

R E S E A R C H P A P E R

## Taxonomic notes on toad bug genus *Nerthra* (Hemiptera: Heteroptera: Gelastocoridae) with description of a new species from Bonaire and Curaçao

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**Abstract.** During an inventory of the Gelastocoridae in the Naturalis Biodiversity Center, Leiden, The Netherlands (formerly Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands), and the Nieser & Chen Collection in Tiel, The Netherlands, we came across an undescribed species of *Nerthra* Say, 1832 (Hemiptera: Heteroptera: Gelastocoridae: Nerthrinae). The specimens were collected from Bonaire and Curaçao, Kingdom of the Netherlands, and we describe them here as *N. papaceki* sp. nov. *Nerthra lurida* Todd, 1959, syn. nov., is synonymized with *Nerthra occidua* Todd, 1959 (both from Indonesia: Sulawesi). In addition, we provide new distributional records of *Nerthra americana* (Montandon, 1905) (Brazil: Paraná), *Nerthra buenoi* Todd, 1955 (Brazil: Pará), and *Nerthra raptorica* (Fabricius, 1803) (Suriname) and provide their differential diagnoses and illustrations.

**Key words.** Hemiptera, Heteroptera, Nepomorpha, Gelastocoridae, Nerthrinae, new species, new synonymy, new records, Caribbean, Kingdom of The Netherlands\*)

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### Introduction

The Gelastocoridae, or toad bugs, belong to the insect order Hemiptera, suborder Heteroptera, infraorder Nepomorpha, superfamily Ochteroidea, and its members live in a riparian and terrestrial environment. Toad bugs were first recognized by BILLBERG (1820) as the family Galgulides, which was based on *Galgulus* Latreille, 1892. However, this name was preoccupied by a genus of birds, *Galgulus* Brisson, 1760. Therefore, KIRKALDY (1897) replaced *Galgulus* Latreille with *Gelastocoris*. Consequently, KIRKALDY (1897) renamed Galgulides as Gelastocoridae. After KIRKALDY (1897, 1906), there was some confusion on the family and generic names in a number of publications (see TODD 1955). After clarifying the detailed classification history of Gelastocoridae, TODD (1955) established its systematic framework. The family Gelastocoridae Kirkaldy, 1897 has been divided into two subfamilies: Gelastocorinae Kirkaldy, 1897 and Nerthrinae Kirkaldy, 1906. For a discussion of the validity of these names, see ŠTYN & JANSSON (1988). From

a morphological point of view, Gelastocoridae, notably the subfamily Nerthrinae, seems most similar to Naucoridae, due to the shape of their fore femora and the short and stout rostrum. This is especially true when considering *Hygropectrocoris* Sites, 2015 (Naucoridae), which bears a striking resemblance to Gelastocoridae and even shares the same habitat association (SITES 2015). However, a phylogenetic analysis (MAHNER 1993) based on morphology has shown that Gelastocoridae is more closely related to Ochteridae, and together they form the superfamily Ochteroidea, which is the sister group to Naucoroidea + Notonectoidea [including Pleoidea] (MAHNER 1993). The results of molecular phylogenetics (HEBSGAARD et al. 2004, WANG et al. 2016, YE et al. 2020) is in agreement with these conclusions.

Contrary to most nepomorphan taxa, toad bugs do not usually live in water, but prefer moist soil and even litter. The recent Gelastocorinae is restricted to the Americas and contains two genera: *Gelastocoris* Kirkaldy, 1897 and the

\*) The Kingdom of the Netherlands consists of a union of states. The first part is The Netherlands in Europe. The second part consists of Aruba, Curaçao, and St. Martin, which are separate states within the Kingdom. The third part consists of Bonaire, Saba and St. Eustatius which are municipalities within the Kingdom. Second and third part are forming together the Caribbean Netherlands.



closely related *Montandonius* Melin, 1929. However, the fossil of *Gelastocoris curiosus* Poinar & Brown, 2016 from Cretaceous Myanmar amber suggests its wider distribution in the past (POINAR & BROWN 2016). Species of Gelastocorinae are diurnal. Several species live on sparsely vegetated mudflats, usually near water, where they hop around like little toads and are easily spotted. The life history of the North American subspecies *Gelastocoris oculatus oculatus* (Fabricius, 1798) has been studied by HUNGERFORD (1922) and BROWN & MCPHERSON (1994).

The second subfamily, Nerthrinae, contains two genera, the extant genus *Nerthra* Say, 1832, which has essentially a pantropical distribution; and the extinct genus *Cratonerthra* Martins-Neto, 2005 from the Lower Cretaceous of Northeast Brazil (LÓPEZ RUF et al. 2005). Most species of *Nerthra* are nocturnal and cryptic (CASSIS & SILVEIRA 2006) and much more difficult to find than species of *Gelastocoris*. Consequently, their life histories are poorly known. There is only one incomplete study of the life cycle of one species, *Nerthra nepaeformis* (Fabricius, 1775) by KEVAN (1942). Toad bugs are so far considered as raptorial, but further research is necessary. *Nerthra* is a large, diverse genus and may have different feeding habits among species. Notably, SITES & NICHOLS (1990) introduced the term ‘retentorial’ for describing the prey operation of naucorids. A comparison with mantids showed the differences in the manner of catching prey with their raptorial fore legs. The two main differences are: i) fore legs of mantids are spinose to retain their prey and ii) operate in a vertical plane. Therefore, mantids are called ‘raptorial’. However, they mentioned that naucorids ‘gather’ and hold their prey during eating with their i) horizontally operating fore legs and ii) without strong bristles for retaining their prey. For this, they introduced the term ‘retentorial’. But as it is well known, the horizontally operating raptorial fore legs of Nepinae are used to catch prey, having no spines or bristles for retaining prey. Unfortunately, we do not know how *Nerthra* obtains its food. KEVAN (1942) fed them with termites and earwigs but did not describe how they ‘catch’ their food. Because this is a pending area of research, we do not make a distinction between raptorial and retentorial in this paper.

Most toad bugs are closely associated with humid habitats, such as the edge of ponds and streams or in water (LA RIVERS 1953 and personal observation). They can also be found by sieving litter, as well as in pitfalls, sometimes far from water (KEVAN 1942; *N. occidua* in this paper). Some species living in humid forest floors can be considered terrestrial. In Australia, some species are even living in desert environments (CASSIS & SILVEIRA 2001). The eggs of *Nerthra martini* Todd, 1954 are laid in small holes in the mud beneath stones near water, and the female seems to guard the eggs until they hatch (USINGER 1956). A small number of *Nerthra* species has the hemelytra immovably fused, which may be associated with a burrowing habit (TODD 1955). Because *Nerthra* is a diverse genus with about 100 described species, it is probable that individual species differ considerably in various details of their life histories.

The most important studies on Gelastocoridae were by E. L. Todd. He published a number of papers on this

family during the period 1954–1961. His most important publications are: i) revision of the family (TODD 1955); ii) descriptions of additional new species and many new country records, especially in eastern Indonesia, New Guinea, Solomon Islands, and Australia (TODD 1957b, 1959, 1960); iii) world checklist of Gelastocoridae (TODD 1961b). These works have laid a good foundation for further study of Gelastocoridae.

The taxonomic history of Nerthrinae is straightforward, but the taxonomy of Gelastocorinae is somewhat complicated. The main argument concerns the species status of *Gelastocoris flavus* (Guérin-Méneville, 1835). More specifically, GUÉRIN-MÉNEVILLE (1844) described three species of *Galgulus*, which was used for *Gelastocoris* at that time, namely *G. flavus*, *G. quadrimaculatus* and *G. nebulosus*. However, these turned out to be the same species (TODD 1955). Todd pointed out that STÅL (1876), who was the first reviser, used the name of *Galgulus nebulosus*. According to the rules of zoological nomenclature, *Galgulus nebulosus* (GUÉRIN-MÉNEVILLE 1844) has priority in a synonymy of these three species. Therefore, Todd treated the three species of Guérin-Méneville as *Gelastocoris nebulosus* (GUÉRIN-MÉNEVILLE 1844). However, the plates belonging to GUÉRIN-MÉNEVILLE (1844) were printed separately from the text. COWAN (1971) found that the plate with the figure of *Galgulus flavus* already appeared in 1835. This illustration of the three ‘species’ described by Guérin-Méneville set the valid name for this taxon as *Gelastocoris flavus* (Guérin-Méneville, 1835) (NIESER, 1972).

DE CARLO (1954) described a number of species of *Gelastocoris* from South America: *G. bergi*, *G. bolivianus*, *G. paraguayensis* and *G. vianai*. TODD (1955) synonymized all of these with *G. nebulosus* (Guérin-Méneville, 1844). DE CARLO (1959) wrote a paper to argue that his species were valid and added another new species, *G. monrosi*, to this complex. TODD (1961a) responded with a paper to stand by his synonymy of De Carlo’s species. NIESER (1972) studied specimens of the various *Gelastocoris* species identified by De Carlo and essentially agreed with Todd, but pointed out that Andean specimens differ somewhat from conspecific lowland specimens. He concluded that this ‘*Gelastocoris nebulosus* complex’ consists of two subspecies: *G. flavus flavus* (Guérin-Méneville, 1835) in the lowlands and *G. flavus quadrimaculatus* (Guérin-Méneville 1844) in the Andes. This conclusion needs to be confirmed by modern biological research techniques. ESTÉVEZ & SCHNACK (1977) described *Gelastocoris decarloi* from Santa Catarina, Brasil, which at present we also consider a synonym of *G. flavus flavus* based on its morphology. SCHNACK & ESTÉVEZ (1979) published a monograph of the Gelastocoridae of Argentina, and ESTÉVEZ & SCHNACK (1980a) revised the Gelastocorinae of South America. In both papers they revalidated the species of De Carlo which were considered synonyms of *G. flavus* by TODD (1955, 1961a) and NIESER (1972). As they apparently overlooked the paper by NIESER (1972) and did not provide argumentation, we keep considering all these names as synonyms of *G. flavus*. BOULARD & JAUFFRET (1984) described *G. vandamepompanoni* from the state of Pará, Brazil. At first sight this species also looks like *G. flavus*,

but closer examination reveals considerable differences in structures of external characters and genitalia of both sexes, which convinced us to consider it as valid species.

