washoe County, Nevada at some time in the future.

Both *Lepidurus packardii* and *L. cryptus* vary in color. In highly turbid water, I have observed both species to be nearly translucent to buff colored with brown mottles. In slightly turbid to clear water, I have observed both species ranging from light green to dark green, dark green mottled with brown, chocolate brown, brown with green mottles, and black.

KEY TO THE *LEPIDURUS* OF NORTH AMERICA

This key is designed for use with mature specimens having a carapace length 1 cm or greater. Typically, mature females or hermaphrodites will bear cysts in the brood pouches on the 11 pairs of thoracic appendages.

1. More than 50 pairs of legs; 30 to 36 body rings 2
- Less than 50 pairs of legs; 24 to 29 body rings 3
2. Nuchal organ behind a line drawn between the posterior apices of eyes (Fig. 4A); caudal lamina truncate; (living animals tend to be shining yellow or grayish silver to light green); common in medium to large hard, alkali playa pools with pH values ranging from 8.2 to 11.3 in deserts of California, Oregon, Nevada, Washington, Wyoming, and Montana, U.S.A. *Lepidurus lemmonii* Holmes
- Dorsal organ intersected by a line drawn between the posterior apices of eyes (Fig. 4B); caudal lamina subquadrate; Colorado, Montana, Utah, Idaho, Nevada, and Wyoming. (Arizona, Oregon?), U.S.A. *Lepidurus bilobatus* Packard
3. Endites of second thoracic appendage short, subequal, not quite extending beyond the margin of the carapace; sulcus with acute spines, 1.5 to 2.5 times

- as long as broad (Fig. 5A); strong carinal spine; 40 to 45 pairs of legs; circumpolar, reported from continuous permafrost regions of North America, Greenland, Iceland, and Eurasia (Johansen, 1922, Vekhoff, 1993) *Lepidurus arcticus* (Pallas)
- Endites of second thoracic appendage long, unequal in length, extending beyond the margin of the carapace (endites are fragile and may be broken off); sulcus with large spines 1 to 1.3 times as long as broad; 30 to 39 pairs of legs 4
4. Sulcus margin lined with large rounded spines separated by twice their width, with an occasional single small spine in between (Fig. 5B); caudal lamina 0.3 to 0.7 times the mid-dorsal length of carapace; Idaho, Montana, Oregon, Utah, Minnesota, and North Dakota, U.S.A., and Saskatchewan, Manitoba, and Alberta, Canada *Lepidurus couesii* Packard
- Sulcus margin lined with large triangulate spines separated by two to three times their width, with numerous, variously shaped small spines in between (Fig. 5C); caudal lamina equal to or less than 0.3 times the mid-dorsal length of carapace 5
5. 12S rDNA with adenine bases at positions 11, 93, 148, 160, 168, 229, and 263; thymine at positions 161 and 305; guanine at position 209; Central Valley of California, U.S.A. *Lepidurus packardii* Simon
- 12S rDNA with guanine bases at positions 11, 93, 148, 160, 168, 229, and 263; cytosine at positions 161 and 305; adenine at position 209; inter-mountain and Great Basin regions of Oregon and California (Nevada?) *Lepidurus cryptus* n. sp.

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