

The prey and predators of Homalopsine snakes

HAROLD K. VORIS and JOHN C. MURPHY

Division of Amphibians and Reptiles, Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605-2496, USA; e-mail: hvoris@fmnh.org

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The diets of all South-East Asian water snakes of the subfamily Homalopsinae are reviewed. New diet observations for 10 species of homalopsine snakes are presented. The data on four of these, Cantoria violacea, Enhydris doriea, E. longicauda and Gerarda prevostina represent the first published diet records for these species. The observations for Fordonia leucobalia, Myron richardsonii and *Enhydris enhydris* represent the first taxonomically detailed diet records for these three species. The records provided for Cerberus rynchops, Enhydris plumbea and Homalopsis buccata add new taxonomic categories to previous records. The records provided for Cerberus rynchops, E. plumbea and Homalopsis buccata add new taxonomic categories to previous records. Four generalities emerge from our findings: (1) freshwater homalopsines feed primarily on fish and the adults and larvae of amphibians; (2) at least four of the eight estuarial species specialize on crustaceans while two primarily prey on fish; (3) feeding on crustaceans appears to have evolved independently at least twice; (4) prey are usually less than 10%of the predator's mass. The known predators of homalopsines are summarized and include both invertebrates and vertebrates. The microhabitats of the estuarial species are discussed and related to prey and habitat preferences.

KEYWORDS: Homalopsinae, water snakes, diet, predators, mud lobster.

Introduction

The 10 genera and 35 species of homalopsine snakes were reviewed by Gyi (1970) in his monograph on these freshwater and estuarial snakes. He devoted a single paragraph to their food habits, in which he cited Schmidt (1927) and Pope (1929) on the frog-eating habits of *Enhydris plumbea*; Boulenger's (1890) hypothesis that *Bitia hydroides* feeds exclusively on fishes (Gyi (1970) erroneously credited Bourret with this information); and Cantor's (1847) observations that *Fordonia leucobalia* inhabits crab-holes and eats crabs. Gyi (1970) also reported finding a 40 mm crab in a specimen of *Fordonia*. He then commented that most species feed on fish and frogs, and that homalopsines may be detrimental in ponds where fish are cultured.

Comments on the food habits of homalopsine snakes are widely scattered in the

literature. Most of the pre-1970 papers simply note stomach contents for one or two specimens (e.g. Flower, 1899; Chang and Fang, 1931) and only a few post-1970s papers provide extensive detail on diet (Jayne *et al.*, 1988, 1995; Voris and Karns, 1996). In fact, the diets of 18 of the 35 homalopsine species Gyi recognized are undocumented. Some of these species have very restricted ranges and are poorly known from museum specimens (e.g. *Cantoria annulata* and *Heurnia ventromaculata*), but for even abundant and widely distributed species (e.g. *Enhydris enhydris* and *Gerarda prevostiana*), the specifics of their diet have been undocumented for more than a century.

Here we review what is known about the diets of homalopsine snakes, report new observations on the food and feeding habitats of 10 species and summarize what is known about the predators of homalopsine snakes. In addition, we comment on the number of prey, prey size and the use of microhabitats.

Materials and methods

For this report we have attempted to accumulate all of the literature pertaining to feeding and predation of homalopsine snakes. We have cited references that report original observations of feeding events or of stomach contents. References with secondary or general statements have been omitted. We have examined more than 450 museum specimens of homalopsines and identified their stomach contents to the lowest taxonomic level possible. Snakes and prey were measured to the nearest mm, and weighed to the nearest 0.1 g. When a prey item was partially digested we estimated its weight by comparing it to intact conspecific specimens.

Field work contributing to this study was carried out in Borneo, Thailand and Singapore between 1992 and 1999. Snakes that were obtained from baited traps were not used for diet analysis. Other snakes were collected by hand, anaesthetized, packed in ice and transported to the laboratory for data collection. When prey were found in stomachs they were measured following the methods outlined above for museum specimens. Most of the field work in Thailand was conducted at Ban Tha Hin on the east side of Lake Songhkla. In Singapore, field work was carried out along the northern coast at Lim Chu Kang and Pasar Ris.