Besides local records in faunistic reports, little work has been published on New World Nerthrinae since TODD (1961b). NIESER (1975) revised the Gelastocoridae of the Guyana Region. POLHEMUS (1972) described *Nerthra spangleri* from Mexico; ESTÉVEZ & SCHNACK (1980) described *N. gaucha* from Rio Grande do Sul, Brazil; and NIESER & CHEN (1992) described *N. undosa* from Chile. POLHEMUS & LINDSKOG (1994) proposed the name *N. toddi* Polhemus & Lindskog, 1994 for *N. mexicana* sensu TODD (1955) (not MELIN 1929) and synonymized *N. usingeri* Todd, 1959 with *N. mexicana* (Melin, 1929). FAÚNDEZ & ASHWORTH (2015) and FAÚNDEZ & CARVAJAL (2017) studied the *Nerthra* of Chile, notably in the south of the country. They found additional material of *N. praecipua* Todd, 1957, describing the male and erecting a new subgenus *Rhinodermacorisis* Faúndez, 2015 for it. In addition, they described *N. subantarctica* Faúndez & Ashworth, 2015 on a subfossil specimen found in the south of Chile. Cladistical analysis by FAÚNDEZ & CARVAJAL (2017) shows that *N. praecipua*, *N. subantarctica* and an undescribed species belong to a clade which is related to the *N. alaticollis*-group from Australia. The other Chilean *Nerthra* are apparently related to the Neotropical *Nerthra*. This points to an Antarctic origin during Gondwana times of the *N. praecipua* clade. In addition, they support the view of CASSIS (2006) that *Nerthra* should be split in several genera.

In the Old World, LANSBURY (1988) described *Nerthra parallela* from New Georgia, Solomon Islands. An important contribution since TODD (1960) is the work by CASSIS & SILVEIRA (2001, 2002, 2004, 2006), who reviewed the Australian and New Caledonian *Nerthra* and described five new species. In addition, KMENT & JINDRA (2008) reviewed the Gelastocoridae from SE Asia west of the Wallace Line, summarized the group in that area and presented illustrations and distributional maps.

The worldwide distribution of the family is peculiar and two main centers of diversification are recognized. The first center of diversification is in the Neotropical Region with 46 species (TODD 1961b, POLHEMUS 1972, ESTÉVEZ & SCHNACK 1980, BOULARD & JAUFFRET 1984, NIESER & CHEN 1992, FAÚNDEZ & ASHWORTH 2015), three of which have penetrated into the Nearctic Region. A second center of diversification is found in Australia and New Guinea with 45 species (TODD 1961b; LANSBURY 1988; CASSIS & SILVEIRA 2001, 2002, 2004, 2006). In Asia west of the Wallace Line, there are only nine species, of which three have penetrated into the eastern Palaearctic Region (China and Japan) (POLHEMUS 1995, KMENT & JINDRA 2008, XIE & LIU 2018). Africa has only two confirmed species and only one species, *N. rugosa* (Desjardins, 1837) is recorded from the western Palaearctic Region from the coast of the Sinai Peninsula (PRIESNER & WAGNER 1961).

Species identification is based on size, arrangement of tubercles on the head, shape of the lateral margin of the pronotum and embolium, callosities and bristles on the dorsum, and male genitalia. Such a set of characters is illustrated

in TODD (1955, 1959). More general morphology with illustrations can be found in POPOV (1971). The important work of POPOV (1971) is written in Russian; its text was translated to English by H. Vaitaitis (year unknown), which was privately organized by M. Parsons. This has resulted in a limited distribution of this handy version.

The males of Gelastocoridae have an asymmetrical abdomen. Abdominal sternite IV is slightly asymmetrical, and sternites V–IX are also asymmetrical, which provide characters for identification of species. However, the male genitalia are always the most reliable character for identification. The two subfamilies both have a well-developed right paramere and vestigial left paramere. For identifying species of Gelastocorinae, the entire male genital capsule should be extracted, as it gives excellent clues for specific identification (TODD 1955, PENDERGRAST 1957). In male *Nerthra*, the tip of the paramere is sufficient for species identification (TODD 1955).

The abdomen of females of Gelastocoridae is usually symmetrical and not useful for identification. However, to identify females in America, the species can be determined by the shape of the abdominal sternites, which are asymmetrical to a variable extent. The abdominal sternites of Old World females of *Nerthra* are more symmetrical and uniform, thus they are rarely useful for species identification. The female genitalia of Gelastocoridae have been studied only in works dealing with Heteroptera in general. PENDERGRAST (1957) studied the spermatheca of *Nerthra annulipes* (Horváth, 1902) and concluded that it is similar to those of Notonectoidea. SCUDDER (1959) studied the female genitalia of *Nerthra grandicollis* (Germar, 1837), and concluded that they are not similar to those of Ochteridae, with which the Gelastocoridae form the superfamily Ochteroidea (MAHNER 1993).

In order to optimally disclose the collections at Naturalis and NCTN, all the gelastocorids in these collections are checked and digitized on specimen-level. The following findings are summarized in this paper: i) Although *N. americana* (Montandon, 1905) and *N. buenoi* Todd, 1955 are so far still confined to Brazil, our new distributional records extend their known range considerably; ii) morphological variation of the paramere in *N. buenoi* is described and illustrated; iii) a new species of *Nerthra* is described here from the Lesser Antilles; and iv) *Nerthra lurida* Todd, 1959 (male) is synonymized with *N. occidua* Todd, 1959 (female). Other species of Gelastocoridae deposited in RMNH have been adequately reported elsewhere, notably in TODD (1955, 1959) and NIESER (1975).

## Material and methods

The specimens studied belong to the following collections; acronyms of the museums are according to ARNETTE et al. (1993).

NCTN	Collection of Nieser & Chen, Tiel, the Netherlands (to be transferred to RMNH in the future);
RMNH	Naturalis Biodiversity Center, Leiden (formerly Rijksmuseum van Natuurlijke Historie, Leiden), the Netherlands;
SEMC	Snow Entomological Museum Collection, University of Kansas, Lawrence, Kansas, U.S.A.

Measurements are in mm and are represented as the range with the average in italics. Length is the median length from the apex of the head to the caudal tip of hemelytra; width is the maximum width of the respective part of body. Both are measured in dorsal view.

To study the genitalic structures of Gelastocorinae, the genitalic segments can be treated in 10% KOH and either stored in pure glycerine, or glued on the labels with the specimen. However, this is not the case for identifying species of *Nerthra*. We followed the method given by TODD (1955): after softening the specimen, one holds it with its head pointing at yourself and then with the ventral side up. Abdominal segments VII–IX are then pulled to the rear and to the left, and the paramere becomes observable. In this way, the genitalia remain with the insect, and it is a quick method for a reliable identification, without extracting the whole capsule. For photography, some specimens were cleaned by soaking in warm water to soften the specimens in order to clean them with a brush.

Specimens were studied using a Zeiss Stemi 2000 binocular and an Olympus BX51 compound microscope. Habitus and paramere photographs were taken using a Zeiss SteREO Discovery V12 microscope with a Zeiss PlanAPO S 1.0x FWD 60 mm lens and AxioVision SE64 Rel. 4.9.1 software. The photographs were further processed using Adobe PhotoShop CC. The distribution maps of the studied specimens were created as follows: collecting localities of the specimens were first georeferenced using Google's Geocoding API (Application Programming Interface). Subsequently, the resulting coordinates were plotted in ArcGIS version 10.2.2, using the geographic coordinate system WGS 1984. The source of the background map to contextualize the coordinates is the U.S. National Park Service.

## Taxonomy

### Neotropical species

#### *Nerthra americana* (Montandon, 1905)

(Figs 1–8, 15, 38)

*Matinus americanus* Montandon, 1905: 404 (original description).

*Nerthra americana*: TODD (1955): 381 (redescription).

**Material examined. BRAZIL: PARÁ:** Bocaiúva [do Sul], 25°08'S, 49°04'W, 1000 m a.s.l., v.1964, leg. F. Plaumann, 1 ♂ 1 ♀ (NCTN).

