Laevicaudata catalogus (Crustacea: Branchiopoda): an overview of diversity and terminology

D. Christopher Rogers * , 1 & Jørgen Olesen 2

1 Kansas Biological Survey, Kansas University, Higuchi Hall, 2101 Constant Avenue, Lawrence, KS 66047-3759 USA; D. Christopher Rogers [Branchiopod@gmail.com] — 2 Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark; Jørgen Olesen [jolesen@snm.ku.dk] — * Corresponding author

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Abstract

The Laevicaudata (smooth clam shrimp) are a small group of freshwater bivalved branchiopod crustaceans in need of taxonomic revision. Here the extant Laevicaudata are defined and diagnosed according to modern standards, and synapomorphies are listed, discussed, and illustrated. A catalogue of the Laevicaudata is presented with synonyms and some taxa are partially revised. One hundred and three recent laevicaudatan taxa are presented, of which thirty-nine are considered valid species. Chresonyms are provided for taxa redescribed according to modern standards. Furthermore we designate a neotype for *Lynceus brachyurus* Müller, 1776. This species catalogue will provide a basis for further taxonomic revision and phylogenetic work within the Laevicaudata.

Key words

*Lynceus*, *Paralimnetis*, *Lynceiopsis*, checklist, synapomorphies.

1. Introduction

The Laevicaudata (smooth clam shrimp; Figs. 7, 8) are a small group of freshwater dwelling bivalved branchiopod crustaceans long grouped with other bivalved branchiopods (Spinicaudata and Cyclestherida), but morphological and molecular studies have recognized them as distinct from these (e.g., Linder 1945; Fryer 1987; Olesen 1998; Richter et al. 2007). Laevicaudatans have been well known since the 1700s with the first species (*Lynceus brachyurus*) described by the Danish naturalist O.F. Müller in 1776 from temporary spring pools, and with very few comprehensive reviews or revisions since. Daday (1913c, 1927) presented 17 species in two genera, however six species presented as new in his 1913c key were not described until his 1927 monograph. Martin & Belk (1988) revising the New World forms, reported 37 species in three genera globally. Brtek (1997) reported 35 species in three genera as valid, and then in 2002, considered only thirty-four valid species in three genera. None of these studies addressed fossil forms. Since that time the only important revisionary work on the genus was Timms (2004) revision of the Australian species.

Current laevicaudatan taxonomy is confusing in several regions and is clearly in need of a revision, initiated already (e.g., Rogers et al. 2016). In many cases the descriptions are ultrabrief or poorly illustrated, which, combined with the occasional apparent absence of accessible type material, make the group difficult to handle taxonomically (Rogers et al. 2016). As a basis for further work with laevicaudatan taxonomy, we provide here a checklist, or catalogue, of the recent species that we consider valid prior to an eventual larger revision of the taxonomy in various parts of the world.

In total there are one hundred and three recent taxa presented in this catalogue under the order Laevicaudata, including one
valid family, three valid genera, and 39 valid recent species. Some 61 taxa are considered synonyms, homonyms, nomina nuda, or nomina dubia. Chresonyms are provided for taxon redescriptions to facilitate identification and evolutionary relationships.

We did not include fossil forms. Branchiopod crustaceans do not preserve well, being very soft bodied (Tasch 1969; Schram 1986), and the fossil laevicaudatan taxa are very poorly understood and described (Tasch 1956, 1969).

We also provide a diagnosis of the Laevicaudata and give a preliminary discussion of some important morphological variation within the group as a basis for future phylogenetic considerations, all primarily based on recent papers on laevicaudatan taxonomy and morphology in which the authors have been involved (Olesen 2005; Pessacq et al. 2011; Olesen et al. 2013, 2016; Kaji et al. 2014; Sigvardt & Olesen 2014; Rogers et al. 2015, 2016).

2. Catalogue structure

The catalog portion follows the format of the recent catalogs on branchiopod (Rogers 2013) and decapod crustaceans (e.g., Ng et al. 2008; De Grave & Fransen 2011). Supraspecific taxa are presented in bold. Genera and species are presented alphabetically. Subgenera and subspecies are presented with the nominate taxon listed first. Synonyms are presented following an equal sign (=). Where an important analysis is presented for a synonymy, a reference is provided as “fide” the synonymizer. For example: = Lynceus caeca (Joseph, 1882) (attributed to L. brachyurus, fide Bretek 1997). Chresonyms are presented parenthetically after the original author and date, and are referred to as “in the sense of” the redescriptor. For example: Lynceus tatei (Brady, 1886) (sensu Timms 2013).


3. Laevicaudata synapomorphies

Laevicaudatans are a morphologically distinct group of clam shrimps within the Branchiopoda. Laevicaudata shares with other clam shrimps (Spinicaudata and Cyclestherida) the presence of a large bivalve carapace which encloses the body, and, at least at the general level, similarly shaped phyllopodous thoracopods of which the first pair(s) in males is modified as claspers composed of quite similar parts. Sars (1867) grouped all clam shrimps in the taxon ‘Conchostraca’, one of the four higher level categories in which he divided the Branchiopoda, the other three being Anostraca, Notostraca, and Cladocera. Lindner (1945) was the first to point out that ‘Conchostraca’ masked significant differences between two groupings of clam shrimps which he named Laevicaudata and Spinicaudata (in which Cyclestheria was included). A first (but not full) step in abandoning ‘Conchostraca’ was taken by Fryer (1987), who supported further Lindner’s (1945) distinction between two separate groups of clam shrimps (Laevicaudata and Spinicaudata, again without separating Cyclestheria). Later phylogenetic approaches involving both morphological and molecular data have indeed shown no basis for upholding ‘Conchostraca’ as a taxon of branchiopod clam shrimps, but instead that these are better treated taxonomically as three separate groups, Laevicaudata, Spinicaudata, Cyclestherida (Olesen 1998, 2000, 2007; Braband et al. 2000; Stenderup et al. 2002; Richter et al. 2007).

