

Oviposition niches and behavior of the genus *Lixus* Fabricius (Coleoptera: Curculionidae, Lixinae)

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Oviposition places in the host plants of 23 *Lixus* Fabricius species in eastern Turkey were identified. *Lixus nordmanni* Hochhuth, *L. subtilis* Boheman, *L. incanescens* Boheman, *L. brevipes* Brisout, *L. sp. n. pr. brevipes* Brisout, *L. ochraceus* Boheman, *L. furcatus* Olivier, *L. rubicundus* Zoubkoff, *L. angustatus* (Fabricius), *L. punctiventris* Boheman, *L. fasciculatus* Boheman, *L. bardanae* (Fabricius), *L. sp. n. pr. korbi* Petri, and *L. scolopax* Boheman deposited eggs in the main stem. *Lixus filiformis* (Fabricius), *L. cardui* Olivier, and *L. korbi* Petri oviposited in the main stem and lateral branch of their host plants. *L. circumcinctus* Boheman laid eggs on both stem and petiole, whereas *L. siculus* Boheman, *L. farinifer* Reitter, *L. cylindrus* (Fabricius), and *L. sp. n. pr. furcatus* Olivier used the petioles, a new ecological niche for the genus *Lixus*. The unique species *L. obesus* Petri selected the seed capsule for laying eggs and completing its generation.

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1. Introduction

The superfamily Curculionoidea, which contains more than 50,000 described species, is the richest organisms known (O'Brien & Wibmer 1978). This diversity is hypothesized to result from invasion of the adaptive zone of strict phytophagy (Anderson 1995). The use of the rostrum in preparing an oviposition site is considered a key adaptation that facilitates entry by circumventing recognized evolutionary barriers to plant feeding and permits the use of a broad spectrum of plant parts as food sources (Anderson 1995). Some structural niches of plants represent a consistent and predictable resource gradient, ranging from the thick stem at the base of the plant to the thin stems at the tip. Hence, for stem-inhabiting spe-

cies, size constraint could play an important role in oviposition and larval development (Eber *et al.* 1999). A study of the different species of endophagous stem borers on thistles showed niche partitioning according to body size (Zwölfer & Brandl 1989). Hence, two or even three different species coexist in different parts of the stem of the same host plant.

The genus *Lixus* has a nearly worldwide distribution and comprises more than 500 species; in the Palaearctic region, more than 150 species are found (Petri 1904/1905, Csiki 1934, Ter-Minassian 1967). Zwölfer & Harris (1984) indicated that genus of the *Lixus*, with long and slender larvae, pupae, and adults is so adapted to mine the stems of herbaceous plants, although a few species attack the roots and buds. The female rostrum

is long, curved, and shaped in such a way that eggs are placed in the interior of the herbaceous stem. Species of *Lixus* has been to a broad spectrum of plant families that provide suitable oviposition sites. Korotyaev & Gültekin (2003) stated that the host range includes several families of higher plants. Majority of the comparatively well-known species develop or at least feed on species of several genera of a single plant family. With some plant families – the Chenopodiaceae, Brassicaceae, and Apiaceae – species of more than one subgenus of *Lixus* are associated. It is not always clear if this reflects a multiple transition of the genus to plants of these families or a broad diversification of the phyletic lineages associated with the respective plant families.

Some of the *Lixus* species are actual (Şenonca 1981) or potential pests of agriculture (Volovnik 1988, Nikulina 1989, Yıldırım & Özbek 1992), but some have potential uses in the biological control of weeds (Julien *et al.* 1984, Freese 1994, Briese 1996, Sobhian *et al.* 1999, Gültekin *et al.* 2000, 2004, Gültekin 2004). There are only two special studies about oviposition niches of the genus *Lixus*. Volovnik (1994) describes the oviposition places and behavior of eight *Lixus* species in Ukraine. Gültekin (2005) reports that *Lixus obesus* Petri, 1904 completes its generation in seed capsules of *Prangos uloptera* DC. This is regarded a new ecological niche for the genus *Lixus*, which is known to be stem-boring. Gültekin (2006) also documented the oviposition behavior of *Lixus nordmanni* Hochhuth. However, the biology of most species of this genus is poorly investigated. This paper aims to elucidate on one of the most important parts of their life cycle, ovipositing.