**Distribution** (Fig. 37). This species is rare in museum collections. MONTANDON (1905) described this species based on two specimens from Espírito Santo, Brazil, which unfortunately lacked more detailed locality information. Because MONTANDON (1905) did not designate a holotype, these two specimens were consequently considered as syntypes, of which one was deposited in the Hungarian National History Museum in Budapest and the other in Montandon's personal collection. The whereabouts of the two specimens are unknown (TODD 1955). TODD (1955) recorded a series of two males and 13 females from São Paulo, Brazil: Mraz Lgt. Jaro Mraz lived in Santa Anna (nowadays Santana), which is now incorporated in the northwest of the metropolis of São Paulo. At the time Mraz collected exclusively for the Czech National Museum (1920–1927) this was a quite isolated rural community bordered in the South by the Rio Tietê and in the North by Serra da Cantateira which was covered by Mata Atlântica (SEKERKA 2020). Todd took two from this

set to be kept in SEMC. Our specimens are the third record of this species, also from Brazil. Bocaiúva do Sul lies in the Serra do Mar, north of Curitiba. This record extends the range of *N. americana* further to the south. The Serra do Mar presently contains an important natural protected area.

**Comparative notes.** This species is somewhat similar to *N. williamsi* Todd, 1955 from São Paulo (TODD 1955). The male can be recognized by its aberrant paramere, which is provided with a large dorsolateral projection (Fig. 15), whereas the paramere of *N. williamsi* is simple. We provide 8 photographs and a drawing (Figs 1–8, 15) to support identification to species level.

#### *Nerthra buenoi* Todd, 1955

(Figs 9–14, 16, 38)

*Nerthra buenoi* Todd, 1955: 365 (original description of female).

*Nerthra buenoi*: TODD (1957a): 2 (description of male, distribution).

**Material examined. BRAZIL: PARÁ:** Capanema, 01°11'45"S, 47°10'W, 17.viii.1959, leg. E.H. Bonn, 1 ♂ (NCTN).

**Distribution** (Fig. 37). This species was described using a single female from 'Bnitp Prov. Pernambuco, Brazil'. This is probably Bonito, a locality somewhat inland of Recife. Later, TODD (1957a) reported two males and two females from Formoso in Goiás, collected during the Machris Expedition. Accompanied with his brief description of the male, TODD (1957a) also presented a very simple outline of the apex of the paramere. Our specimen is from Capanema, Pará, which is 160 km WNW of Belém (Fig. 37).

**Comparative notes.** *Nerthra buenoi* and *N. raptoria* (Fabricius, 1803) are very similar small toad bugs, which share the widened fore femora. The differences between them are: i) *N. buenoi* (length 4.2, width 2.6) (Figs 9–10) is smaller than *N. raptoria* (length 5.0–5.5, width 3.1–3.4) (Figs 19–20). iii) in *N. buenoi* the distal edge (Fig. 13) of the widening of the fore femur has a sharper point than in *N. raptoria* (Fig. 21). However, this is difficult to evaluate on a single specimen. iii) The parameres of these species are acuminate, in *N. buenoi* the narrowed tip is long and straight (Figs 14, 16), whereas in *N. raptoria* it is short and curved (Figs 18, 22, 23). However, the apex of the paramere of our specimen from Capanema (Fig. 16) differs from the specimens from Formoso (Fig. 14). More male specimens are needed to evaluate the variation of its paramere.

#### *Nerthra raptoria* (Fabricius, 1803)

(Figs 18–23)

*Naucoris raptoria* Fabricius, 1803: 111 (original description).

*Nerthra raptoria*: TODD (1955): 366 (definition, redescription, distribution); NIESER (1975): 42 (redescription, records for Suriname, distribution).

**Material examined. SURINAME:** road to Matta, km 4–5, 5°27'N, 55°15'W, mudflat with some ponds, 3.x.1969, leg. N. Nieser, 1 ♂; Paramaribo, Fernandesweg at Polderweg naar Zee, 5°53'N, 55°14'W, 10.x.1969, leg. N. Nieser, 1 ♀ (NCTN); Tijgerkreek, Dirkschoop, 26.vii.1978, from cow dung, leg. A. van Assen, 2 ♂♂ (RMNH).

**Distribution.** A common and widespread species from Mexico through Central America, and South America east through the Andes to northern Argentina. For more detailed data on distribution and synonymy see TODD (1955) and NIESER (1975). We provide five photographs (Figs 19–23) to support identification to species level.

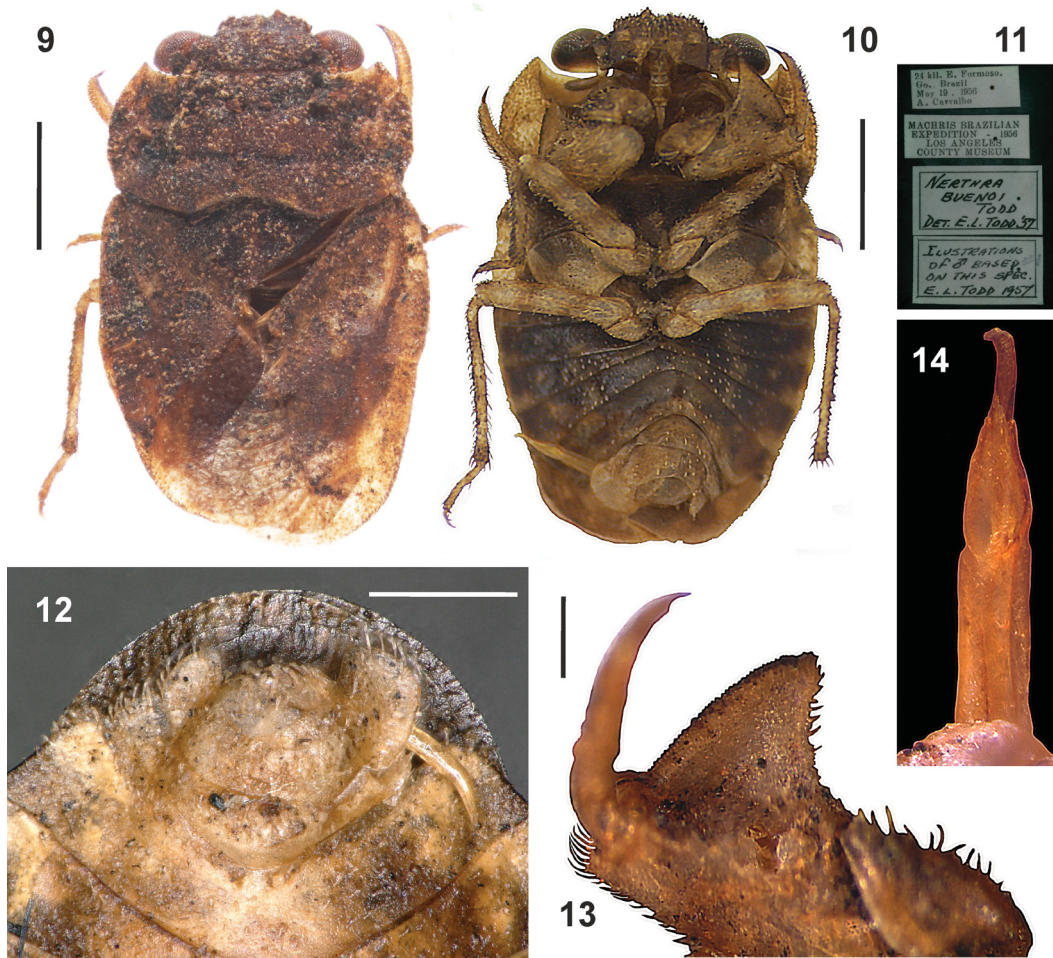
**Comparative notes.** See under *N. buenoi*.



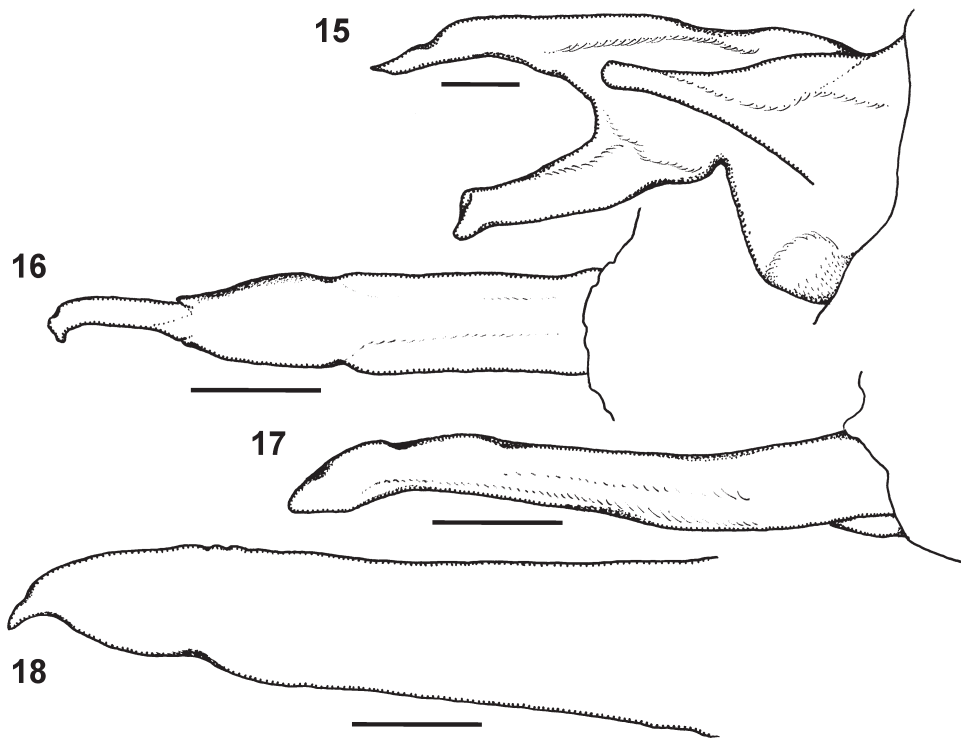
Figs 1–4. Habitus of *Nerthra americana* (Montandon, 1905): 1–2 – male (1 – dorsal view, 2 – ventral view); 3–4 – female (3 – dorsal view, 4 – ventral view).