Since the first characterization of Laevicaudata by Lindner (1945) no serious concerns about its validity or monophyly has been expressed, probably due to the shared distinct morphology of its members. In the few phylogenetic treatments involving molecular data there is always support for the Laevicaudata, but only rather few species of Lynceus have been included (e.g., three in Richter et al. 2007), and never any species of Paralimnetis or Lynceopsis.

We present the more obvious of the many synapomorphies of the Laevicaudata mostly relating to external morphology of both adults and larvae. We treat some of the known variation within Laevicaudata in order to identify possible character systems for a future morphology based laevicaudatan phylogeny. We also will consider the morphological origin within the Branchiopoda of some aspects of the unusual laevicaudatan morphology.

3.1. Carapace: smooth, globular, true hinge dorsally. Several aspects of the bivalved laevicaudatan qualify as putative separate synapomorphies: (1) It is smooth (Figs. 1D,E, 2M–O), e.g., without growth lines as those seen in Spinicaudata, Cyclestherida, and some cladocerans (see Olesen 1998). Lindner (1945) reported on an undescribed laevicaudatan with one growth line on its carapace, but this material has never been restudied. (2) The two valves of the carapace form a rather globular/rounded unit. (3) The two valves of the carapace are dorsally hinged to-
gether in a more complicated way than in Spinicaudata and Cyclesterida. In these two latter taxa the hinge is a simple anterior-posterior fold in the dorsal midline of the carapace, whereas the fold area in Laevicaudata is invaginated (Fig. 2J,N,O) yielding two distinctly separate carapace valves (= a truly bivalved carapace). The invaginated hinge area is seen clearly when the carapace is closed (Fig. 2J), while it is hidden by the dorsal margins of the carapace valves when the carapace is open (Fig. 2K). This type of dorsal hinge seemingly prevents the carapace being opened more than about 45°, an angle seen very common in for example mating males (Figs. 2K, 3A; Siguardt & Olesen 2015).

3.2. Head size, articulation between head and body, rostrum shape. Several aspects of the laevicaudatan head qualify as separate synapomorphies: (1) The head of laevicaudatans (= part anterior to dorsal cervical suture where the mandibles insert) is characteristically crescent shaped and very large occupying sometimes more than half of the entire body volume (e.g., females of L. grandirostris, Fig. 1). (2) Another speciality of the Laevicaudata is the articulation between the head and the remaining part of the body (the cervical suture) allowing for extending the head anteriorly between the carapace valves, something which, to our knowledge, is not seen in Spinicaudata or Cyclesterida. (3) The rostrum is a large and dominating part of the head in Laevicaudata. There is much variation in shape and ornamentation of the rostrum, which may be of phylogenetic importance but only a few aspects are highlighted here. In males the rostrum is wide and truncated distally (to maintain position on female carapace during mating, Fig. 2K and Siguardt & Olesen 2014), sometimes terminating in a dorsoventrally flattened margin as in L. brachyurus and L. grandirostris (e.g., Siguardt & Olesen 2014; Rogers et al. 2015), sometimes in a large, setose field as in L. insularis (Olesen et al. 2016). The shape of the rostrum in females vary between being truncated (e.g., Paralimnetis texana), rounded (e.g., L. gracilicornis), or pointed (e.g., L. brachyurus and L. grandirostris). Much variation is also seen in the ornamentation of the rostrum, such as in the extension of the rostral median carina, which, to mention two extremes, sometimes extends to the tip of the rostrum (e.g., both sexes of L. brachyurus and L. grandirostris), but at other times (in Paralimnetis, Lynceiopsis, and some Lynceus) it bifurcates before the tip of the rostrum. Variation is seen in the lateral setation of the rostrum (e.g., very distinct in L. grandirostris, Fig. 1G), in the specific shape of the fornix which may or may not have sharp ridges on each side (Fig. 1G), in the specific ornamentation of the distal edge of the rostrum which may sometimes be strongly spinose (e.g., L. tatei, Fig. 1J). Much of this variation is probably of phylogenetic significance but will not be explored further here.

3.3. Frontal setal field. In all known laevicaudatans there is a pair of oval or circular setal fields located on either side of the midrostral carina just anterior to the compound eyes (Fig. 1C,K,L). They have been suggested to have sensory (mechanical or chemical) function and are unique to laevicaudatans (Cash-clark & Martin 1994; Fritsch et al. 2013).

3.4. First antennae. Among branchiopods the first antennae of all known laevicaudatans have a unique morphology in being composed of two antennomeres, the distal of which carries setules on the anteriodistal side (Figs. 1B, 2A–C). There is some variation in the relative size of the two antennomeres in various species but the phylogenetic importance of this remains to be tested. In species of Paralimnetis the first antennae are inserted on a short antennomere-like protrusion (Martin & Belk 1988), which seemingly is absent in Lynceus, which therefore is another character of potential importance for the intrinsic phylogeny of the Laevicaudata.

3.5. Second antennae. The second antennae are broadly speaking composed of a proximal peduncle of two antennomeres (coxa and basis) and pair of flagellar rami (endopod and exopod) of approximately the same length (e.g., Fig. 1C,H). There are general similarities to the second antennae of Spinicaudata and Cyclesterida, but the laevicaudatan second antennae are different from these with respect to shorter ramal antennomeres (annuli) and the generally higher number of these. There is some variation in the specific number of rami antennomeres between species but the phylogenetic significance needs to be explored.

