Taxonomy, ecology, and phylogeny of species of *Lophyra* Motschulsky 1859, subgenus *Eriolophyra* Rivalier 1948 (Coleoptera Cicindelidae)

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A key is provided for the identification of the five species of the subgenus *Eriolophyra* Rivalier 1948 of the genus *Lophyra* Motschulsky 1859 (Coleoptera Cicindelidae): *L. (E.) alba* (Horn 1894); *L. (E.) albens* (Horn 1895); *L. (E.) arnoldi* (Horn 1904); *L. (E.) barbifrons* (Boheman 1848); and *L. (E.) somalia* (Fairmaire 1882). The taxonomy of this subgenus is reviewed and *Lophyra (Eriolophyra) barbifrons marqueza* (Périniguey 1896) is placed as a synonym of *L. (E.) barbifrons*. Information about the ecology of species of *Lophyra (Eriolophyra)* is summarized: *Lophyra (Eriolophyra) alba*, *L. (E.) albens*, and *L. (E.) arnoldi* are associated with sandy riverine areas in southern, central, and west-central Africa, respectively, while *L. (E.) barbifrons* and *L. (E.) somalia* are associated with coastal sand beaches in southern and eastern Africa, respectively. Descriptions of adult foraging, thermoregulatory, reproductive, and defensive behaviors are provided for *L. (E.) alba*, based on recent observations at sites along the Letaba River in Kruger National Park, South Africa. A hypothesis of phylogenetic relationships is proposed for the five species of the subgenus *Eriolophyra* on the basis of adult morphological characteristics. Morphological characters suggest that this group forms a monophyletic clade within the broader complex of species allied to *Lophyra*.

**KEY WORDS:** *Eriolophyra*, Cicindelidae, ecology, phylogeny, morphology, distribution.
INTRODUCTION

Tiger beetles (Coleoptera Cicindelidae) have long been one of the most popular insect groups among amateur and professional entomologists (Acorn 2001, Pearson & Vogler 2001). In recent years, these beetles have also come to the attention of conservation biologists, due to the fact that population declines have been noted in many species. Many of these declines can be attributed to human activities, including urbanization, dam construction, and recreational use of sensitive habitat areas (Graves & Brzoska 1991, Knisley & Schultz 1997). As a result, species of tiger beetles are protected under the biodiversity laws of many countries (Pearson & Cassola 1992, Cassola & Pearson 2000, Pearson & Vogler 2001, Pearson et al. 2006).

Coastal and riverine tiger beetle species appear to be especially sensitive to anthropogenic disturbances (Knisley & Schultz 1997). Human recreational use of coastal and riverine beaches has been directly responsible for declines in several North American tiger beetle species, including Cicindela dorsalis dorsalis Say 1817 and Cicindela puritana Horn 1871, whose larvae are easily trampled by vehicular and human foot traffic on beaches (Hill & Knisley 1993, 1994).

Information about the ecology and taxonomy of tiger beetles has played an important role in the development of conservation strategies for these insects (Knisley & Schultz 1997). While much is known about the ecology of North American and European tiger beetles (Knisley & Schultz 1997, Pearson et al. 2006), very little has been published on the ecology of most African tiger beetle species (Guppy et al. 1983, Fähr 1998, Mawdsley & Sithole 2008).

The present paper is an outgrowth of recent ecological studies of riverine tiger beetles in Kruger National Park, South Africa (Mawdsley & Sithole 2008). These surveys have produced the first detailed information about the ecology of the riverine species Lophyra (Eriolophyra) alba (Horn 1894), which is presented for the first time below. In preparing the notes on this species for publication, however, it became apparent that a more substantial paper was needed on the taxonomy of the subgenus Eriolophyra Rivalier 1948 of Lophyra Motschulsky 1859. Although the five species of this subgenus were recently illustrated by Werner (2000), this work did not include a key to the species of this subgenus, nor did it include an analysis of the phylogenetic relationships among species of Lophyra (Eriolophyra) using modern cladistic approaches. I have therefore reviewed the taxonomy of this group and prepared a key to species and a provisional cladistic analysis of the species of this subgenus.
Genus *Lophyra* Motschulsky 1859

Subgenus *Eriolophyra* Rivalier 1948

References. Rivalier 1948 (as genus); 1957 (subgenus of *Lophyra*); Wiesner 1992 (subgenus of *Lophyra*); Werner 2000 (subgenus of *Lophyra*).

Type species. Cicindela barbifrons Boheman 1848 (designation by Rivalier 1957).