Results

Table 1 summarizes what is known about the diets of homalopsine snakes and it incorporates new diet observations for 10 species of homalopsine snakes. To our knowledge, the data on four of these, *Cantoria violacea, Enhydris doriae, E. longicauda* and *Gerarda prevostina*, represent the first published diet records for these species. The observations for *Fordonia leucobalia, Myron richardsonii* and *Enhydris enhydris* represent the first taxonomically detailed diet records for these three species. The records provided for *Cerberus rynchops, E. plumbea* and *Homalopsis buccata* add new taxonomic categories to previous records. Three generalities emerge from a review of table 1 and figure 1: (1) freshwater homalopsines feed primarily on fish and the adults and larvae of amphibians; (2) at least four of the eight estuarial species specialize on crustaceans while two primarily prey on fish; (3) feeding on crustaceans appears to have evolved independently at least twice (figure 1).

Estuarial and mangrove piscivorus

Among the estuarial species, *Cerberus rynchops* is a generalist that takes a variety of fish representing several families and, in at least one instance, a crustacean

(Alpheidae, table 1). Jayne *et al.* (1988) examined 262 *C. rynchops* in 1984 and found 37% contained food; in a 1985–1986 sample, 349 snakes were examined, and 27% contained food. Jayne *et al.* (1988) present data demonstrating that *C. rynchops* take relatively small prey (usually Oxydercine gobies) and often multiple items. For example, in 86% of the *C. rynchops* that contained prey, the prey weighed 10% or less of the predator's mass. In this same sample of 181 snakes with stomach contents, the stomachs of 72 snakes (40%) contained two or more prey items. One of us (J.C.M.) examined 12 specimens of *C. rynchops* that contained food at the Museum and Art Gallery of the Northern Territory, Australia, seven (58%) contained multiple fish.

Bitia hydroides, as Boulenger (1890) suggested, feeds on fish (table 1). The only detailed diet data for *B. hydroides* suggests that it may specialize on gobies (Jayne *et al.*, 1995). Of 117 *B. hydroides* examined, the stomachs of only six snakes (5.1%) contained food. Of the six prey items, two were complete and represented 13% and 38% of the respective snake's mass.

Estuarial and mangrove crustacean feeders

Fordonia leucobalia was the first homalopsine to be recognized as a crustacean feeder (Cantor, 1847). Of 32 *F. leucobalia* examined between 21 November 1985 and 8 February 1986 at Parit Jawa, Malaysia, five (16%) contained the remains of crabs (Voris and Jayne, field notes). Of another 30 museum specimens examined, six (20%) were found to contain the remains of crabs or, in one case, a mud lobster (*Thalassina anomala*). In five cases where prey items were complete and snake masses were measured, we found the prey to be relatively small, ranging from only 0.5 to 7.4% of the snake's mass.

Shine (1985) has described two distinct feeding behaviours for *F. leucobalia*. In one behaviour *F. leucobalia* pushes the crab into a muddy substratum with its forebody to immobilize it for swallowing, a behaviour we have recorded on videotape (Jayne and Voris, personal communication) and have termed 'chin-pinning'. Shine (1985) also reported the observations of Paul Horner, that a captive *F. leucobalia* held a crab in a coil of its body, while eating each of the crab's legs. Other authors have apparently picked up on this description. Green (1997: 182) wrote, 'This species tears the legs off larger crabs before swallowing their bodies...' O'Shea (1996: 112) described this as, 'Crabs are pinned in their burrows and "chewed" until they are dismembered'. It is very likely that snakes do grasp crabs by their legs, and that the snakes will swallow the legs and not the rest of the crab, since we have found crab legs in a snake's stomach without the crab's body. However, it seems much more probable that the crab autonomizes its leg(s) when the appendage(s) are seized by the snake, rather than having the snake tear or chew them off.

Gerarda prevostiana ranges along sea coasts from the vicinity of Bombay, India to the Philippines. Despite this huge range, discovering this snake's habitat and habits has been long in coming. Descriptions of its habitat include general statements such as '...tidal rivers and estuaries, and often wanders out along the coasts' (Gharpurey, 1944). Deraniyagala (1955) considered it rare in India and Ceylon, while Taylor (1965) described collecting 15 specimens in the mangroves at Ang Hin, Thailand, and stated he could have collected more.