3.6. Mandibles. The mandibles of large branchiopods are most often of the rolling-grinding type with a large molar surface occupying most of the gnathal edge (richter 2004). However, among the exceptions are the Laevicaudata, where the gnathal edge of the mandibles is composed of a row of transverse teeth becoming larger and more disparately positioned posteriorly and with a single distinct tooth at the posterior corner (Fig. 2E,F), a type of morphology probably linked to feeding on detritus (see Fryer & Boxshall 2009). A comparable type of morphology of the gnathal edge is present in notostracans (richter 2004), but a phylogenetic signal seems unlikely in the light of the current view on branchiopod phylogeny (Olesen 2007, 2009; Richter et al. 2007). The gnathal edge is known only for relatively few species at the SEM level, but some variation of potential phylogenetic importance seems to be present, both regarding the number of transverse teeth and their ornamentation.

3.7. First and second maxilla. In the few taxa where the first maxilla has been examined in detail, they all have practically the same morphology. In Lynceus insularis (see Fig. 2A,G,H) the first maxilla is a small, lobate, curved structure situated behind the mandible with a setose inner margin and the posterior corner with 3 shorter robust, denticulate spiniform setae, and an additional even shorter seta. Since the same morphology is seen in L. brachyurus (see Sars 1896) and in L. simiaefo-
cies (Fryer & Boxshall 2009) this first maxilla morphology is a candidate for constituting a synapomorphy for Laevicaudata. According to Sars (1896) the second maxilla in *Lyneceus brachyurus* are represented only by a pair of simple, delicate, membranous lobes, but it remains to be determined whether this is unique to Laevicaudata.

3.8. Thoracopods, general shape of exopods, scraper setation, specific type of serial homology. Many unique laevicaudatan features relate to the thoracopod morphology (Fig. 5). Some of them are as follows: (1) A unique shape of the exopods of many limbs, involving a very large, lobate dorsal part. (2) Endites 4 and 5 and endopod elongate and digitiform with rows of scraping setae. Despite the general similarity between thoracopods of laevicaudatans, there seems to be significant variation among the setae of possible phyletic importance but which remains to be explored further. In *Lyneceus insulare*, for example, the endopod and endites 4 and 5 have scraper setae (Fig. 5B,C,F) of a morphology rather similar to those described for *L. simiaeaces* (see Fryer & Boxshall 2009). In contrast the setae on the same limb structures in *L. brachyurus* have a very different morphology. Here the endopod in *L. brachyurus* has no scraper setae and the scraper setae of endites 4 and 5 are very short and characteristically ending in three hooks (Fig. 5D,E).

3.9. Male claspers. The first pair of male thoracopods is modified as claspers by which it clings to the female carapace margin during mating (Fig. 3; Sigvardt & Olesen 2014). Spinicaudata and Cyclestherida males also have claspers. The claspers in all three taxa appear superficially similar being composed of apparently the same parts, but a study of their development suggested partly convergent evolution. In all three taxa the clasper part of the limb consist of basal swollen part on which the other three parts insert, a ‘movable finger’ which is the part operating as a hook during the clasping process and two palps which probably have sensory functions (Kaji et al. 2014). The ‘movable finger’ is homologous across taxa and is the modified endopod of a nonmodified thoracopod. However, the swollen basal part is only partially homologous. Unique to the Laevicaudata, it is composed of elements of three normal thoracopod limb parts, which are endites 3, 4, and 5 (and their corresponding limbs parts). This is contrasted with the Spinicaudata where this part of the clasper does not involve elements of endite 3 (Kaji et al. 2014). Another aspect of the clasper unique to Laevicaudata is a larger diversity in setal forms compared to the Spinicaudata (Fig. 3F–J; Sigvardt & Olesen 2014). Clasper morphology has traditionally been an important taxonomic character within Laevicaudata (e.g., Daday 1927; Martin & Belk 1988; Rogers et al. 2016; Olesen et al. 2016), especially characteristics such as shape and size of the movable finger and the two palps, and the shape of the swollen basal part on which they insert. Probably the morphological diversity of these structures and the specific setal patterns will prove important (for phylogeny) also at higher taxonomic levels.

3.10. Female modified exopods of t9 and t10. In those female laevicaudatans for which details are known (e.g., *Lyneceus brachyurus*, *L. biformis*, *L. insularis*), the egg clusters are carried by specialized, curved exopods with distal setation of thoracopods 9 and 10 (Sars 1896; Ferrari & Grygier 2012; Olesen et al. 2016; see Fig. 4C,D,G–H). Eggs/embryos are also carried by exopodal prolongation in both Spinicaudata and Cyclestherida, but not the exact same limbs are involved and the egg carrying part of the exopod is not modified the exact same way. There is some variation in the length of these parts of the exopods in various laevicaudatan species which may be of phylogenetic importance (see Daday 1927).

3.11. Lamina abdominalis. Females have a laterally protruding extension of the posterolateral trunk somites, termed the lamina abdominalis or dorsal lamina. It is shaped as a flattened, lobate, process, the lateral margin and dorsal side of which is subdivided in a varying number of branches and assists in holding the egg mass. A recent study of *L. brachyurus* suggest that the lamina abdominalis also assist in guiding the newly extruded egg mass to the tip of the egg carrying exopods (Sigvardt & Olesen 2014). The presence of a lamina abdominalis is unique to Laevicaudata and a synapomorphy for this taxon. The specific shape of the lamina abdominalis has proven important at the species level since there is variation in the specific number of branches in which it is divided and in their shape and morphology. This variation will likely prove important for establishing a morphology-based phylogeny for the Laevicaudata, but a restudy of many species will be required to establish homologies between various lobes etc.