**Diagnosis.** Important diagnostic features for the genus *Eriolophyra* include:

- Elytra predominantly ivory-white; dark elytral ground color reduced to narrow dark linear markings or entirely absent; one species with four dark quadrate areas on each elytron;
- Frons, pronotum, antennomeres 1-4, venter, and legs metallic coppery (occasionally metallic green);
- Frons, pronotum, scape, antennomeres 3-4, venter, and legs with dense suberect and erect white setae;
- Pretarsal claws enlarged and elongate, nearly as long as tarsomeres;
- Antennomeres 1-4 metallic coppery-black; antennomeres 5-11 yellow;
- Antennomere 4 in male often with erect sensory setae, which may take the form of a “penicillum” (sensu Cassola 1983);
- Associated with coastal beaches or sandy riverine microhabitats in sub-Saharan Africa.

Separation from allied genera and subgenera. Species belonging to two other tiger beetle taxa, *Habrodera* Motschulsky 1862 and *Lophyra* (*Lophyra*) Motschulsky 1859, have elytra with expanded white or pale yellow markings and are found in riverine or coastal beach habitats in sub-Saharan Africa where they might be confused with species of the subgenus *Eriolophyra* (Werner 2000). Species of *Lophyra* (*Lophyra*) can be readily separated from species of subgenus *Eriolophyra* by the lack of dense white setae, especially on the frons, scape, pronotal disc, and legs, and by the less extensive white or yellow areas on the elytra. The few species of *Lophyra* (*Lophyra*) with expanded white or yellow elytral markings (such as *L. (L.) candida* Dejean 1825) can be readily distinguished from the species of subgenus *Eriolophyra* by the lack of dense white setae on the frons, scape, pronotal disc, and legs. Species of the genus *Habrodera* have expanded lobes on either side of the pronotal base which give the pronotum a trapezoidal shape when viewed from above. In addition, the species of *Habrodera* have the dark areas of the elytra distinctly impressed, whereas the dark areas of the elytra of species of subgenus *Eriolophyra* are not impressed.

Notes on status. *Eriolophyra* was described by Rivalier (1948) as a separate genus, distinguishable from *Lophyra* on the basis of the significant differences in vestiture and elytral markings. Rivalier (1957) subsequently placed *Eriolophyra* as a subgenus of *Lophyra*, based on similarities in the structure of the internal sac of the male genitalia. This classification was followed by subsequent authors, including Wiesner (1992) and Werner (2000)
in their treatments of global and African Cicindelidae, respectively. Although
the exact relationships of the species currently classified within *Lophyra* and
allied genera are unclear, the group of species now classified in subgenus *Eriolophyra*
forms a distinct and probably monophyletic group. Other, similar
groups of species within the broader *Lophyra* complex are now recog-
nized at the generic level, including *Habrodera* Motschulsky 1862 and *Chaeto-
todera* Jeannel 1946 (Wiesner 1992, Werner 2000). It is possible that similar
treatment will eventually be proposed for subgenus *Eriolophyra*. However,
the status of the group of species currently classified in the subgenus *Lophyra*
(*Lophyra*) is far from clear, and *Lophyra* (*Lophyra*) may well be paraphyle-
etic relative to *Lophyra* (*Eriolophyra*). Any nomenclatural change would
need to be based on a more comprehensive revisionary study of the *Lophyra*
generic group that identifies clearly monophyletic lineages within the group
of species now classified in the subgenus *Lophyra* (*Lophyra*).

### KEY TO SPECIES

1. Elytra elongate, slender, more than 1.7 times longer than wide; associated
with sandy beaches and other riverine microhabitats in Cameroon, Chad,
Mali, Niger, and Senegal, possibly also the Central African Republic..........
........................................................................................................... *L. (E.) arnoldi* (Horn 1904)
  — Elytra stouter, 1.7 times longer than wide or less; Congo River basin, eastern
Africa, or southern Africa................................................................. 2

2. Frons with two clusters of dense white setae along anterior margin; sea
beaches of eastern South Africa and southern Mozambique....................
........................................................................................................... *L. (E.) barbifrons* (Boheman 1848)
  — Frons with two linear bands of dense white setae, extending from anterior
margin to vertex; distribution not as above............................................ 3

3. Each elytron white with four quadrate brownish-black markings; sea
beaches of northern Kenya and southern Somalia.................................
........................................................................................................... *L. (E.) somalia* (Fairmaire 1882)
  — Elytra white with narrow linear markings; riverine species.......................... 4