2. Materials and methods

Investigations were conducted in the provinces of Adıyaman, Artvin, Bayburt, Elazığ, Erzincan, Erzurum, Gümüşhane, Iğdır, Kars, Kayseri, Malatya, Nevşehir, Niğde, and Trabzon in the eastern part of Anatolia. Several expeditions were conducted to describe the biodiversity of Lixini (Coleoptera: Curculionidae; Lixinae) from 1997 to 2005. The area includes extensive agricultural land and natural habitats, with altitudes

ranging from 50 to 2,400 m. The climate is cold and snowy during winter; it is warm and dry during summer.

The main goal was to investigate the biodiversity of Lixini tribe, describe host plant linkages, and determine its ecological niche in eastern Anatolia. In studying weevil and host association, oviposition marks were located and places where eggs were laid were observed by opening the plant stems and other plant organs. These observations were done in the natural habitats of weevils and associated host plants. The oviposition behavior of some species was likewise observed in the field.

3. Results

All the *Lixus* species studied had early activity compared with other species from Lixinae, especially *Larinus* Dejean. Generally, male individuals associated with their host plants in the early spring before the females. Most adult species fed on leaves of plants, even if the species have special feeding characteristics. For instance, *L. subtilis*, *L. bardanae*, *L. filiformis*, *L. cardui*, and *L. korbi* fed on leaves, opening several small round holes. *Lixus nordmanni* and *L. ochraceus* fed on the outer margin leaves, making wide semi-circular holes. *Lixus circumcinctus* fed on *Crambe orientalis* L. and *Crambe tataria* Sebeok, chewing directly on the stem, bud, or petiole. Secondary adult food sources of *Lixus* are plant stems and petioles upon opening excavations for eggs. Apparently, overwintered adults need to feed for some period before mating and ovipositing.

Before laying eggs, the females mated several times with the males. Some species even continued mating during oviposition (*L. cardui*, *L. filiformis*). Furthermore, some male species preferred to mate while the females were opening oviposition holes (*L. furcatus*) or inserting eggs in the oviposition cavity (*L. sp. n. pr. korbi*). The females did not try to escape or show antagonistic behavior against the male during this time. Furthermore, they continued opening the cavity and pushing the egg into the hole. The rostrum is a unique organ used to make oviposition holes instead of the ovipositor, one of the main organs to be captured of female pronotum or on the scu-