3.12. Subanal plate. Posterior to the last pair of trunk limb is a plate that extends backwards beneath the telson on both females and males here termed the ‘subanal plate’ (following Martin & Belk 1988), but which has sometimes been termed ‘opercular lamella’, ‘lamina infra analis’ (Day 1927) or ‘anal plate’ (Timms 2013). The position of the subanal plate immediate posterior to the last pair of trunk limbs and its bilobed nature in many taxa suggest that it is made up of modified thoracopods. One function of the subanal plate in males may be to assist in opening the female’s carapace prior to mating (see Fig. 2L; Sigvardt & Olesen 2014). As far as is known a subanal plate is present in all laevicaudatan species and as such constitute as synapomorphy of the taxon. Daday (1927) paid much attention to the specific shape of the sub-anal plate at the species level, but the morphological variation may also be important from a phylogenetic point of view. Morphological variation of the subanal plate is seen in (1) its size (length versus width), (2) in its shape (bilobed or not), and (3) in the marginal setation (with a couple of setae or glabrous) (Sars 1896; Daday 1927; Timms 2013; Olesen et al. 2016). Before this char-
character can be used phylogenetically many taxa need re-study.

3.13. Telson. Among Branchiopoda the laevicaudatan telson (sometimes called ‘anal somite’) has a unique morphology, which can be considered synapomorphic for the taxon. The anterior part of the telson is a conical structure tapering into a pair of triangular hirsute protrusions, each of which, at least in most taxa, terminates in a short spine (Fig. 21). Dorsally a pair of long telson setae is present as in all other Phyllopoda. The laevicaudatan telson is significantly different from its counterpart in all other branchiopods in the lack of distinct caudal rami, and different from all Onychocaudata (Spinicaudata, Cyclostherida, and Cladocera) in the lack of any dorsal spine. There is some variation in the specific shape of the posterior triangular parts between taxa (e.g., *Daday 1927; Timms 2013*), but the usefulness of the character for phylogeny will require a re-study of many taxa.

3.14. Larval morphology. Larvae have only been studied for a few laevicaudatan species, but in the cases where larvae are known, they have a very distinct morphology (*Olesen & Martin 2014*). Among the unique features are the presence of a dorsal, univalved head shield, which gives the larvae a UFO shaped appearance, and specialised first antennae, which are shaped as large, curved horns (Fig. 6). Most larval information is available for *Lynceus* *brachyurus* and *L. biformis* and less for *L. andronachensis* (*see Olesen 2005; Olesen & Martin 2014; Olesen et al. 2015; Botnaruc 1947; Botnaruc & Orghidan 1953*). Regarding the detailed structure of naupliar feeding appendages (antennae 2 and mandibles) the larvae of all three taxa are very similar. However, some of them are remarkably different with respect to the extension of the dorsal, univalved head shield (absent in stage 1 of *L. biformis*), the morphology of the caudal spines (long in *L. biformis*), and of the labrum (e.g., large plate in *L. brachyurus*, small with four marginal spines in *L. biformis*). In the light of these distinct differences in the larval morphology, a broader study of larval morphology is promising for phylogeny of the Laevicaudata.

### 4. Systematics

#### CLASS BRANCHIOPODA Latreille, 1817

#### SUBCLASS PHYLLOPODA Täsch, 1969

#### ORDER LAEVICAUDATA Linder, 1945 (Figs. 7, 8)

**Diagnosis (synapomorphy based).** Carapace bivalved, globular, smooth surface, with invaginated hinge dorsally. Head large and crescent shaped. Rostrum large. Head with pair of anterior setal fields. First antennae short and composed of two antennomeres. Second antennae with high number of short ramal antennomeres. Mandible gnathal edge with row of transverse teeth becoming larger and more disparately positioned posteriorly. Thoracopod exopods with large, dorsal lobate part. Thoracopod endites 4 and 5 elongate and digiform with rows of scraping setae. Male thoracopods with one pair of claspers on t1 with large diversity in setae and spines. Female exopods of t9 and t10 digiform, curved, and carries egg clusters distally. Females with flattened, lobate, posterior lateral extension of trunk somites (lamina abdominalis). Posterior to last pair of trunk limbs with ventral plate (sometimes bilobed) (subanal plate). Telson conical, tapering into a pair of triangular hirsute protrusions. Larvae with dorsal, univalved shield and hornlike first antennae.

**Order.** *Lynceidae Stebbing, 1902* = *Estheriidae Packard, 1874* (pro partim) = *Limnetidae Simon, 1886* (not *Sars, 1896*, in *Barnard, 1929* and *Tasch, 1969*) = *Lynceioidea Stebbing, 1902* = *Lynceidae Sayce, 1902* **Diagnosis.** As for the order. Type genus: *Lynceus* Müller, 1776

**Comments.** The genera are defined based on the amount of modifications on the male second thoracopod. In *Lynceiospis* and *Paralimnetis* there are extensive modifications, whereas in *Lynceus* there are no modifications to the male second thoracopod except for *L. aequatorialis* and *L. simaificies*, which both have limited modifications on one or both endites IV and V. Future study may suggest that these two taxa do not belong in *Lynceus*.

**Family.** *Lynceinae Stebbing, 1902* **Diagnosis.** As for the order. *Lynceiospis* *Daday, 1912* (sensu Martin & Belk 1988) **Diagnosis.** (Modified from Martin & Belk 1988) Male claspers thin, nonglobose, dimorphic. Male thoracopod II strongly modified but lacking protopodal hooked process. Thoracopod II distal endites fused into a large four lobed process bearing a circular knob on one end and small sharp knob on the other. Endite 4 not modified. Type species: *Lynceiospis perrieri* *Daday, 1912* by monotypy.