4. Elytra broad and robust in both sexes, 1.4-1.5 times longer than wide;
lateral margin of elytra strongly expanded at basal third in both sexes;
smaller species, length 10-13 mm; Congo River basin..........................
........................................................................................................... *L. (E.) albens* (Horn 1895)
  — Elytral form sexually dimorphic: broad and robust in female only, elytra
1.3 times longer than wide in female, 1.6 times longer than wide in male;
lateral margin of elytra expanded at basal third in female only; larger spe-
cies, length 14-16 mm; Mozambique, Namibia, South Africa, Tanzania,
Zimbabwe.......................................................................................... *L. (E.) alba* (Horn 1894)

*Lophyra* (*Eriolophyra*) *alba* (Horn 1894)

References. Horn (1894: 112; 1915: 268; 1926: 144; 1938: pl. 39 f. 8), Peringuey
Taxonomy of *Lophyra* (*Eriolophyra*)

*Type locality.* “Africa orient. (Quelimane)” (Horn 1894).

*Diagnosis.* A large tiger beetle (length 14-16 mm) with predominantly white elytra associated with riverine sandbars and other unconsolidated sand deposits along major river systems in southern Africa. The elytral shape is sexually dimorphic, with males having elongate elytra with acuminate apices (length 1.6-1.7 times longer than width) and females having very broad, trapezoidal-shaped elytra which are broadly rounded at the apex (length 1.3-1.4 times longer than width). The elytra are predominantly ivory-white, with narrow linear coppery-brown markings.


*Lophyra (Eriolophyra) albens* (Horn 1895)


*Type locality.* “Brazzaville (Afr. occid.)” (Horn 1895).

*Diagnosis.* A moderately sized (length 10-13 mm) tiger beetle with white elytra associated with riverine sand bars in the Congo River basin. The elytra are broadly expanded in both sexes, with length 1.4-1.5 times the width. The elytra are predominantly ivory-white with narrow linear brown or black markings.

*Known distribution.* République Democratique du Congo: Kasai Province, Djeka (Werner 2000); Kondu (Burgeon 1937); Lusambo (Werner 2000); Mobayi-Mbongo [formerly Banzyville]; Pool Malebo [formerly Stanley Pool] (Burgeon 1937). République du Congo: Brazzaville (Horn 1895).

*Lophyra (Eriolophyra) arnoldi* (Horn 1904)

Type locality. “Benue sup.” (HORN 1904).

Diagnosis. A smaller (length 9-11 mm) riverine tiger beetle with predominantly white elytra from West Africa. The elytra are more slender than other species of *Lophyra (Eriolophyra)*, with length 1.8-1.9 times the width. Elytral markings are similar to those of *L. (E.) alba* and *L. (E.) albens*, with narrow greenish or coppery markings on otherwise ivory-white elytra.


Specimen examined. Mali: Koulikoro (1 male, NMNH).

*Lophyra (Eriolophyra) barbifrons* (Boheman 1848)


Type locality. “in Caffraria interiore” (BOHEMAN 1848).


Diagnosis. A smaller (length 9-11 mm) tiger beetle with white or predominantly white elytra, occurring on coastal sea beaches in South Africa and Mozambique. The elytra are either entirely white or have a series of small vittate and/or maculate coppery-brown markings. When present, the dark markings of the elytra are not impressed as in species of *Habrodera*. The presence of dense white pubescence on the pronotum, antennal scape, antennomeres 3-4, and legs will readily separate it from sympatric species of *Lophyra (Lophyra)* and *Habrodera*.

Known distribution. Mozambique: Inhambane Province, Praia de Quissico; Joao Belo Province, Praia de Chidenguela (CASSOLA 1975); Maputo Province, Maputo Bay [formerly Delagoa Bay] (HORN 1915). South Africa: Eastern Cape Province: Port Elizabeth (HORN 1915); KwaZulu-Natal Province: Durban (PÉRINGUEY 1896); mouth of Tugela River (CASSOLA 1975, WERNER 2000, BRZOSKA & CASSOLA 2005); Manzengwenya (WERNER 2000); Sipongo [formerly Tsipongo] (PÉRINGUEY 1896).