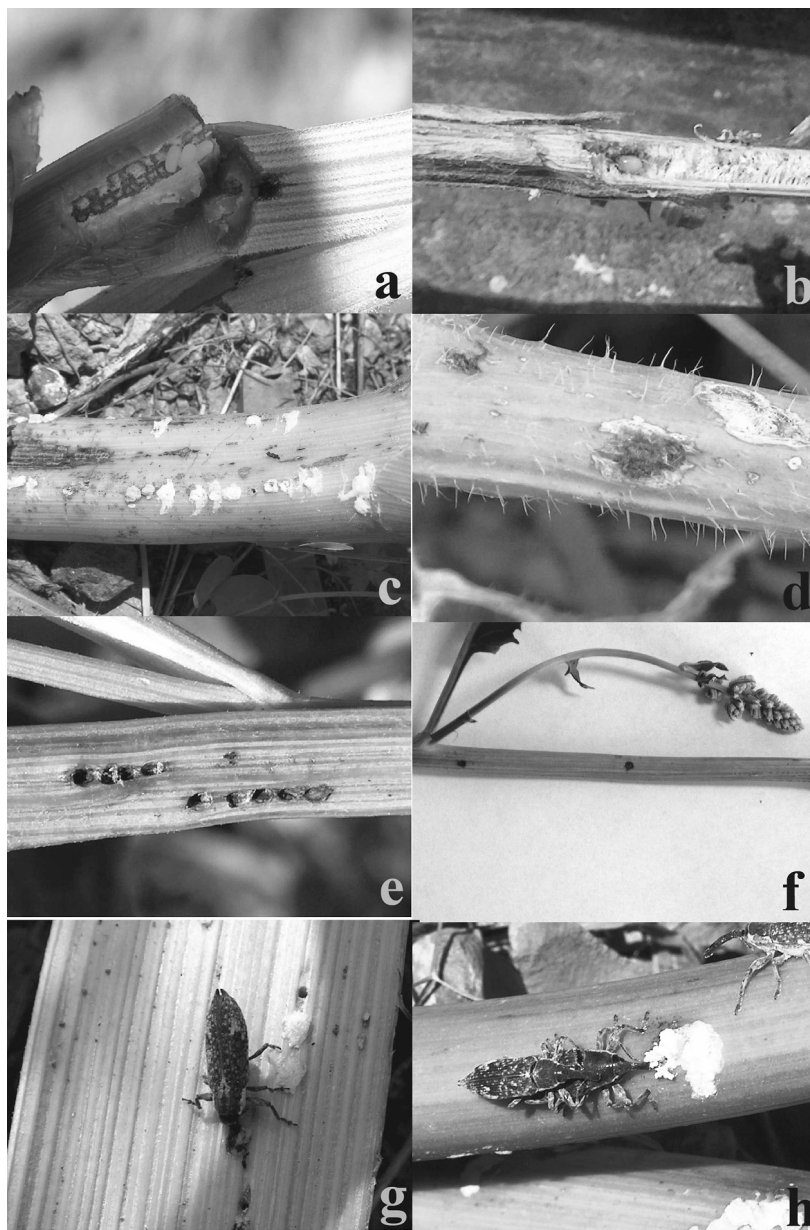


Fig. 1. Eggs and oviposition marks of *Lixus* F. genus. – a. *Lixus nordmanni* Hochhuth (eggs). – b. *Lixus scolopax* Boheman (egg). Oviposition marks. – c. *Lixus furcatus* Olivier. – d. *Lixus circumcinctus* Boheman. – e. *Lixus* sp. n. pr. *korbi* Petri; and – f. *Lixus korbi* Petri. Excavating oviposition holes by female. – g. *Lixus* sp. n. pr. *furcatus* Olivier and – h. *Lixus furcatus* Olivier (and mating position).

tellar area by the male at the mating position.

In preparing to excavate, the ovipositing female moved in such a way that forelegs were positioned anterolaterally and the hind legs posterolaterally, and all tarsi held the stem or petiole, sometimes with legs embracing the stem in form of a ring if the plant stem is thin enough. The female (*L. sp. n. pr. korbi*) started to remove the epidermal tissue of the stem or petiole, biting off small pieces of plant tissue. The rostrum was

moved toward the inside of the hole. From time to time, the female removed the rostrum from the hole. The rostrum was completely inserted into the hole when drilling of the hole is almost finished. Upon completion, the female walked away slowly and tried to position the tip of the abdomen in the cavity. Staying in this position without any movement, only the abdomen extended and retracted several times, with the rostrum touching the plant tissue and helping keep the female mo-

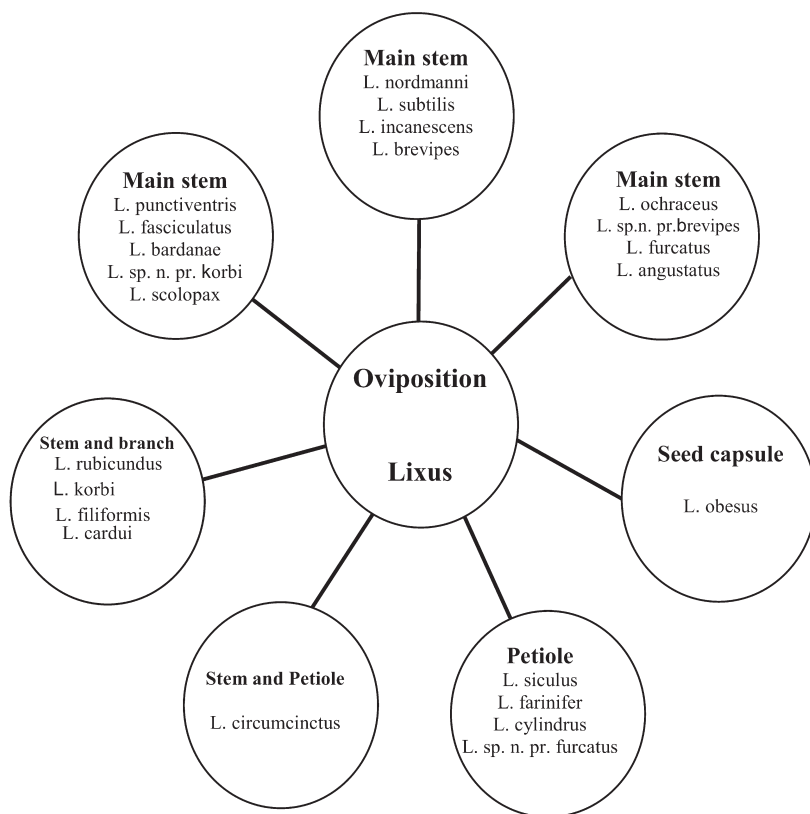


Fig. 2. Matrix of oviposition niches of the *Lixus* F. in eastern Turkey.

tionless. After eggs were laid in the hole, the female used the rostrum to push eggs in the bottom of the oviposition hole.