**Lynceiospis perrieri** *Daday, 1912* (sensu Martin & Belk 1988) = *Lynceiospis perrieri* aber. *dextrosa* *Daday, 1912* = *Lynceiospis perrieri* aber. *sinistrosa* *Daday, 1912*


**Type Locality.** Niger: Niger River Valley.

**Distribution.** Known only from the type locality.

**Comments.** Redescribed by Martin & Belk (1988).

**Lynceiospis sanctijohanni** *Thiéry, 1986* = *Lynceiospis sancti-johanni* *Thiéry, 1986* (fide Martin & Belk 1988)

Type Locality. Chad: Near N’Djamena. A temporary pool with dense hydrophytic vegetation, at approximately 12°N and 15°E, 250 m asl.

Distribution. Known only from the type locality.

Lynceus Müller, 1776 (sensu MARTIN & BELK 1988)

= Hedessa Liévin, 1884
= Limnetis Lovén, 1847 (fide STEBBING 1902)
= Lynnetis (in error) Packard, 1875
= Eulynceus Daday, 1913

Diagnosis. (Modified from MARTIN & BELK 1988) Second male thoracopod unmodified, or, if modified, never with hooked process on protopodite or large distal lobed process. Type species: Lynceus brachyurus Müller, 1776 by monotypy.

Comments. STEBBING (1902) demonstrated that Lynceus Müller, 1776 has priority over Limnetis Lovén, 1847, and that Lynceus (Lynceidae) has priority over Lynceus (Chydoridae).

Lynceus aequatorialis Daday, 1927

= Lynceus (Eulynceus) aequatorialis Daday, 1913 nomen nudum

Type Locality. Venezuela: near the junction of Rio Arauca and Rio Apure.


Comments. Redescribed by MARTIN & BELK (1988). ROESSLER (1995) suggested that this species may also occur in the Colombian lowlands east of the Andes and in the vicinity of the Orinoco River. Two additional collections (one of 15 specimens and one of 4 specimens) are also present in the MNHN, and were also examined by Daday. More recent material is deposited in the United States National Museum, catalogue number USNM 1143987, accession number 2021738. In addition, unlike other members of the genus Lynceus, the male second thoracopod endite V has a series of lobes that are serrate posteriorly and the endopod has a series of transverse grooves (MARTIN & BELK 1988). The generic assignment of this species should be investigated.

Lynceus argillaphilus Timms, 2013

Types. WAM, Holotype, male: accession number C52151; Allotype, female: accession number C52152.

Type Locality. Australia: Western Australia: Pilbara: De Grey Claypan, 20°17′42″S 119°25′21″E, 88.5 km E of Port Hedland, 14 May 2004, A. Pinder and H. Barron.

Distribution. Known only from two localities in the Pilbara Region.

Lynceus baylii Timms, 2013

Types. WAM, Holotype, male: accession number 51627; Allotype, female: accession number 51628.

Type Locality. Australia: Western Australia: 30°59′29″S 117°50′47″E, middle gnamma (rock pool) of five in a row, 14.6 km NNE of Trayning, 20 October 2011.

Distribution. Australia: Western Australia, South Australia.

Lynceus bicarinatus Barnard, 1924


Type Locality. Namibia (Ovamboland)


Comments. BARNARD (1929) provides further descriptive notes and figures.

Lynceus biformis (Ishikawa, 1895)

= Limnetis biformis Ishikawa, 1895
= Lynceus dauricus Thiele, 1907 (fide YOON & KIM 2000)

Types. No types designated or deposited of L. biformis. Types of L. dauricus, deposited: MNHB, type series: 3861 (collection contains 17 specimens).

Type Locality. For L. biformis, Japan: Tokyo Prefecture: Yoshiharatambo District: in rice paddies. For L. dauricus, Russia: Siberia: Burutiyai (Transbaikal), Dorasim (Dauria); the mountains east of Lake Baikal.

Distribution. Japan (ISHIKAWA 1895); South Korea (YOON & KIM 2000); Taiwan; China; Russia: Transbaikal Region (Thiele 1907), Zabaykalsky Krai (Chita Oblast), and Tyumen Oblast (DOBRYNINA 2011).

Comments. Redescribed by DADAY (1927) based on material from Japan. YOON & KIM (2000) redescribed L. biformis based on material from South Korea. YOON & KIM (2000) provide persuasive arguments concerning the synonymy of L. dauricus; however they did not compare the type material of the two taxa, and did not examine any L. dauricus material (ROGERS et al. 2016). Thus, this synonymy must be revisited.

Lynceus bouvieri Daday, 1927

= Lynceus bouvieri Daday, 1913 nomen nudum


Distribution. Known only from the type locality.

Lynceus brachyurus Müller, 1776 (sensu SARS 1896, MARTIN & BELK 1988)

= Hedessa Sieboldi Liévin, 1848
= Hedessa brachyura Siebold, 1849
= Limnetis brachyurus Grube, 1853
= Limnetis Gouldi Baird, 1862
= Estheria caeca Joseph, 1882 (fide DADAY 1927)
= Limnetis zichiyi Daday, 1901 (fide STRASKRABA 1965)
= Lynceus acutirostris Daday, 1912 nomen nudum (fide BRTEK 1997)
= Lynceus brachyurus isorhynchos Daday, 1912
= Lynceus acanthorrhynchos Bowkiewicz, 1923 (fide STRASKRABA 1965)
= Lynceus brachyurus var. typicus Daday, 1927 (fide STRASKRABA 1965)
= Lynceus andronachensis Botnariuc, 1947
= Lynceus andronachensis aber. spinosa Botnariuc, 1947
Types. None deposited or designated. We designate neotypes: ZMUC, Neotype, male: accession number CRU-4788; Topotype, female: accession number CRU-4789; Topotypes, 10 females, 26 males: accession number CRU-4790.