Specimens examined. Mozambique: Gaza Province: Chonguene, XII.1972 (1 male, NMNH). Maputo Province: Beach E of Rikatla, XII (4 males, 1 female, NMNH); Inhaca,
Taxonomy of *Lophyra* (*Eriolophyra*)

I.1973 (1 male, TMSA, 2 females, NMNH, 1 female, SANC); Lourenco Marques, XII.1908 (1 male, 1 female, TMSA), II.1957 (1 male, 1 female, NMNH). South Africa: KwaZulu-Natal Province: Cosy Bay mouth, sandy sea-shore, 5.XII.1992 (10 males, 2 females, TMSA); Doonside, 10.XII.1937 (1 female, SANC); Durban, 1896 (1 female SANC), III (3 males, 1 female, NMNH), 27.III.1920 (1 male, 1 female, TMSA); Gingindlovu, 30.XII.1977 (1 female, SANC); Illovo Beach, 25.I.1984 (1 male, 1 female, TMSA); Isipingo, XII.1895 (1 female, TMSA); Manzengwenya, 30.XII.1979 (1 female, SANC); Mtuzini, II.1953 (13 males, 8 females, TMSA); N. Lemare, II.1953 (1 male, TMSA); Sordwana Bay, I.1939 (1 male, 1 female, SANC), I.1949 (2 males, 1 female, SANC); Tongaat, 1909 (6 males, TMSA); Turton, 30.I.1971 (1 male, 3 females, TMSA), 15.II.1971 (3 males, 4 females, TMSA); Umdoni Park, 18.III.1971 (1 male, TMSA); Umgeni (1 male, TMSA). Western Cape Province: Jackalswater, between Springbok and Uranoep, II.1953 (1 female, TMSA).

Discussion of synonymies. Péringuey (1896) treated the species now known as *L. (E.) barbifrons* under the name *Cicindela chrysographa* Dejean 1831. However, the taxon originally described by de Jean (1831) as *Cicindela chrysographa* is not conspecific with *L. (E.) barbifrons* and is in fact now considered a doubtful subspecies or synonym of *Habrodera capensis* (Linnaeus 1764) (Wiesner 1992, Werner 2000). *Cicindela chrysographa* Péringuey 1896 must therefore be considered a primary junior homonym of *Cicindela chrysographa* Dejean, as well as a synonym of *Cicindela barbifrons* Boheman.

Péringuey (1896) also described a form *Cicindela chrysographa* var. *marqueza* from Delagoa Bay, Mozambique. This form differed morphologically from the nominate form in having its elytra entirely white, without any dark ground color present (Péringuey 1896). *Cicindela chrysographa* var. *marqueza* was subsequently placed as a synonym of *Cicindela barbifrons* Boheman by Horn (1915, 1926). It was not treated as a valid taxon by Rivalier in his revision of *Lophyra* (Rivalier 1948) or his more comprehensive treatment of African cicindelines (Rivalier 1957). The name was treated by Wiesner (1992) as a subspecific epithet and it was considered a doubtful subspecies of *L. (E.) barbifrons* by Werner (2000).

As noted by Péringuey (1896), adults which have the elytra entirely white are found in populations of *L. (E.) barbifrons* in both Mozambique and KwaZulu-Natal. In the NMNH collection, I examined a small series from Durban, KwaZulu-Natal, which contained one entirely white specimen, two specimens with the dark elytral markings as described by Boheman (1848), and two specimens with reduced dark markings. I also examined an entirely white specimen from Rikatla, Mozambique, as well as two specimens from Delagoa Bay which had the dark elytral markings as described by Boheman (1848). Although morphologically distinct, the form with entirely white elytra is not localized to a specific geographic area and is therefore not worthy of recognition on a subspecific level. The name *Cicindela chrysographa* var. *marqueza* Péringuey should therefore be treated as a synonym of *L. (E.) barbifrons* (Boheman).

*Lophyra* (*Eriolophyra*) *somalia* (Fairmaire 1882)

Type locality. Not specified in the original description, but the introduction to Fairmaire (1882: 1) indicates that it should be “le pays des Comalis.”

Diagnosis. A small (length 10-12 mm) white tiger beetle of coastal sea beaches in northern Kenya and southern Somalia. Each elytron has four quadrate dark brownish-black maculae which are subequal in size and arranged in a line on the elytral disc. The maculae may be more or less distinct in individual specimens.


Specimens examined. Somalia: Gesira, 20 km SW Mogadishu, 29.IV.1987 (1 male, 1 female, SANC).

ECOLOGY

Species of the subgenus Eriolophyra are inhabitants of riverine or coastal sand beaches in sub-Saharan Africa. Werner (2000) provided an overview of the biology of the species of this genus. Two species, L. (E.) barbifrons and L. (E.) somalia, are associated with coastal sand beaches in southern and eastern Africa, respectively (Perringuey 1896, Cassola 1975, Werner 2000). The remaining species are associated with sandy riverine areas in southern Africa (L. (E.) alba), central Africa (L. (E.) albens), and west and north-central Africa (L. (E.) arnoldi) (Werner 2000). Lophyra (Eriolophyra) alba has also been collected at lights at night (Werner & Wiesner 1994).