Figs 5–8. *Nerthra americana* (Montandon, 1905): 5 – male, head and prothorax (ventral view); 6 – male, left fore leg (ventral view); 7 – female, left fore leg (ventral view); 8 – male, right middle leg (ventral view).



Figs 9–14. *Nerthra buenoi* Todd, 1955, male: 9–10 – habitus (9 – dorsal view, 10 – ventral view); 11 – labels of specimen; 12 – abdominal end with paramere exposed; 13 – right fore leg (ventral view); 14 – paramere (medial view).



Figs 15–18. *Nerthra* spp., apex of paramere, ventral view: 15 – *N. americana* (Montandon, 1905); 16 – *N. buenoi* Todd, 1955; 17 – *N. occidua* Todd, 1959; 18 – *N. raptoria* (Fabricius, 1803).



Figs 19–23. *Nerthra raptoris* (Fabricius, 1803): 19–21 – female: 19 – habitus (dorsal view), 20 – habitus (ventral view); 21 – fore legs (ventral view); 22–23 – male, paramere (22 – ventral view; 23 – apex, dorsal view).

*Nerthra papaceki* sp. nov.  
(Figs 24–30, 38)

**Type locality.** Bonaire, Lac, Cai, 12°11'N, 68°22'W.

**Type material.** HOLOTYPE: ♂: **BONAIRE:** Lac, Cai, 12°11'N, 68°22'W, *Rhizophora*, 16.ix.1967, leg. P. W. Hummelinck 880 (RMNH). PARATYPES: **BONAIRE:** same data as holotype, 1 ♀ (RMNH); Cay, entrance of Lac, *Avicennia* leaves, 1.ix.1948, leg. P. W. Hummelinck 180a, 1 ♀ (NCTN). **CURAÇAO:** Groot St. Joris, shore, 12°12'N, 68°83'W, *Rhizophora* in muddy sand, 9.iv.1949, leg. P. W. Hummelinck 326, 2 ♀♀ (NCTN).

**Description.** *Dimensions* (in mm). Male (Figs 24–26): Length 5.21, width of pronotum 3.58, width of abdomen 3.61, width of hemielytra over embolia 3.72. Female (Figs 28–29): length 5.77–5.87–5.96 mm, width of pronotum 3.70–3.85–3.99, width of abdomen 3.83–4.16–4.34, width of hemielytra over embolia 3.99–4.10–4.31.

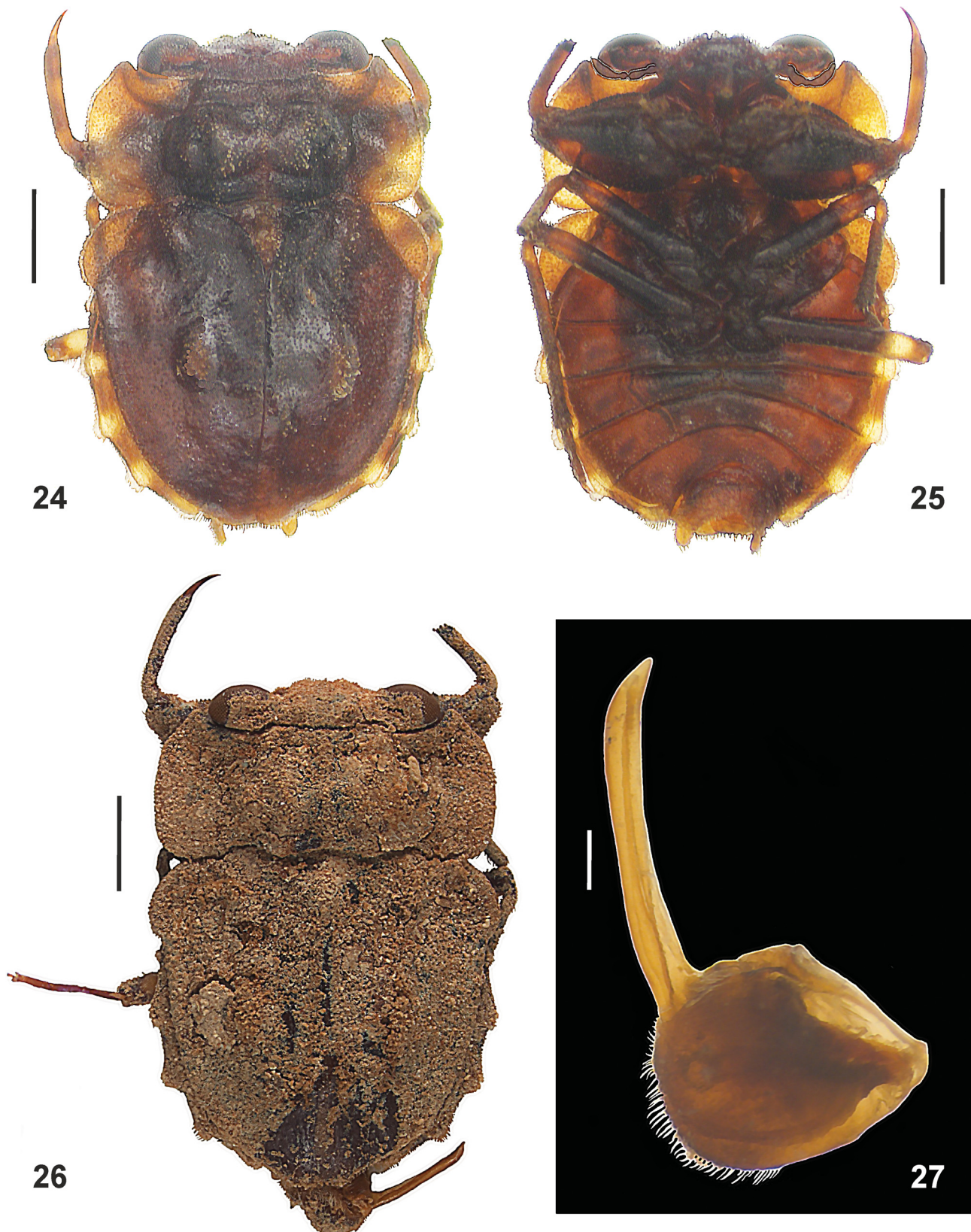
**Colouration.** Castaneous, pronotum laterally and legs lighter, usually covered with mud and sand.

**Structure.** *Head.* Front of head with apex concavely excavated, with a stout, short and blunt tubercle on either edge of the excavation. Lateral tubercles apparently absent, a small pointed tubercle in centre of frons and two low, blunt, distinct tubercles laterally on vertex. Ocelli absent. *Pronotum* with a pair of strongly elevated submedian elevations accentuated by clavate bristles, anterior quarter of lateral margins convergent, virtually straight; posterior edges rounded, remainder of lateral margins parallel, straight. Width of pronotum subequal to width of abdomen in male, slightly less than width of abdomen in females.

Posterior margin of pronotum sinuate, with a pair of short, submedian caudal projections. *Scutellum* with a central elongate elevation beset with clavate bristles, basal width of scutellum about 1.5 times its median length. *Hemielytra* fused, membranes reduced. Just behind pronotum midway between scutellum and lateral margin of embolium a small longitudinal elevation beset with clavate bristles, caudally from this halfway between posterior margin of pronotum and caudal tip of the hemielytron a more pronounced elevation also accentuated by clavate bristles. Embolium covering abdomen, its lateral margin rounded, hemielytra leaving a narrow strip of connexivum uncovered. Latero-caudal edges of abdominal segments rounded, accentuated by clavate bristles. Body dorsally sparsely beset with clavate bristles, more densely on the elevations. *Legs.* Fore trochanter with two blunt projections, fore femur anteriorly not strongly dilated.

**Male.** *Abdominal venter.* Sternites II–IV symmetrical, V–VI only slightly asymmetrical, much less so than in other species of *Nerthra*, sternite VIII with posterolateral corners somewhat produced caudally; sternites VII–IX distinctly asymmetrical (Fig. 25). *Genitalia.* Pygophore globular; left paramere reduced; right paramere (Figs 30a,b) a simple rod with slightly curved apex, middle part of shaft slightly narrowing. (See also Differential diagnosis and discussion.)

**Female** abdominal sternites almost symmetrical, last sternite (VII) without tumescences, its median length only slightly shorter than that of all preceding segments together,



Figs 24–27. *Nerthra papaceki* sp. nov., holotype, male. 24–26 – habitus: 24 – dorsal view (cleaned, genital capsule removed); 25 – habitus, ventral view (cleaned, genital capsule removed); 26 – dorsal view (before cleaning, genital capsule extended). 27 – genital capsule (ventral view).





Figs 28–29. *Nerthra papaceki* sp. nov. paratype, female, habitus (28 – dorsal view, before cleaning; 29 – ventral view, cleaned).

its posterior margin straight, nearly covering the lobes of ovipositor (Fig. 29).

**Etymology.** Named in honor of the late Professor Dr. Miroslav Papáček (1953–2019) for his wide ranging contributions on biology. Notably the morphology and taxonomy of Gerromorpha and Nepomorpha (see DITRICH et al. 2020).