Type Locality. O.F. Müller did not deposit material and only mentions having found *Lynceus brachyurus* ‘in palustribus’ (meaning ‘in the swamp’). The water bodies in the area where O.F. Müller made his original collections have been destroyed, but before this, about 100

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**Fig. 5.** Laevicaudatan key characters relating to structure of thoracopods. A: *Lynceus insularis*, female, thoracopod 4, right side, anterior view. B: *L. insularis*, male, thoracopod 5, right side in anterior aspect. C: *L. insularis*, female, thoracopod 3 endopod scraper setae. D: *L. brachyurus*, female, thoracopod 1, left side, setation of endopod and endites 4, 5. E: *L. brachyurus*, female, scraper setae of endite 5 (close-up of D, dorsomedial view). F: *L. insularis*, thoracopod 5, scraper setae of endopod (close-up of B).
years after its description, P.E. Müller (1873) reported to have found the species in a small water filled depression with grass vegetation at the bottom on a field in front of Frederiksdal Castle, which he assumed most likely was one of O.F. Müller’s localities (O.F. Müller was appointed as tutor for a young nobleman at Frederiksdal Castle in the period). The sample from which we have designated neotypes was located in the Zoological Museum, University of Copenhagen; the original label only says ‘collected in 1872 by P.E. Müller; a later label suggests that the material is likely a misidentification or an undescribed species; probably based on P.E. Müller (1873).

**Distribution.** Holartic from temperate and subarctic regions. Belgium; Canada; Czech Republic; Finland; France; Denmark; Germany; Hungary; Norway; Pakistan; Russia; Slovakia; Sweden; Ukraine; USA (Kaisila et al. 1963; Strøskræba 1965; Martin & Belk 1988).

**Comments.** Redescribed by Martin & Belk (1988). This taxon is a widespread holartic temperate species. Material reported from Sarawak, Borneo (Sapandi. 1925) and from Tamil Nadu, India (Nayar & Naïr 1968) are most certainly misidentifications. The Sarawak material is most likely an undescribed species. The Tamil Nadu material is likely a misidentification or an undescribed species (Rogers & Padhye 2015).

**Lynceus brevifrons** (Packard, 1877) (sensu Martin & Belk 1988)

= *Limnetis brevifrons* Packard, 1877
= *Lynceus* (Eulynceus) *brevifrons* (Packard, 1877)

**Types.** None designated.

**Type Locality.** USA: Kansas: Ellis, well vegetated playas. The type locality has been destroyed.

**Distribution.** Mexico: Chihuahua, Durango, Guanajuato, San Luis Potosi; USA: Arizona, Colorado, Kansas, Montana, New Mexico, Texas (Martin & Belk 1988; Maeda-Martínez et al. 2002).

**Comments.** Redescribed by Martin & Belk (1988).

**Lynceus decaryi** Gauthier, 1936

**Types.** MNHN, type series: IU-2007-811 (= MNHN-Bp 520), ten specimens.

**Type Locality.** “Madagascar”.

**Distribution.** Madagascar.

**Comments.** Gauthier (1936) provides one of the best early descriptions of any *Lynceus*, and compares this species with the others reported from Madagascar at that time.

**Lynceus denticulatus** (Gurney, 1930) species complex

= *Limnetis denticulatus* Gurney, 1930
= *Lynceus allepeyensis* Balaranan & Nayar, 2004
= *Lynceus vasishti* Battish, 1981

**Types.** Lynceus species. Types of *L. allepeyensis*: Southern Regional Station, Zoological Survey of India, Chennai, Holotype, female: accession number CC7ZSI/SRS; Allotype, male: accession number CC8 ZSI/SRS; Paratypes: accession number CC6 ZSI/SRS. Types of *L. vasishti*: Zoological Museum of the Department of Zoology, Punjab Agricultural University, Ludhiana, Punjab, India.

**Type Locality.** India: Tamil Nadu: Madura District: Ammayanayakanur, temporary pools across from the Koniakanal Road Station. Of *L. allepeyensis*: India: Allepey District: Nangyarkkulangara, seasonally astatic wetland (abandoned rice paddy), 9.5’N 76.5’E, on west side of National Highway 47. Of *L. vasishti*: Punjab: “muddy pond” at Rakhra Village on Patiala-Nabha Road.

**Distribution.** India: Tamil Nadu (Gurney 1930; Royan & Alfred 1971), Punjab (Batish 1981); Sri Lanka: Jaffna Peninsula (Selvarajah & Costa 1979).

**Comments.** Rogers & Padhye (2015) treated this taxon as a species complex in need of closer examination. No types were deposited of *L. serratus*. *Lynceus allepeyensis* and *L. vasishti* are apparently known only from the type localities. All attempts (telephone calls, emails, certified letters, and personal visits) to inquire about, examine, borrow or collect any information on the type specimens at the Indian Museum, the Zoological Survey of India, and the Punjab Agricultural University have been ignored over a three year period. Therefore we assume that the types are lost or destroyed. Based upon the original descriptions, we can find no consistent differences between these taxa and treat them all as *Lynceus denticulatus*.