Cavities and oviposition marks have some distinct characteristics, depending on weevil species, rostrum length, and plant tissue. Both interspecific and intraspecific peculiarities among species exist starting from the aspect of site selection for laying eggs. *Lixus nordmanni* laid creamy white eggs solitarily or 2–3 eggs together in the same oviposition hole (Fig. 1a). *Lixus bardanae* and *L. punctiventris* laid yellowish ellipsoid eggs in hollow parts solitarily. The eggs of both of species were observed from the base to the tip of the plant stem, 5–9 cm apart from each other. *Lixus subtilis*, *L. incanescens*, and *L. rubicundus* laid yellowish, nearly rounded eggs one at a time in the main stem of their host plants, 4–5 cm from the base of the stem. *Lixus brevipes* and *L. sp. n. pr. brevipes* deposited yellowish eggs in the hollow part of the main stem. Even if eggs, 4–5 eggs in one stem, of *L. brevipes* occur along the stem, *L. sp. n. pr. brevipes* eggs, usually one egg

in one stem, inspected only the little upper of root crown of plant. *Lixus ochraceus* deposited eggs, one by one, into the stem, opening cavities in the plant tissue. Eggs were abundant along the median parts, usually 7–8 eggs were placed in one stem; at times, this number reached 11–12. *Lixus fasciculatus* oviposited in the main stem; usually 1 or 2 eggs can be found in one stem in the upper part of the plant. *Lixus filiformis* and *L. cardui* deposited yellowish green eggs, one by one, or very near each other solitarily from the base to the tip of the stem, including the lateral branch of the plant. *Lixus angustatus* preferred to lay solitary yellowish eggs, approximately in the upper 15 cm of the stem up to the tip. *Lixus korbi* laid yellowish green eggs in the hollow part of the main stem and in the thick lateral branches, solitarily at 7–8 cm distance (Fig. 1f), but *L. sp. n. pr. korbi* eggs touched each other in groups of 4–5 (Fig. 1e). Both these species protected the eggs by a secretion that hardened and turned brownish black in time. While *L. furcatus* oviposited in the main stem of their host plants (Fig. 1h), *L. sp. n. pr.*

furcatus (Fig. 1g), *L. farinifer*, *L. cylindrus* and *L. siculus* laid eggs on the plant petioles only. *Lixus furcatus*, including four petiole borers, deposited eggs solitarily, closed the holes with a secretion mixed with thin plant fibril remnant. Pale brownish oviposition marks can be seen easily on the plant (Fig. 1c). On the other hand, these plants strongly respond to excavation damage by secreting a resin-like liquid that sometimes closed the oviposition holes too. *Lixus scolopax* laid eggs one by one (Fig. 1b) and closed holes with a thick layer of secretion. These brownish black oviposition marks were seen easily. The female of *L. circumcinctus* laid eggs on the stem and petiole of leaves, opening the cavity with the rostrum. Then, the surface of the eggs and their surroundings were covered by a secretion prepared by chewing plant fibers while opening the cavity. These places turned purplish brown-black in the course of time (Fig. 1d). Each plant has 1–21 eggs, depending on plant size and number of adults.

4. Discussion

The use of the rostrum for excavating an oviposition site in a plant structure can be seen clearly as a key point in explaining the diversity within superfamily Curculionoidea (Zwölfer 1975). Subfamily Lixinae, one of the richest groups in family of Curculionidae and in this present study, *Lixus* oviposition takes place in live plant tissue using the rostrum for excavating oviposition places. This paper found that most *Lixus* species laid eggs usually in the stems of plants; 13 species in main stem, four species stem and lateral branches, a species stem and petiole (Fig. 2; Table 1). However, only some *Callistolix* Reitter (*L. farinifer*, *L. cylindrus*, and *L. sp. n. furcatus*) and the *Eulixus* Reitter (*Lixus siculus*) species laid eggs in the petioles of their host plants. Furthermore, larval and pupal growth occurred in these ecological niches. In addition, these four *Callistolix* species and *L. circumcinctus*, *L. scolopax*, *L. korbi* and *L. sp. n. pr. korbi* applied a greater amount of secretion to close the oviposition holes. This peculiarity gives greater egg protection and avoids predation, parasitism, and desiccation.