**Habitat and distribution.** This species is known only from the Caribbean Islands Bonaire and Curaçao (Fig. 38), where it apparently lives in mangroves. This species should be looked for in the mangroves of Aruba, Trinidad, and the northern coast of South America. Apparently it burrows in mud because the holotype (Fig. 26) and paratypes (Fig. 28) were covered by a layer of fine silt concealing its real colouration (Figs 24, 25, 29). Fused hemielytra have been suggested to enable a burrowing way of life (TODD 1955).

**Differential diagnosis and discussion.** The shape of right paramere of *N. papaceki* is very similar to that of *N. parvula* (Signoret, 1864) from Chile. However, the aedeagal furrow of *N. papaceki* is entirely dorsal (Fig. 30b), whereas in *N. parvula* it is visible in ventral view in the apical part of the right paramere. In addition, *N. parvula* is larger, with the body length of males 5.8–6.1 mm (TODD 1955), and the hemielytra are not fused and have well-developed membranes.

This species does not run well with the key of TODD (1955). It runs either to *N. americana* or to *N. rugosa* (Desjardins, 1837), but only the latter is closely related to

*N. papaceki*. Males of *N. americana* have a large dorso-lateral projection on the paramere (Fig. 15), which is lacking in *N. papaceki* (Fig. 30). Females of *N. americana* have the caudal margin of the last abdominal sternite deeply incised, leaving the large asymmetrical lobes of the ovipositor uncovered (Fig. 4), whereas the caudal margin of the last abdominal sternite of females of *N. papaceki* is straight, almost covering the ovipositor lobes (Fig. 29). Alternatively, it could run to *N. rugosa*, which was described from Mauritius but also recorded from Panamá (Pearl Islands, on the Pacific side, TODD 1955) and Florida, U.S.A. Additional records from Belize, Brazil: São Paulo and Egypt (POLHEMUS 1995) suggest a possible pantropical distribution. There is also a doubtful record from ‘N.G. Nat. Ver.N. Holl.’ which TODD (1957b) interpreted as Australia. TODD (1959) wrote that it is not known whether ‘N. G.’ referred to New Guinea or ‘N. Holl.’ refers to New Holland, an old name for Australia. However, ANDERSEN & WEIR (2004) did not mention this species in their book on Australian water bugs, so apparently there are no other records of this species from Australia. *Nerthra papaceki* is similar to *N. rugosa*, (Figs 28, 29; TODD 1955: 471, fig. 121). The lateral margins of the pronotum are straight in *N. papaceki* and somewhat convex in *N. rugosa*. More differences between these species are given below.

Please note that *N. papaceki* sp. nov. is based on a single male and four females. So far, no males of *N. rugosa* have been reported. TODD (1955: 470) gave the so far only

Table 1. Differences between the females of *Nerthra rugosa* (Desjardins, 1837) and *Nerthra papaceki* sp. nov.

Characters	<i>Nerthra rugosa</i>	<i>Nerthra papaceki</i>
Body length	6.00–7.10 mm	5.77–5.96 mm
Excavation in anterior margin of head	missing	developed
Posterior edge of pronotum	produced backwards	rounded, at the same level as posterior margin
Embolium	more or less straight	rounded and convexly curved
Width of pronotum	4.10–5.00 mm	3.70–3.99 mm
Width of abdomen	4.20–5.10 mm	3.83–4.34 mm
Width of hemielytra across embolium	unknown	3.99–4.31 mm
Apex of hemielytra	slightly pointed	more or less truncate

illustration showing the outline of the female of *N. rugosa*. The differences between the females of these two species are listed in Table 1.

The presence or absence of an excavation in the anterior margin of the head is considered an important differential character in this genus (TODD 1955); the remaining differences between the females of *N. rugosa* and *N. papaceki* sp. nov. further support that *N. papaceki* is an undescribed taxon. More material, specifically males and specimens from Brazil, Egypt, and Florida of *N. rugosa* is needed to further define the boundaries of variability of both species.

### Australasian species

#### *Nerthra occidua* Todd, 1959

(Figs 17, 31–37, 39)

*Nerthra occidua* Todd, 1959: 71 (original description).

*Nerthra lurida* Todd, 1959: 72 (original description), **syn. nov.**

**Type material examined.** *Nerthra lurida*: HOLOTYPE: ♀, INDONESIA: SULAWESI SELATAN (Fig. 39): Rantepao, Nanggala, 900 m, vii.1937, leg. Drescher (RMNH).

**Additional material examined.** INDONESIA: SULAWESI TENGAH: Lore Lindu NP, Sopa River Pools, 930 m a.s.l., 6.xii.1985, leg. J. Krikken & J. van Tol, 1 ♀, det. P. Lindskog (identified by comparing with type) (RMNH); Lore Lindu NP, Sopa River Pools, 930 m a.s.l., 6.xii.1985, leg. J. Krikken & J. van Tol, 2 ♀♀ (RMNH); Lore Lindu N.P., Dongi Dongi shelter, 940 m a.s.l., 4.–8.xii.1985, multistratified evergreen forest, 2 fish traps, leg. J. Krikken, 3 ♀♀ (NCTN); same, garage, 950 m a.s.l., 4.–9.xii.1985, multistratified evergreen forest, 4 dung traps, leg. J. Krikken, 4 ♂♂ 7 ♀♀, 1 L (instar 5) (2 ♂♂ 2 ♀♀ NCTN, 2 ♂♂ 5 ♀♀ RMNH); Lore Lindu NP Dongi Dongi shelter, 940 m a.s.l., 4.–8.xii.1985, multistratified evergreen forest, 2 human excrement traps, leg. J. Krikken, 1 ♂ 1 ♀, 3 L (instar 4) (RMNH); Lore Lindu NP, Danau Taming forest, 1600 m a.s.l., 5.–09.xii.1985, multistratified evergreen forest, 4 human excrement traps, leg. J. Krikken, 1 ♀ (RMNH).

**Discussion** (Fig. 39). TODD (1959) described two species in the same paper, namely *N. occidua* (holotype male, deposited in Museum für Naturkunde, Berlin) and *N. lurida* (holotype female, deposited in RMNH), and mentioned a number of small differences between them. Both the species were collected from Sulawesi but each of them was based on an unique specimen of different sex, therefore comparison of male genitalia was not possible. *Nerthra occidua* was distinguished from *N. lurida* by a wider head (equal to combined length of pronotum and scutellum), the front of the head rounded, scutellum moderate with

median and basal portions depressed, and the pronotum and abdomen wider. According to the drawing given by TODD (1959: 63, figs 14–15), little difference can be seen except that *N. lurida* is very slightly broader.

After the work of Todd, additional gelastocorids were collected in Sulawesi by Dr. J. Krikken and other colleagues of RMNH during the Project Wallace in 1985. It is interesting to note that the specimens were collected in pitfalls baited with excrement or rotting fish as collateral catch of research on dung beetles. There are other records of species of *Nerthra* found in cow dung: the Neotropical *N. manni* Todd, 1955 (LAUCK & WHEATCROFT 1958) and *N. raptoria*, specimens in RMNH (see above). This does not necessarily imply that these species eat dung, but more likely the bugs are able to find prey near this kind of smell. We have compared the later samples with the holotype of *N. lurida*. Running the key of TODD (1959: 62), the males of this series from Sulawesi (Figs 30–32) can be identified as *N. occidua* by the shape of paramere (TODD 1959: 69, Fig. 45). However, the front of the head (Figs 31–34) is flat and its width is less than the combined length of the pronotum and the scutellum (4.5 / 5.0), which would agree with *N. lurida* according to TODD (1959). In some females, the front of the head is slightly convex (Figs 31–34), but