In 1921, Wall speculated on the food habits of *G. prevostiana*, 'No observations have been made, but it is fairly certain to subsist upon fishes'. He was incorrect. We have examined 16 museum specimens of *G. prevostiana* and found six (37.5%) to

	Table 1. Diet records for Homalopsine snakes.	
Predator	Prey	Reference
Estuarial/marine Bitia hydroides	Pelagic fishes	Cantor, 1847
Cantoria violacea Cerberus rynchops	Oxydercine gobies Alpheus macrorhynchus (Alpheidae) (2), snapping shrimp (Alpheidae) (3) Caranx ire Amhivochius su Synodus evernani Alpheus su (Alpheidae)	Jayne <i>et al.</i> , 1995 This study Annandale, 1907 Auffenherer 1980
	Eels, gobies, apogonids, signids Oxydercine gobies, other gobies, catfish, mullet Periophthalmus sp.	Gorman <i>et al.</i> , 1981 Jayne <i>et al.</i> , 1988 Pauwels <i>et al.</i> , 2000
Fordonia leucobalia	Arius sp. (2), Eleotridae, Talapia mosambica Crabs	This study Cantor, 1847; and others
	Sarmiatium germani (Grapsidae), Macrophthalmus sp. Sesarmine crab (Grapsidae) Dotillopsis brevitarsis (Ocypodidae) (3)	This study This study This study
Gerarda prevostiana Myron richardsonii	<i>Uca</i> sp. (Ucypoundae) (many) <i>Thalussina anomala</i> (Thalassinidae) <i>Dotillopsis</i> sp. (Ocypodidae), crabs (4) Crabs	Gow, 1989; Shine, 1991b; this study This study Worrell, 1963
	Fish Gobiidae and other fish	Shine, 1991b This study
Freshwater Enhydris bocourti	Fishes Five fishes in one stomach	Deuve, 1970 Saint Girons, 1972
Enhydris chinensis	Anabas scandens Fish and frogs Fish and amphibians	Chang and Fang, 1931 Gressitt, 1940, 1941 Kuntz, 1963
Enhydris doriae Enhydris enhydris	Macropodus viridiauratus, Erythroculter aoki, Carassius or Cyprinus spp. Systomus cf. orphoides and fish (2) Small fish Anabas testudineus, Rasbora sumatrana, Trichopsis vittata	Pope, 1929, 1935 This study Taylor and Elbele, 1958 This study

Predator	Prey	Reference
Enhydris innominata Enhydris longicauda Enhydris plumbea	Fish Trichogaster trichopterus Fish, frogs, crustaceans Loaches and amphibians Rana limnocharis, Microhyla sp., frogs Rana sp., Microhyla sp. Polypedates leucomystax, Claris teysmanni Anabas testudineus, Macropodus opercularis, Monopterus alba (2),	Saint Girons, 1972 This study Gresssitt, 1940, 1941 Kuntz, 1963 Pope, 1929, 1935 Schmidt, 1927 Voris and Karns, 1996 This study
Enhydris polylepis	Eleotridae, Limnonectes limnocharis (2), Microhyla pulchra (6) Small frogs Marshachium en (Dolosmoridae) Electridae Mardone cuminoidae	1 his study Kinghorn, 1928 Thompson, 1935 Shina, 10015
Enhydris sieboldii Erpeton tentaculatum	Fish and frogs Fish and frogs Small fish	Wall, 1907 Campden-Main, 1970 Saint Girons, 1972
Homalopsis buccata	Fiant mactual (probably accuental matchal) Fish Tilapia, Lebistes, Mystus, Fluta alba Fluta alba, Claris sp., Chana sp. Puntius binotatus Fish, frogs, freshwater crustaceans 30 cm fish	Monce, 1075 Bergman, 1951 Berry and Lim, 1967 Lim Boo-Lait, 1964 Deuve, 1970 Hoesel, 1959
The genera and species of snake prey type exceeded one the number	The genera and species of snakes are listed alphabetically within the two major ecological categories. When the number of snakes with a particular type exceeded one the number is given in parentheses. Family names are provided in brackets for crustacean prey. The authors are unaware of	When the number of snakes with a particula srustacean prey. The authors are unaware of

Table 1. (Continued).

prey type exceeded one the number is given in parenuceses raming names are provined in contrasting. E. bennetti, E. dussumieri, E. indica, diet records for the following taxa: Cantoria annulata, Cerberus microlepis, Enhydris albomaculata, E. alternans, E. bennetti, E. dussumieri, E. indica, E. innominata, E. jagorii, E. maculosa, E. matannensis, E. pakistanica, E. pahangensis, E. punctata, E. smithi and Heurnia ventromaculata.