**Lynceus dovei** Daday, 1927

= *Lynceus dovei* Daday, 1913 nomen nudum


**Type Locality.** Madagascar: Antananarivo Province: Vinaninony.

**Distribution.** Known only from the type locality.

**Comments.** Gauthier (1936) provides additional, useful figures of this species. Two collections are present at MNHB (18362 and 18363).

**Lynceus gracilicornis** (Packard, 1871) (sensu Martin et al. 1986, Martin & Belk 1988)

= *Limnetis gracilicornis* Packard, 1871
= *Lynceus* (Eulynceus) *gracilicornis* (Packard, 1871)

**Types.** No types designated.

**Type Locality.** USA: Texas: Bosque County. Packard (1883) in error reported this as Waco (Geiser 1933; Martin et al. 1986).

**Distribution.** Mexico, Puebla (Maeda-Martínez et al. 2002); USA, Florida, North Carolina, Texas (Martin et al. 1986; Martin & Belk 1988).


**Lynceus grandirostris** Rogers, Olesen & Martin, 2015


**Type Locality.** Canada: Northwest Territories: A tempo-
rare tundra pool 20 km west of Yellowknife, 62°30′32″N 114°48′25″W.

**Distribution.** Known only from the type locality.

*Lynceus indicus* Daday, 1927

= *Lynceus indicus* Daday, 1913 nomen nudum

**Types.** ZSIC.

**Type Locality.** India: Uttarakhand.

**Distribution.** India: Uttarakhand, Bhim Tal, Bhowali, Kumaon, Nainital. Found at high altitudes in the Himalaya Mountains.

*Lynceus insularis* Olesen, Pöllabauer, Sigvardt & Rogers, 2016

**Types.** ZMUC, Holotype: male, CRU-4783, Allotype: female, CRU-4784, and paratypes: CRU-4785 and 4786. Holotype and allotype transferred to MNHN.

**Type Locality.** New Caledonia: South Province: Le Mont-Dore: doline (limestone sink hole) at 22°19′32.26″S 166°54′07.24″E.

**Distribution.** Known only from scattered locations in South Province, New Caledonia.

*Lynceus jeanneli* Daday, 1927

= *Lynceus jeanneli* Daday, 1913 nomen nudum

**Types.** None designated. Possible types deposited at the McGregor Museum, Kimberley, Northern Cape, Republic of South Africa.

**Type Locality.** Kenya: Nyandarua District: Kinangop Constituency.

**Distribution.** Kenya: Kinangop.

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**Fig. 6.** Laevicaudatan key characters relating to structure of larvae. 

Lynceus lobatianus Barnard, 1929
Types. SAM, type series: A7625.
Type Locality. Botswana: South East District: Lobatse.
Comments. Known only from the type locality.

Lynceus macleayanus (King, 1855) (sensu Timms 2013)
= Limnetis macleayana King, 1855, nomen nudum
= Lynceus macleayanus (Brady) error in Daday 1927
= Lynceus macleayanus (King-Sars) error in Daday 1927
Types. AM, Neotype, male: accession number P90062
(whole animal) and P90062.1 (thoracopod I).
Distribution. Widespread across Australia, including Tasmania.

Lynceus planifascius Rogers, Saengphan, Thaimuangphol & Sanoamuang, 2016
= Lynceus alleppeyensis Rogers et al., 2012
Types. ZMUC, Holotype, male: accession number CRU-8316.
Distribution. Division Collection (Catalogue #33.944) and should be compared with L. mulliensis.
Type Locality. Thailand: Khon Kaen Province: road side ditch on northeast side of Highway 208 flooded by rainwater, 16°18’45.88”N 102°52’31.37”E, south of Don Han.

Distribution. Thailand: Khon Kaen, Maha Sarakham, Roi Et, and Udon Thani provinces.

Lynceus rotundirostris (Daday, 1902) = Limnetis rotundirostris Daday, 1902

Types. HNHM, Holotype, female: accession numbers 1182/1, 1203/1901.

Type Locality. Argentina: Santa Cruz Province: Amenkelt, 50°03’S 69°W. (Not Chubut Province as reported in Martin & Belk 1988, per Crespo 1996.)

Distribution. Known only from the type locality.

Comments. Known from a single female specimen in very poor condition, with certain salient characters missing or damaged (Martin & Belk 1988). This is the only species described with a possible umbo, which was mentioned as appearing in Daday’s drawings by Martin & Belk (1988), but was not mentioned by Daday (1927) in the original description.

Lynceus rotundus Thiele, 1907 = Lynceus madagascarensis Thiele, 1907 (fide Gauthier 1936)

Types. MNHB, Holotype of L. rotundus: 11153 (nine specimens in three tubes). Type of L. madagascarensis: 11144 (20 specimens in four tubes).

Type Locality. Madagascar: Annanarivo (= Antananarivo?).

Distribution. Madagascar: known from the type locality and Anosy, Andrahomana.

Comments. Described by Gauthier (1936). The specimen label for L. rotundus provides two sets of coordinates: 12°S 49°14’E and 25°3’S 46°48’E. These coordinates lie at the extreme north and south ends of Madagascar, and probably represent the location of the island, rather than collection localities. The specimen label for L. madagascarensis has the coordinates: 18°56’S 47°31’E, which is Antananarivo, the Capital City of Madagascar.

Lynceus simiaefacies Harding, 1941

Types. BMNH, Type Series: 1939.10.25-40; Paratypes: 1940.7.23.1-3.

Type Locality. Yemmen: Jebel Jihaf: temporary pool, 2164 m asl.

Distribution. Known only from the type locality.

Comments. Unlike most other species of Lynceus, this species has a modified male second thoracopod. Endite V bears a row of lobiform projections that are not known in other Lynceus species (Harding 1941). This was further discussed by Fryer & Boxshall (2009) who also provide excellent figures of many characters. The generic placement of this species should be re-evaluated.