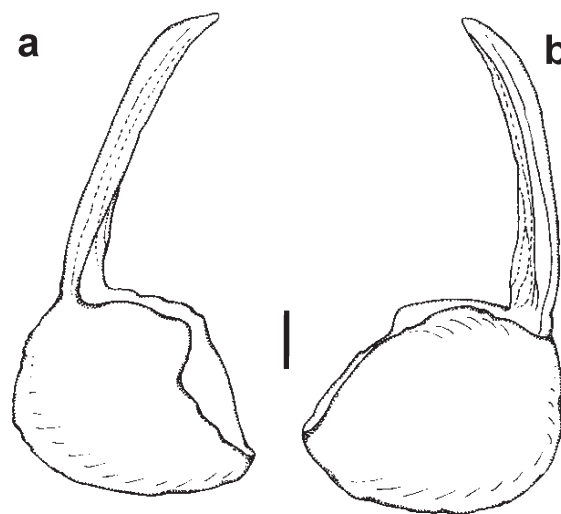
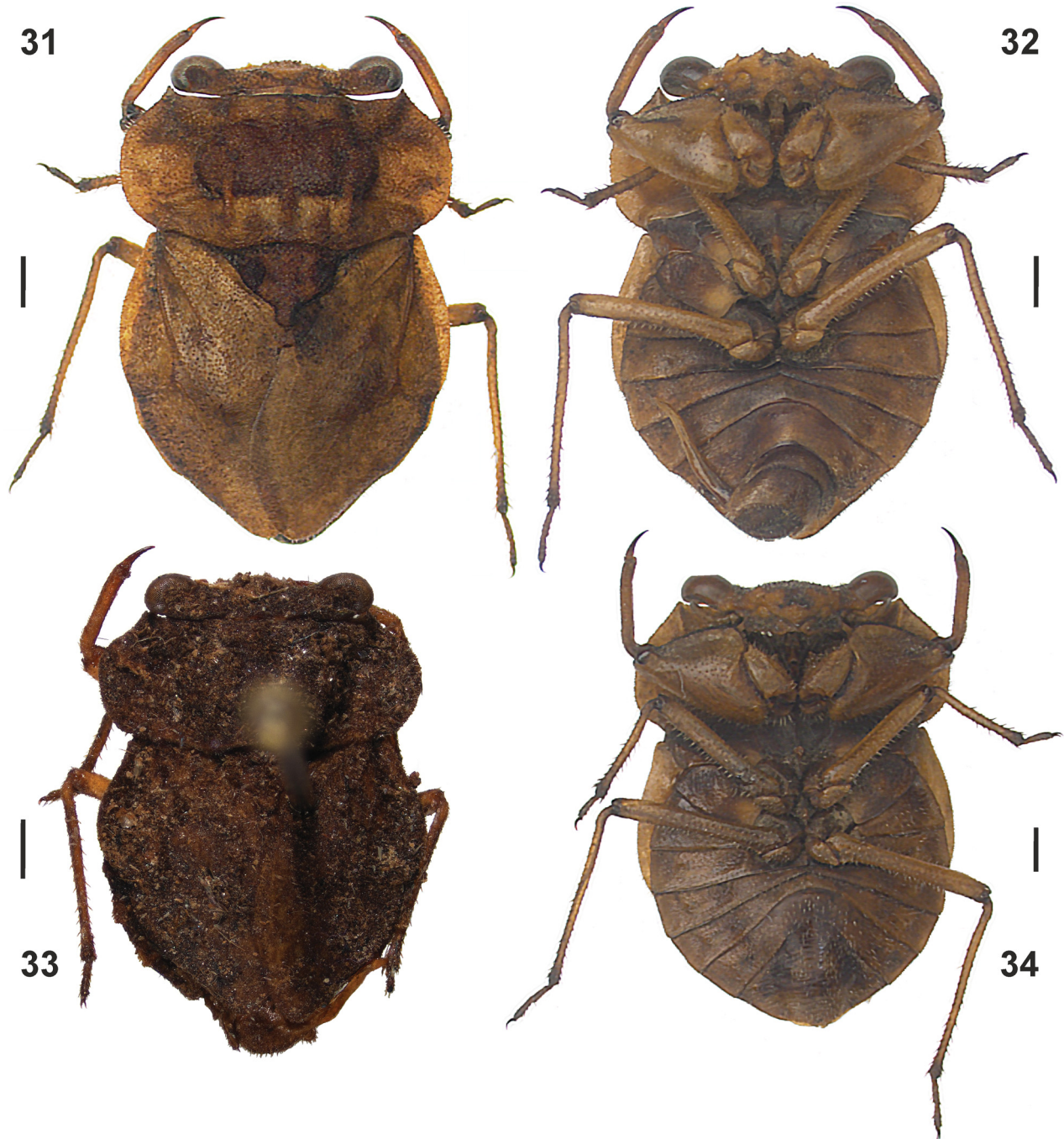


Fig. 30. *Nerthra papaceki* sp. nov., paramere and pygophore (a – ventral view, b – dorsal view).



Figs 31–34. *Nerthra occidua* Todd, 1959. 31–33 – male, habitus (31 – dorsal view, cleaned; 32 – ventral view, cleaned; 33 – dorsal view, before cleaning). 34 – female, habitus (ventral view, cleaned).

in most, as in *N. occidua*, the width of head is less than the length of the pronotum and the scutellum combined (4.7 / 5.1) as in *N. lurida*. The scutellum itself is not elevated but all three tumescences are strongly elevated in both males and females. Therefore, we conclude that *N. occidua* and *N. lurida* refer to the same species. We choose *N. occidua* as the valid name because it was described on a male, and *N. lurida* becomes its junior subjective synonym.

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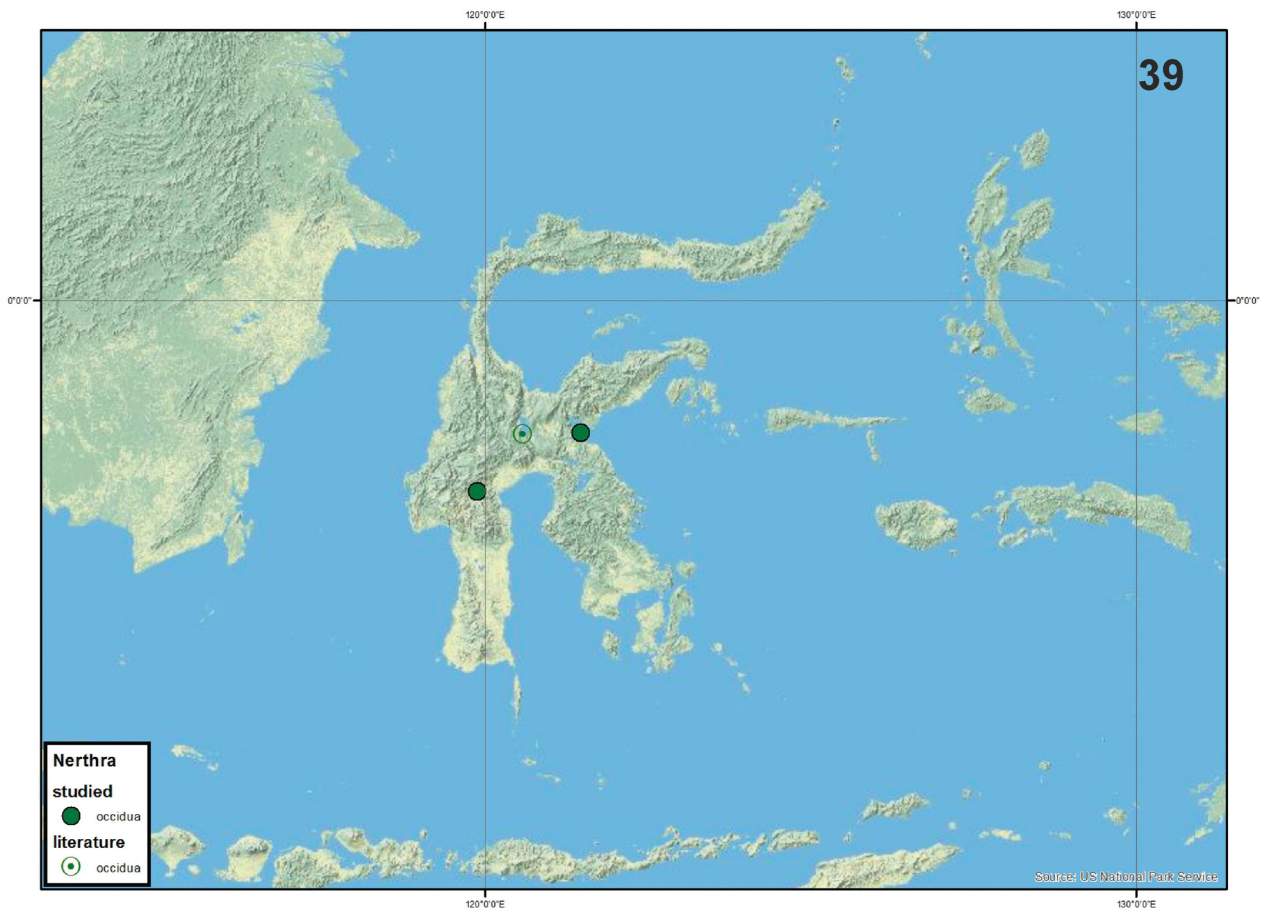
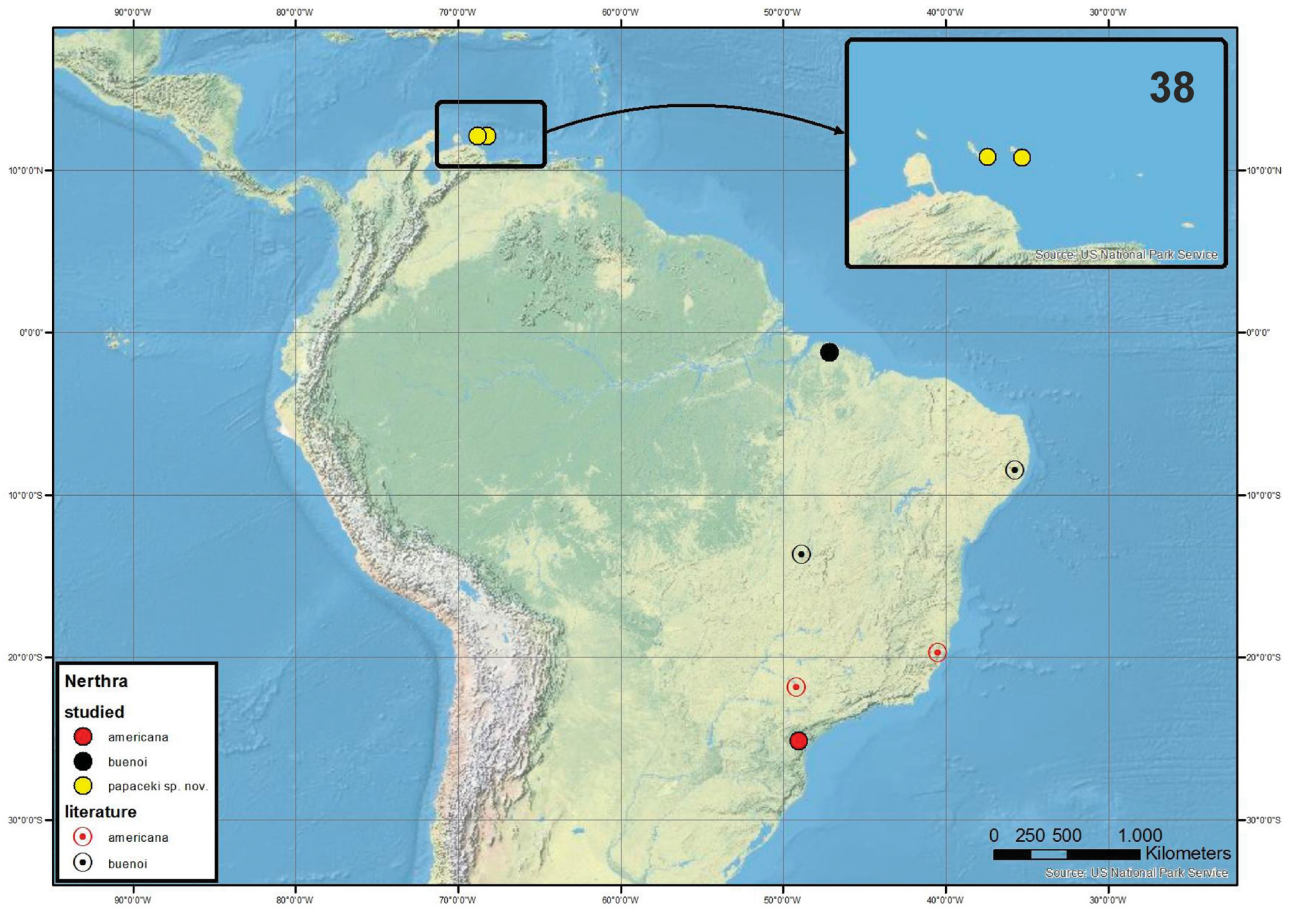
*buanoi* from Goiás. We would like to thank our colleagues in Naturalis, Leiden: Yvonne van Dam for preparing most of the photographs of the RMNH and NCTN specimens, Godard Tweehuysen for access to literature, Luc Willemsse for his support to our work in many ways, Maarten van 't Zelfde for his aid in making the distribution maps and to Reshma Dijkstra and Ant Brandenburg for digitizing all RMNH and NCTN specimens. In addition, we thank Dr. D. Rédei (National Chung Hsing University, Taichung) for providing pieces of literature which were difficult to get. Finally, we would like to thank Dr. P. Kment and Dr. R.W. Sites for their comments and linguistic correction of the manuscript, which have considerably improved this paper.