Cassola (1975) presented information about the ecology of L. (E.) barbifrons at sites in Natal and Mozambique. He characterized this species as a “halophilous, seashore-inhabiting species” and noted that “large ocean beaches” were its “typical habitat” (Cassola 1975). Earlier, Perringuey (1896) had noted that this species “do[es] not occur far from the seashore.” Brzosa-Ka & Cassola (2005) reported recent collections of this species at the mouth of the Tugela River, where adults were collected “on the sea-facing slope of the coastal sand dunes”.

Cassola & Miskell (1990), Naviaux (1980), and Werner (2000) presented information about the ecology of L. (E.) somalia, which appears to have similar habits to L. (E.) barbifrons, except that it is found on sea beaches in Somalia and northern Kenya (“sur les grande plage de sable” according to Naviaux 1980: 220).

In November, 2007, I studied the ecology of L. (E.) alba at sites along the Letaba River in Kruger National Park, South Africa. A single male of this species was collected at 2 PM on 18 November, 2007, during routine surveys for riverine tiger beetle species (described by Mawdsley & Sithole 2008). This individual was collected away from the main river channel on a dry, sandy riverbank overlooking the riverine floodplain. This section of
riverbank was actively eroding and the single individual of *L. (E.) alba* was collected in an area of dry, eroding, unconsolidated sand. Other tiger beetle species present at this site included *Lophyra (Lophyra) differens* (Horn 1892) and *Lophyra (Lophyra) neglecta intermediola* (Horn 1921).

On 19 November, 2007, I found a large population of *L. (E.) alba* on a very large sand dune located in the floodplain of the Letaba River (Fig. 1). The dune was triangular in shape, approximately 30 m wide, 50 m long, and 5 m high, with a broad, flat top and steep sides. The dune was composed entirely of fine dry unconsolidated yellow sand, and lacked associated vegetation. Over 50 adult *L. (E.) alba* were observed on or near this dune. Activity of the adults of *L. (E.) alba* was confined to the top surface and sides of the sand dune and to a small wash or gully that cut through the dune and led to the main channel of the Letaba River approximately 100 m away.

Foraging, reproductive, and thermoregulatory behaviors of *L. (E.) alba* were observed at this site. In general, these behaviors are similar to those described for other tiger beetles (Knisley & Schultz 1997). Foraging behavior consists of short (1-3 m) runs, after which the beetle pauses briefly, and then runs again. This behavior is repeated continuously. Adult *L. (E.) alba*

![Fig. 1. — View of the Letaba River in Kruger National Park, photographed from the south end of the high water bridge on the H1-6 main tourist road northwest of Letaba Rest Camp. The white arrow indicates the most productive collecting site for *Lophyra (Eriolophyra) alba*, while the black arrow indicates a collecting area for *Chaetodera regalis*.](image-url)
were observed feeding on small ants and other small arthropods: as with other cicindelids, prey is captured using the mandibles, masticated using the mandibular bases, and held by the maxillary and labial palpi against the buccal cavity for feeding. Beetles along the base of the dune and along the course of the small wash or gully exhibited amplexus, mating, and oviposition behaviors. All oviposition sites were in loose dry unconsolidated sand. Adult beetles exhibited the full range of thermoregulatory behaviors reported in tiger beetles (Knisley & Schultz 1997), including basking, stilting, shuttling, and burrowing in loose sand.

The ivory-white dorsal coloration of *L. (E.) alba* is strongly cryptic on the loose yellow sand surface, and the adult beetles are not easily detected except when disturbed. Adult *L. (E.) alba* have several defensive behaviors. If approached closely, their first response is to stop moving and remain motionless for a short period. This behavior renders them quite inconspicuous against the sand. If the disturbance continues, the beetles will fly. Escape flights are short and straight, with most between 5-10 m. Upon landing, the beetles often remain motionless for a short period of time, after which they resume normal foraging behaviors. If captured, the beetles will attempt to bite and will also regurgitate a black liquid from the digestive tract. I did not detect a chemical odor when collecting the adult beetles.