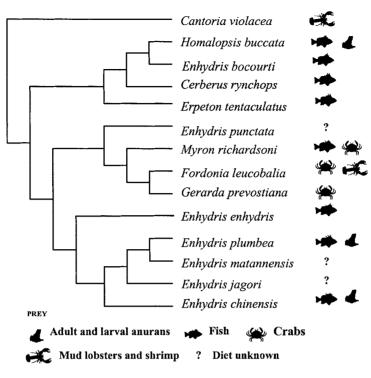


FIG. 1. The known diets of 14 species of homalopsine snakes are indicated on a hypothetical phylogenetic tree based on parts of two ribosomal genes. The data include 313 base pairs of the 16S gene and 462 base pairs of the cytochrome *b* gene. The parsimony analysis was done using PAUP 4.0 and both transitions and transversions.

contain the remains of grapsoid crabs (Crustacea: Decapoda: Grapsidae). In only two (FMNH 179103; BM 1904.10.18.7) of these six specimens were the prey nearly complete and in each case represented less than 1% of the snake's mass.

We have collected *G. prevostiana* at two localities on the north coast of Singapore. On 16 February 1996 a snake was discovered in a burrow during the excavation of a mud lobster (*Thalassina anomala*) mound near Lim Chu Kang. This snake (ZRC 2.3460) contained the back legs from one side of a 3-4 cm (estimated carapace width) grapsoid crab. On 13 and 14 July 1999 between 1830 and 2000 h at Pasar Ris, Singapore, at least eight *G. prevostiana*, several *F. leucobalia* and *C. rynchops* were seen in a total of 3h of observation over the two evenings. The site was a restored mangrove forest with abundant mud lobster mounds and the snakes were swimming in tidal pools formed in depressions around the bases of mud lobster mounds. As *G. prevostiana* foraged, they moved in and out of the water and crab burrows on the outer surface of the mounds.

Cantoria violacea ranges from the coast of Myanmar and the Andaman Islands eastward following coastlines throughout the Greater Sunda Islands, and ascending tidal rivers for at least short distances (Wall, 1924; Smith, 1943; Tweedie, 1983). Frith and Boswall (1978) described one specimen collected on a mud flat on Phuket Island, Thailand, with its head down a crab burrow but they provided no diet data. One of us (H.K.V.) collected four specimens on Phuket Island of which two had stomach contents. One *C. violacea* (FMNH 250115, 95.0 mm svl (short vent length),

19.5 mm tail lg (length), 127 g) was collected on the edge of a mud bank in a tidal creek at about 21:00 h on a rising tide on 31 July 1992. Its stomach content consisted of one complete female giant mangrove snapping prawn, *Alpheus microrhynchus* (Crustacea: Decopoda: Alpheoidea) (thorax length 20 mm, total length 57.5 mm, claw length 30.3 mm, mass 5.1 g). Thus, in this case, the prey amounted to 4% of the snake's mass. A second specimen, a male *C. violacea* (FMNH 250118, 75.5 mm svl, 15.8 mm tail lg, 65 g) was collected at Saphan Hin mud flats and tidal creek on the night of 16 August 1992. The stomach content consisted of one complete but digested claw of a *A. microrhynchus* (claw length 25.7 mm, estimated mass of claw 0.95 g based on the previous prawn claw), one digested decapod (the remains of a *A. microrhynchus* or a grapsoid crab); one piece of wood 16 by 8 mm and one piece of leaf 20 mm diameter. The estimated mass of the claw was 1.5% of the snake's mass.

Worrell (1963) reported that *Myron richardsonii* feeds on crabs. Our examination of the stomachs of seven museum specimens of *M. richardsonii* uncovered one snake with a mostly digested fish and one snake with a partially digested fish of the family Gobiidae. Thus, it appears that this species may prey on both fish and crabs.

Diets of freshwater homalopsines

Table 1 presents the first taxonomically detailed diet records that demonstrate that *E. enhydris* feeds on a variety of small freshwater fish. At the edge of Lake Songkhla, Thailand, the number of *E. enhydris* hand-collected from fish bays with food in their stomachs varied greatly from year to year. In 1996 the entire sample of 28 snakes lacked food in their guts. In 1997 five of 20 (25%) contained food in their guts, and in 1999 three of seven (43%) contained fish. The five fish that were complete amounted to between 2.1 and 10.9% of the snake's mass.

The new records provided for *E. plumbea* include four fish species and two frog species (table 1). In a sample of 17 *E. plumbea* collected in Vietnam, 59% contained food, and of these 90% were anurans and 10% were fish. In a sample of 20 *E. plumbea* from Borneo, Voris and Karns (1996) reported 90% with stomach contents, composed of 77% anurans and 23% fish.

Table 1 provides two new prey taxa records for *Homalopsis buccata*, both fish. Although the prey we observed for this species were incomplete, Bergman (1951) reported on complete fish in two *H. buccata* and in each case the fish was 25% of the snake's mass.