Figs 35–37. *Nerthra occidua* Todd, 1959. 35–36 – female, habitus dorsal view (35 – before cleaning, 36 – cleaned). 37 – apex of paramere (ventral view).

## References

- ANDERSEN N. M. & WEIR T. A. 2004: *Australian water bugs. Their biology and identification (Hemiptera-Heteroptera, Gerromorpha & Nepomorpha)*. Entomograph Vol. 14. Apollo Books, Stenstrup & CSIRO Publishing, Collingwood, 344 pp.
- ARNETTE R. H. JR., SAMUELSON G. A. & NISHIDA G. M. 1993: The insect and spider collections of the world (Second edition). *Flora & Fauna Handbook* **11**: i–vii + 1–310.
- BILLBERG G. J. 1820: *Enumeratio Insectorum in Museo Gust. Joh. Billberg*. Gadelianis, Stockholm, 128 pp.
- BOULARD M. & JAUFFRET P. 1984: Description d'un *Gelastocoris* nouveau du Brésil et précisions sur les genitalia males et femelles de ce genre d'Hémiptères (Gelastocoridae). *Nouvelle Revue d'Entomologie (Nouvelle Série)* **1**: 7–18.
- BRISSON M. J. 1760: *Ornithologia sive synopsis methodica sistens avium divisionem in ordines, sectiones, genera, species ipsarumque varietates. Vol. 2. Augustinorum*, Parisiis, xvii + 516 pp + 46 pls.
- BROWN L. N. & McPHERSON J. E. 1994: Life history and laboratory rearing of *Gelastocoris oculatus oculatus* (Fabricius) (Hemiptera: Gelastocoridae) with descriptions of immature stages. *Proceedings of the Entomological Society of Washington* **96**: 516–526.
- CASSIS G. 2006: A phylogenetic reclassification of the toad bug family Gelastocoridae (Insecta: Heteroptera). P. 3. In: *Third Quadriennial Meeting of the International Heteropterist's Society*. WICC Wageningen, 18–21 July 2006. Abstracts, 31 pp.
- CASSIS G. & SILVEIRA R. 2001: A revision and phylogenetic analysis of the *Nerthra alaticollis* species group (Heteroptera: Gelastocoridae: Nerthrinae). *Journal of the New York Entomological Society* **109**: 1–46.
- CASSIS G. & SILVEIRA R. 2002: A revision and phylogenetic analysis of the *Nerthra elongata* species group (Heteroptera: Gelastocoridae: Nerthrinae). *Journal of the New York Entomological Society* **110**: 143–181.
- CASSIS G. & SILVEIRA R. 2004: A redescription of *Nerthra tuberculata* (Montandon) (Heteroptera: Gelastocoridae: Nerthrinae) and a discussion of its systematic position. *Journal of the New York Entomological Society* **111** [2003]: 194–201.
- CASSIS G. & SILVEIRA R. 2006: A new species and first record of a toadbug (Insecta: Heteroptera: Gelastocoridae) from New Caledonia and zoogeography. *Russian Entomological Journal* **15**: 147–150.
- COWAN C. F. 1971: On Guérin's Iconographie: particularly the insects. *Journal of the Society for Bibliography of Natural History* **6**: 18–29.
- DE CARLO J. A. 1954: Subfamilia Gelastocorinae. Nuevas especies de los géneros *Gelastocoris* Kirkaldy y *Montandonius* Melin (Gelastocoridae – Hemiptera). *Misión de Estudios de Patología Regional Argentina* **24** (83–84) [1953]: 87–102.
- DE CARLO J. A. 1959: Géneros *Gelastocoris* y *Montandonius* (Hemiptera-Gelastocoridae) revisión de las especies de Guérin y De Carlo consideradas sinonimas. *Acta Zoologica Lilloana* **17**: 53–85.
- DESJARDINS J. 1837: Note sur un insect nouveau faisant partie de la faune de l'île Maurice. *Annales de la Société Entomologique de France* **6**: 239–242.
- DITRICH T., PETR J., LEPŠ J. Š. & KMENT P. 2020: In memoriam of Professor Miroslav Papáček (1953–2019): biography, memories, bibliography and list of described taxa. *Acta Entomologica Musei Nationalis Pragae* **60** (1): 1–14.
- ESTÉVEZ A. L. SCHNACK J. A. 1977: Una nueva especie del genero *Gelastocoris* Kirkaldy. *Neotropica* **23**: 81–83.
- ESTÉVEZ A. L. SCHNACK J. A. 1980: Descripción de una nueva especie del genero *Nerthra* Say (Hemiptera, Gelastocoridae). *Revista de la Sociedad Entomológica Argentina* **39**: 59–61.
- FABRICIUS J. C. 1775: *Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Libraria Kortii, Flensburgi et Lipsiae, xxx + 832 pp.
- FABRICIUS J. C. 1798: *Systema entomologiae emendata et aucta, secundum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus*. Supplement Proft, Hafniae, 572 pp.
- FABRICIUS J. C. 1803: *Systema Rhyngotorum secundum ordines, genera, species, adiectis synonymis, locis, descriptionibus*. Reichard, Brunsvigae, vi + 324 pp.
- FAÚNDEZ E. I. & ASHWORTH A. C. 2015: Notas sobre la familia Gelastocoridae (Hemiptera: Heteroptera) en el extremo sur de Chile, con descripción de un subgénero y especie nuevos. *Anales Instituto Patagonia* **43**: 69–74.



Figs 38–39. Distribution of treated *Nerthra* species: 38 – *N. americana* (Montandon, 1905), *N. buenoi* Todd, 1955 and *N. papaceki* sp. nov.; 39 – *N. occidua* Todd, 1959.