Three other species of tiger beetles were observed in the small gully near the dune with *L. (E.) alba*: *Lophyra (Lophyra) differens* (2 individuals), *Lophyra (Lophyra) neglecta intermediola* (1 individual), and *Chaetodera regalis* (Dejean 1831) (1 individual). Continued investigation of this general area led to the discovery of large populations of tiger beetles on a very large riverine sandbar which was located approximately 100 m from the dune. Tiger beetles observed on this sandbar included *Chaetodera regalis* (over 100 individuals) and *Calomera fimbriata imperatrix* (Srńka 1891) (2 individuals).

Potential predators or parasites of *L. (E.) alba* were not observed at this site, although large robber flies (Diptera Asilidae) and dragonflies (Odonata Anisoptera) capable of capturing adults of *L. (E.) alba* were observed at the large riverine sandbar nearby.

Voucher specimens from these observations are deposited in the following collections: KNPC, NMNH, SANC, TMSA (see Acknowledgments for explanation of abbreviations).

**PHYLOGENETIC RELATIONSHIPS**

The phylogenetic relationships of *Lophyra* and several closely allied genera and subgenera (the genera *Chaetodera* and *Habrodera*, and the subgenera *Lophyra* (*Eriolophyra*) and *Lophyra* (*Stenolophyra* Rivalier 1957)) have not been studied in detail. The following 10 morphological characters have been used by previous authors (Horn 1915; Rivalier 1948, 1957; Werner 2000) to diagnose and separate species within the subgenus *Eriolophyra*.

1. Clypeus with white setae laterally, glabrous medially (0) / clypeus setose across entire width (1).
2. Scape lacking white setae (0) / scape with white setae (1).
3. Antennomeres 3-4 lacking white setae (0) / antennomeres 3-4 with white setae (1).
4. Frons with dense white setae limited to clusters along the anterior margin (0) / frons with lines of white setae extending onto vertex of head (1).
5. Pronotal disc glabrous (0) / pronotal disc with dense white setae (1).
6. Elytra not broadly expanded in female, length 1.5 times width or greater (0) / elytra broadly expanded in female, length 1.3-1.4 times the width (1).
7. Elytral epipleurae in female straight or broadly and uniformly rounded, lacking lobe-like lateral expansion at basal third (0) / with lobe-like lateral expansion at basal third (1).
8. Elytral shape subequal in both sexes (0) / sexually dimorphic, broader in female than in male (1).
9. Dark elytral ground color extensive, covering 50% or more of elytral surface (0) / dark elytral ground color reduced, with more than 50% of elytral surface white (1).
10. Abdominal sternites with white setae laterally (0) / with white setae medially as well as laterally (1).

The distribution of these characters within the subgenus *Eriolophyra* is shown in Table 1. I have included a species of *Lophyra* (*Lophyra*), *L. (L.) neglecta* Dejean 1825, as an outgroup taxon for purposes of cladistic analysis. *Lophyra* (*Lophyra*) *neglecta* is a fairly generalized species of *Lophyra* (*Lophyra*) and is widespread throughout sub-Saharan Africa (Wiesner 1992, Werner 2000). Character states present within *L. (L.) neglecta* were provisionally interpreted as plesiomorphic (0) while the character states absent in *L. (L.) neglecta* but present within various species of *Eriolophyra* were provisionally interpreted as apomorphic (1).

The matrix in Table 1 yields a single most parsimonious cladogram (Fig. 2) under standard maximum parsimony analysis using the algorithm of Farris (1970). This cladogram shows four clear synapomorphies for this

<table>
<thead>
<tr>
<th>Species</th>
<th>Character number</th>
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<tbody>
<tr>
<td>L. (L.) neglecta</td>
<td>0 0 0 0 0 0 0 0 0 0</td>
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<tr>
<td>L. (E.) somalia</td>
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subgenus (the derived states of characters 2, 3, 5, and 9) relative to \textit{L. (L.) neglecta}. \textit{Lophyra (Eriolophyra) barbifrons} is the sister-species to the four other species of \textit{Eriolophyra}, which are united by two synapomorphies (the derived states of characters 1 and 4). Within this group of four species, \textit{Lophyra (Eriolophyra) somalia} is the sister-species to the three other species, which are united in a clade by one synapomorphy (the derived state of character 10). These three species also share a similar elytral color pattern (Werner 2000). Finally, \textit{L. (E.) alba} and \textit{L. (E.) albens} are clearly sister-species, united by two synapomorphies (the derived states of characters 6 and 7). The derived state of character 8 is an autapomorphy of \textit{L. (E.) alba}.

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Taxonomy of Lophyra (Eriolophyra)