Anderson (1995) suggested that the development of a longer rostrum by the female species of Curculionoidea allowed the invasion of a new adaptive zone through excavation of oviposition sites in plant parts, which are otherwise not previously available as food sources for immature stages. The most interesting example shown by Gültekin (2005) is *L. obesus*, which had the unique behavior of laying eggs in the seed capsule of *Prangos uloptera*, in contrast to the general biological records of the genus *Lixus*.

Studying the different species of endophagous stem borers on thistles, Zwölfer & Brandl (1989) showed niche partitioning according to body size. Hence, two or even three different species coexist in different parts of the stem of the same host plant. Selection of different plant organs on which to lay eggs in may avoid interspecific competition between species. According to the present data set, *Prangos* plant stems were used by *L. furcatus* in immature biological stages and *P. uloptera* was one of the host plants of *L. furcatus* in eastern Anatolia. However, *L. obesus* has the same plant host. Apparently, this weevil may have jumped to the seed capsule to avoid interspecific competition with each other.

In all species studied, only one egg is laid per cavity, except for *L. nordmanni*, which occasionally laid three eggs in one hole. Common European species *Lixus iridis* Olivier, 1807 laid eggs in hollow parts of stem of the *Anthriscus nemorosa* (Bieb.) Spreng (Volovnik 1994) which is not found in eastern part of Turkey. In this region, *L. nordmanni* is widespread on several Apiaceae (Gültekin 2006).

The selection of the petiole as oviposition site by four *Lixus* species (*L. siculus*, *L. farinifer*, *L. cylindrus*, and *L. sp. n. pr. furcatus*) reflects a new ecological niche where both oviposition and growth of immature stages take place. This may be possible, depending on the structure of main stem tissue, asynchronous vegetation, and lack of competition with other species. For instance, the host plant of *L. farinifer* has only leaves in the beginning of summer; the stem shows up in late summer when the oviposition period of the weevil has already passed. The main stem and lateral branch of the host plant of *L. siculus* is an extremely hard tissue. Thus, the softer petiole is preferred for oviposition and growing of larvae.

Table 1. Oviposition niches of the *Lixus* F. in eastern Turkey.

Weevil species	Host plants	Niches of eggs	References
<i>Lixus nordmanni</i> Hochhuth	<i>Heracleum trachyloma</i> Fisch. et Mey. <i>H. sosnowskyi</i> Manden <i>H. pastinacifolium</i> C. Koch <i>H. platytaenium</i> Boiss. <i>Angelica sylvestris</i> L. <i>Pastinaca urens</i> Req. et Godr.	Main stem	Gültekin 2006
<i>Lixus subtilis</i> Boheman	<i>Chenopodium vulvaria</i> L.	Main stem	
<i>Lixus incanescens</i> Boheman	<i>Salsola kali</i> L. <i>Chenopodium foliosum</i> Asch. <i>C. vulvaria</i> <i>Beta vulgaris</i> L.	Main stem	
<i>Lixus brevipes</i> Brisout	<i>Gypsophila</i> sp.	Main stem	
<i>Lixus</i> sp. n. pr. <i>brevipes</i> Brisout	<i>Silene vulgaris</i> (Moench) Garcke	Main stem	
<i>Lixus ochraceus</i> Boheman	<i>Tchihatchewia isatidea</i> Boiss.	Main stem	Korot. & Gült. 2003
<i>Lixus furcatus</i> Olivier	<i>Prangos uloptera</i> <i>P. ferulacea</i> <i>P. lophoptera</i> Boiss.	Main stem	
<i>Lixus angustatus</i> (Fabricius)	<i>Cirsium</i> sp.	Main stem	
<i>Lixus punctiventris</i> Boheman	<i>Senecio</i> sp.	Main stem	
<i>Lixus fasciculatus</i> Boheman	<i>Artemisia vulgaris</i>	Main stem	
<i>Lixus bardanae</i> (Fabricius)	<i>Rumex crispus</i> L. <i>R. patientia</i> L.	Main stem	Gültekin <i>et al.</i> 2004
<i>Lixus</i> sp. n. pr. <i>korbi</i> Petri	<i>Beta trigyna</i>	Main stem	
<i>Lixus scolopax</i> Boheman	<i>Echinops sphaerocephalus</i> L. <i>Centaurea solstitialis</i> L. <i>Centaurea</i> sp.	Main stem	
<i>Lixus rubicundus</i> Zoubkoff	<i>Kochia prostrata</i> (L.) Schrad. <i>Chenopodium</i> sp.	Stem and branch	
<i>Lixus korbi</i> Petri	<i>Beta corolliflora</i> Zoss. <i>B. trigyna</i> Waldst. et Kit.	Stem and branch	
<i>Lixus filiformis</i> (Fabricius)	<i>Carduus nutans</i> L. <i>C. crispus</i> L.	Stem and branch	Gültekin 2004
<i>Lixus cardui</i> Olivier	<i>Onopordum bracteatum</i>	Stem and branch	Gültekin <i>et al.</i> 2000
<i>Lixus circumcinctus</i> Boheman	<i>Crambe orientalis</i> L. <i>C. tataria</i> Sebeok	Stem and petiole	
<i>Lixus siculus</i> Boheman	<i>Ferula orientalis</i> L.	Petiole	
<i>Lixus farinifer</i> Reitter	<i>Ferula szowitsiana</i> DC.	Petiole	
<i>Lixus cylindrus</i> (Fabricius)	<i>Prangos ferulacea</i> (L.) Lindl.	Petiole	
<i>Lixus</i> sp. n. pr. <i>furcatus</i> Olivier	<i>Prangos</i> sp.	Petiole	
<i>Lixus obesus</i> Petri	<i>Prangos uloptera</i> DC.	Seed capsule	Gültekin 2005