Lynceus spinimanus Rogers, Saengphan, Thaimuangphol & Sanoamuang, 2016 = Lynceus n.sp. Rogers et al. 2013

Types. ZMUC, Holotype, female: accession number CRU-8213; Allotype, male: accession number CRU-8218; Paratypes, 2 females: accession number CRU-8270.

Type Locality. Thailand: Suphan Buri: Donchedi District: road side ditch flooded by rainwater, 14°40’N 99°50’E, between Thap Luang and Sra Krachom.

Distribution. Thailand: Suphan Buri Province.

Lynceus susanneae Timms, 2013

Types. WAM, Holotype, male: accession number 51613; Allotype, female: accession number 51614; paratypes: accession number 51615. AM, Paratypes: accession number P90027.

Type Locality. Australia: Western Australia: Nullarbor Plain: Cocklebiddy, ca 32°02’S 126°06’E.

Distribution. Australia: Western Australia: western Nullarbor Plain, in limestone gnammas (rock pools).

Lynceus tatei (Brady, 1886) (sensu Timms 2013) = Limnetis tatei Brady, 1886 nomen nudum

Types. HNHN, Holotype, presumably female: accession number 7641.

Type Locality. Australia: “Sydney”. Neotype locality: South Australia: 37°44’44”S 140°37’47”E, pond 29.5 km southeast of Milicent.

Distribution. Southern Australia and Tasmania, north to the Paroo.


Lynceus triangularis Daday, 1927 (fide Forro & Brtek 1984)

= Lynceus triangularis “Wolf in Litteris” Daday, 1913 nomen nudum

Types. Deposited NMW (many specimens), accession number 25739, and HNHM (two specimens), accession number D 1913-163; I/C-190.

Type Locality. Republic of South Africa: Eastern Cape: Port Elizabeth.

Distribution. Only known from the type locality.

Comments. Daday provides a brief description with poor drawings, but does not refer to any material. Daday gives authority to Wolf, but does not cite a specific reference.

Lynceus tropicus Daday, 1927 = Lynceus (Eulynceus) tropicus Daday, 1913 nomen nudum

Types. MNHN, Holotype, presumably female: accession number Bp 521.

Type Locality. Venezuela: “Guanaaro”.

Distribution. Known only from the type locality and from a single specimen.

Comments. The type specimen is represented only by an empty carapace. The remaining body is missing (Martin & Belk 1988).

Lynceus truncatus Barnard, 1924

Types. SAM, Types: SAM A6740.
Type Locality. Namibia (Ovamboland): Ukualuthi.
Distribution. Namibia; South Africa, Natal (Reyn & Bowland 1985); Zimbabwe (Nhiwatiwa et al. 2014). 
Comments. Barnard (1929) provides additional descriptive comments and figures.

Paralimnetis Gurney, 1931 (sensu Martin & Belk 1988)
Diagnosis. (Modified from Martin & Belk 1988) Male thoracopod I very large and globose, relatively larger than in Lynceus. Male thoracopod II with protopod modi-
fied on right or left side as large sclerotized hooklike projection. Thoracopod II, endite 6 distal apex with a minute hook on one or both sides. Type species: Paralimnetis rapax Gurney, 1931 by monotypy.

Paralimnetis mapimi Maeda-Martínez, 1987 (sensu Martin & Belk 1988)
Types. USNM, Holotype, male: accession number 222988; Allotype, female: accession number 222989; Paratypes: accession number 222990.

Type Locality. Mexico: Chihuahua/Durango states: Bolson de Mapimi.

Distribution. Mexico: Chihuahua, Durango, Sinaloa, Sonora, Tamaulipas (Maeda-Martínez et al. 2002); Colombia? (see Comments).

Comments. Redescribed by Martin & Belk (1988). Roessler (1995) reports *P. mapimi* from Colombia. However, as *P. mapimi* is a species from the arid deserts of northern Mexico, we suspect that Roessler’s tropical material may represent a new, undescribed species.

Paralimnetis rapax Gurney, 1931 (sensu Martin & Belk 1988)

Types. BMNH, Syntypes: accession number 1928.2.23. 21 – 23.

Type Locality. Paraguay: Presidente Hayes Department: Maktlawaiya, −23°25′S −58°19′W.

Distribution. Known only from the type locality and one other adjacent pool.

Lyncceus sp. [undescribed] Naganawa, Zagas & Enkhtsetseg, 2001

Types. None designated.

Distribution. Known from one locality (“Station 9”), a saline pool in Mongolia, Dundgovi aimag: 1 km W of Mandalgovi (Naganawa et al. 2001; Naganawa & Zagas 2002).

Comments. This putative species was reported as a “localized-endemic” from central Mongolia (Naganawa et al. 2001; Naganawa & Zagas 2002). No material was reported as deposited in any museums.

† Palaeolynceinae Tasch, 1956 nomen dubium

Tasch (1956) created this subfamily for all fossil forms attributed to the Laevicaudata based on a lack of growth lines and few to no preserved soft parts. Tasch (1956) did this to reflect the “great uncertainty” of the placement of these forms. Tasch later (1969) treated this taxon as a nomen nudum, despite the fact that he defined it in his original (1956) paper. Only two fossil laevicaudans have preserved soft parts: *Paleolynceus stchunkini* and *Prolynceus beipiaensis* (Tasch 1969; Zhang et al. 1990). Laevicaudatan clam shrimp are particularly rare in the fossil record (Zhang et al. 1990). We cannot comment on the validity of the described taxa.

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6. References