- FAÚNDEZ E. I. & CARVAJAL M. A. 2017: New data on the subgenus *Rhinodermacoris* (Insecta: Heteroptera: Gelastocoridae), with comments on its Gondwanian origin and relationships. Pp. 321–324. In: GUAQUIL I., LEPPE M., ROJAS P. & CANALES R. (eds): *Visiones sobre Ciencia Antártica. Libro de Resúmenes del IX Congreso Latinoamericano de Ciencia Antártica. Punta Arenas, Chile, 4 al 6 de octubre 2017*. Instituto Antártico Chileno, Punta Arenas, 931 pp.
- GUÉRIN-MÉNEVILLE F. E. 1835, 1844: *Iconographie du règne animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables, et souvent non encore figurées, de chaque genre d'animaux*. Ballière, Paris, 576 pp. [1835 plate 57; 1844 text].
- HEBSGAARD M. B., ANDERSEN N. M. & DAMGAARD J. 2004: Phylogeny of the true water bugs (Nepomorpha: Hemiptera-Heteroptera) based on 16S and 28S rDNA and morphology. *Systematic Entomology* **29**: 488–508.
- HORVÁTH G. 1902: Descriptions of new Hemiptera from New South Wales. *Természeti Füzetek* **25**: 611–612.
- HUNGERFORD H. B. 1922: The life history of the toad bug. *University of Kansas Science Bulletin* **24**: 145–171.
- KEVAN D. K. McE. 1942: Some observations of *Mononyx nepaeformis* (Fabricius, 1775) a toad bug. *Proceedings of the Royal Entomological Society of London (A)* **17**: 109–110.
- KIRKALDY G. W. 1897: Synonymic notes on aquatic Rhynchota. *Entomologist* (London) **30**: 258–260.
- KIRKALDY G. W. 1906: List of the genera of the pagiopodous Hemiptera-Heteroptera, with their type species, from 1758 to 1901 (and also of the aquatic and semiaquatic Trochalopoda). *Transactions of the American Entomological Society* **32**: 117–156.
- KMENT P. & JINDRA Z. 2008: Review of the family Gelastocoridae (Heteroptera: Nepomorpha) of south-eastern Asia. Pp. 189–213. In: GROZEVAS & SIMOV N. (eds.): *Advances in Heteroptera research. Festschrift in honour of 80th anniversary of Michail Josifov*. PenSoft Publishers, Sofia, Moscow, 417 pp.
- LA RIVERS I. 1953: New gelastocorid and naucorid records and miscellaneous notes with a description of a new species *Ambrysus amargosus*. *Wasmann Journal of Biology* **11**: 33–96.
- LANSBURY I. 1988: Gelastocoridae (Hem.-Het.) in the Hope Entomological Collections, University Museum, Oxford. *Entomologist's Monthly Magazine* **124**: 243–250.
- LAUCK D. R. & WHEATCROFT D.G. 1958: Notes on a new habitat for *Nerthra*. *Entomological News* **69**: 20.
- LOPEZ RUF M. PEREZ GOODWYN P. & MARTINS-NETO R.G. 2005: New Heteroptera (Insecta) from the Santana Formation, Lower Cretaceous (Northeastern Brazil), with description of a new family and new taxa of Naucoridae and Gelastocoridae. *Gaea* **1**: 68–74.
- MAHNER M. 1993: Systema Cryptoceratorum Phylogenticum (Insecta, Heteroptera). *Zoologica* **143**: i–ix + 1–302.
- MELIN D. 1929: Hemiptera from South and Central America, I. Revision of the family Gelastocoridae and the American species of *Mononyx*. *Zoologiska Bidrag från Uppsala* **12** [1929]: 151–198.
- MONTANDON A. L. 1905: Trois nouvelles espèces d'Hémiptères Cryptocérates des collections du Musée National Hongrois. *Annales Musei Nationalis Hungarici* **3**: 404–406.
- NIESER N. 1972: The *Gelastocoris nebulosus* complex (Heteroptera – Gelastocoridae). *Studies on the Fauna of Suriname and other Guyanas* **13**: 57–67.
- NIESER N. 1975: The water bugs (Heteroptera: Nepomorpha) of the Guyana Region. *Studies on the Fauna of Suriname and the other Guyanas* **16**: 1–308.
- NIESER N. & CHEN P. P. 1992: Notes on Gelastocoridae and Ochteridae (Heteroptera) with the description of five new species. *Storkia* **1**: 2–13.
- PENDERGRAST J. G. 1957: Studies on the reproductive organs of Heteroptera with consideration of their bearing on classification. *Transactions of the Royal Entomological Society of London* **109**: 1–63.
- POINAR G. JR. & BROWN A. E. 2016: Toad bugs (Hemiptera: Gelastocoridae) in Myanmar amber. *Cretaceous Research* **63**: 39–44.
- POLHEMUS J. T. 1972: Notes on the genus *Nerthra*, including the description of a new species (Hemiptera: Gelastocoridae). *Proceedings of the Entomological Society of Washington* **74**: 306–309.
- POLHEMUS J. T. 1995: Family Gelastocoridae Kirkaldy, 1897 – toad bugs. Pp. 23–25. In: AUKEMA B. & RIEGER CH. (eds.): *Catalogue of the Heteroptera of the Palaearctic Region. Vol. 1, Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha and Leptopodomorpha*. The Netherlands Entomological Society, Amsterdam, xxvi + 222 pp.
- POLHEMUS J. T. & LINDSKOG P. 1994: The stridulatory mechanism of *Nerthra* Say, a new species, and synonymy (Heteroptera: Gelastocoridae). *Journal of the New York Entomological Society* **102**: 242–248.
- POPOV YU. A. 1971: Istoricheskoe razvitiye poluzhestkokrylykh infraotryada Nepomorpha (Heteroptera). [Historical development of true bugs of the infraorder Nepomorpha (Heteroptera)]. *Trudy Paleontologicheskogo Instituta AN SSSR* **129**: 1–230 + pls 1–9 (in Russian). [English translation: VAITATAITIS H., unknown: *Historical Development of Hemiptera Infraorder Nepomorpha* (Heteroptera)].
- PRIESNER H. & WAGNER E. 1961: Supplement to <<A review of the Hemiptera heteropteran known to us from Egypt>>. *Bulletin de la Société Entomologique d'Égypte* **45**: 323–339.
- SAY T. 1832: *Descriptions of new species of Heteropterous Hemiptera of North America*. New Harmony, Indiana, 39 pp.
- SCUDDER G. G. E. 1959: The female genitalia of the Heteroptera: morphology and bearing on classification. *Transactions of the Royal Entomological Society of London* **11** [1914]: 405–465.
- SEKERKA L. 2020: Commented catalogue of Cassidinae (Coleoptera: Chrysomelidae) of the state of São Paulo, Brazil, with remarks on the collection of Jaro Mráz in the National Museum in Prague. *Acta Entomologica Musei Nationalis Pragae* **60** (2): 667–707.
- SIGNORET V. 1864: Révision des Hémiptères du Chili. *Annales de la Société Entomologique de France, Série 4* **3**: 541–588.
- SITES R. W. 2015: New taxa of Cryphocricinae (Heteroptera: Naucoridae) from the Guiana Shield: *Hygropetrocoris* Sites, n. gen. and two new species of *Ambrysus* Stål. *Zootaxa* **4033** (3): 427–438.
- SITES R. W. & NICHOLS B. J. 1990: Life history and description of immature stages of *Ambrysus lunatus lunatus* (Hemiptera: Naucoridae). *Annals of the Entomological Society of America* **83**: 800–808.
- SCHNACK J. A. & ESTÉVEZ A. L. 1979: Monographia sistemática de los Gelastocoridae de la República Argentina. *Limnobiós* **1**: 346–380.
- ŠTYS P. & JANSSON A. 1988: Check-list of recent family-group and genus-group names of Nepomorpha (Heteroptera) of the world. *Acta Entomologica Fennica* **50**: 1–44.
- TODD E. L. 1954: New species of *Nerthra* from California. *Pan-Pacific Entomologist* **30**: 113–118.
- TODD E. L. 1955: A taxonomic revision of the family Gelastocoridae (Hemiptera). *University of Kansas Science Bulletin* **37**: 277–475.
- TODD E. L. 1957a: The Machris Brazilian Expedition Entomology: Gelastocoridae (Hemiptera) from Central Goiás. *Los Angeles County Museum Contributions in Science* **14**: 1–3.
- TODD E. L. 1957b: Five new species of Gelastocoridae with comments on other species (Hemiptera). *Proceedings of the Entomological Society of Washington* **50**: 145–162.
- TODD E. L. 1959: The Gelastocoridae of Melanesia (Hemiptera). *Nova Guinea (N. S.)* **10**: 61–94.
- TODD E. L. 1960: The Gelastocoridae of Australia (Hemiptera). *Pacific Insects* **2** (2): 171–194.
- TODD E. L. 1961a: Synonymical notes on some South American species of *Gelastocoris* Kirkaldy (Hemiptera: Gelastocoridae). *Proceedings of the Biological Society of Washington* **74**: 57–64.
- TODD E. L. 1961b: A checklist of the Gelastocoridae (Hemiptera). *Proceedings of the Hawaiian Entomological Society* **17**: 461–476.
- USINGER R. L. 1956: Aquatic Hemiptera. Pp. 182–228. In: USINGER R. L. (ed.): *Aquatic Insects of California*. University of California Press, Berkeley and Los Angeles, Second printing, [1963], 508 pp.
- WANG Y. H., CUI Y., RÉDEI D., BAŇAŘ P., XIE Q., ŠTYS P., DAMGAARD J., CHEN P. P., YI W. B., WANG Y., DANG K., LI C. R. & BU W. J. 2016: Phylogenetic divergences of the true bugs (Insecta: Hemiptera: Heteroptera), with emphasis on the aquatic lineages: the last piece of the aquatic insect jigsaw originated in the Late Permian/Early Triassic. *Cladistics* **32**: 390–405.
- XIE T.-Y. & LIU G.-Q. 2018: Notes on some toad bugs from China (Hemiptera, Heteroptera, Gelastocoridae). *ZooKeys* **759**: 137–147.
- YE ZH., DAMGAARD J., YANG H.-H., HEBSGAARD M. B., WEIR T. & BU W.-J. 2020: Phylogeny and diversification of the true water bugs (Insecta: Hemiptera: Heteroptera: Nepomorpha). *Cladistics* **36**: 72–87.