Twenty-three *Lixus* species used plants from six different plant families as host plant and oviposition sites; 14 Apiaceae, 11 Compositae, 8 Chenopodiaceae, 4 Brassicaceae, 2 Polygonaceae, and 2 Caryophyllaceae species were used. The highest number of *Lixus* species is associated with plant families Apiaceae (7), Compositae (6), and Chenopodiaceae (6) (Table 1). Of these plants, *C. nutans*, *O. bracteatum*, *C. solstitialis*, and *R. crispus*, are important weeds in the region

(Gültekin *et al.* 2000, 2004, Gültekin 2004, Cristofaro *et al.* 2002).

Associations of host plants with *Lixus* at the subgeneric level show an overlap with different plant families in some subgenera. The subgenus *Eulixus* used Apiaceae, Caryophyllaceae, Chenopodiaceae, Brassicaceae; *Dilixellus* Reitter used Chenopodiaceae, Compositae, and Polygonaceae. Some subgenera deal with host plant groups as a tribe or a family level in this study

area-*Epimeces* Billberg used only Cardueae tribe (Compositae); *Callistolix* used only Apiaceae; *Compsolix* Reitter and *Lixogylptus* Reitter used only Brassicaceae.

The species *Prangos* Lindl., *Ferula* L. and *Tchihatchewia isatidea* Boiss. can be important bio-indicators of the degree of erosion. *T. isatidea* grows in the peculiar conditions of steep, dry detritus or clay slopes in the northeastern Anatolian mountains, this highly moveable substrate, though providing easy access to water is subjected to erosion and abrasion and holds the characteristic vegetation of a few species of Brassicaceae (Korotyayev & Gültekin 2003). *Prangos* and *Ferula* species grow under similar characteristic conditions of dry detritus or clay slopes in the high afforested mountains in eastern Anatolia, also subjected to erosion and abrasion where apparently, these plants can be highly important plant groups in avoiding the negative effect of erosion and abrasion.

Differences in oviposition places and marks can help distinguish related species in the field. Also, these ecological characteristics can help differentiate near species. For instance, *L. furcatus* and *L. sp. n. pr. furcatus* are sibling species. It is not easy to distinguish these two species taxonomically, except for the apical part of aedeagus. On the other hand, ecological niches of immature stages are clearly different as indicated above. *Lixus korbi* and *L. sp. n. pr. korbi* are closely related species, but their oviposition behaviors are different. The latter lays eggs connected to each other (Fig. 1e), the former lays eggs clearly distant from each other (Fig. 1f). Consequently, these behavioral traits can serve to reflect taxonomic characters and thereby clarify relationships between species. The data could be useful as a systematic tool, but more so in understanding these behaviors in the ecological context.

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