Stomachs of 15 *Enhydris doriae* from Borneo were examined and three were found to contain the remains of fish. One item was identified to the genus *Systomus*, a group of relatively fast swimming barbs.

Predators of homalopsine snakes

Crustaceans as snake predators were documented by Voris and Jeffries (1995). They found snake scales in about 5% (n=22) of the stomachs of the mangrove crabs (*Scylla serrata*) they examined; fishermen on Phuket Island, Thailand described seeing crabs feeding on *C. rynchops*; and 106 staged encounters between crabs and *C. rynchops* resulted in the snakes being consumed by the crabs about 25% of the time. In addition, in 1999, fishermen on Thailand's Pak Pang Peninsula reported to us that crabs there ate the local water snake, *C. rynchops*.

Among the vertebrates the homalopsines have a variety of predators. Lyle and Timms (1987) reported *C. rynchops* and *F. leucobalia* in the stomachs of the tiger shark, *Caracharhinus caustus*. A photograph in Shine (1991a) illustrates the

Australian long-necked turtle, *Chelodina rugosa*, regurgitating an *E. polylepis*, and Taylor (1979) reported *M. richardsonii* from the stomach of a salt-water crocodile, *Crocodylus porosus*. The Museum and Art Gallery of the Northern Territory, Australia has a *F. leucobalia* (svl=35.0 cm) that was removed from the gut of a *Varanus indicus* (svl=40.0 cm).

Snakes may be the most important predators of homalopsines in many localities. The pipe snake, *Cylindrophis ruffus*, is known to feed on *H. buccata* (Smith, 1914) and *Enhydris alternans* (Iskandar, 1987). We observed a captive sunbeam snake, *Xenopeltis unicolor* feeding on *E. enhydris*. The cobra, *Naja naja*, and the krait, *Bungarus multicintus*, are reported to feed on *E. plumbea* (Mao, 1970) and field notes from Jayne (personal communication) report the krait, *Bungarus fasciatus*, with a *F. leucobalia* in its stomach.

The white-bellied sea eagle, *Haliaeutus leucogaster*; the brahminy kite, *Haliaster indus*; and the pariah kite, *Milyus migrans*, are known predators on *C. rynchops* (Saha, 1983; Murthy and Rao, 1986). Jabiru storks, *Xenorhynchus asiaticus*, have been reported by Guinea to feed on homalopsines (Greer, 1997). The bandicoot rat, *Bandicota indica*, has been observed feeding on *E. enhydris* (Nandi, 1984). Humans use the skin of *C. rynchops* for ornamental leather products and kill them from fear (Hoesel, 1959; Silva, 1980; Dutta, 1989). Humans eat *E. polylepis*, *E. bocourti* and *E. chinensis* (Thomson, 1935; Angel, 1950; Irvine, 1954; Parker, 1982; Stuart, personal communication). In addition, Stuart *et al.* (2000) reported that in Cambodia, large numbers of *E. enhydris*, *E. bocourti*, *E. longicauda* and *H. buccata* were collected from Grand Lac and then sold as feed to crocodile farms in Siem Reap.

Discussion and conclusions

Prey type, size and number

The majority of homalopsines feed on fish. Several species also take amphibians and at least three species consume only crustaceans. Our observations, as well as those in the literature, substantiate the assertion that most homalopsines take relatively small prey (e.g. Campden-Main, 1970; Saint Girons, 1972) and often will take multiple items (e.g. Jayne *et al.*, 1988).

Role of mud lobster mounds

Mud lobster mounds have been overlooked by herpetologists as potential refuges and foraging sites for snakes but it is clear from our observations that these mounds may be very important to the ecology of as many as five species of homalopsine snake. The mud lobster, *Thalassina anomala* (Crustacea: Decapoda: Thalassinidae) appears to have a geographical distribution that encompasses the distribution of all of the estuarine homalopsines. *T. anomala* ranges from the vicinity of Bombay, India eastward to Manila Bay, Philippines and Moreton Bay, Queensland, Australia (Pearse, 1911; Sankolli, 1963; Macnae, 1968). The mud lobster colonizes areas between the mean low tide and mean high tide, thus they are using the landward side of the mangrove forest. *Thalassina* filters the mud for food, digesting the organic matter and shovelling the undigested material out of its burrow with its first pair of appendages. The mud lobster and crabs of the genus *Uca* (Crustacea: Decopoda: Ocypodidae) are the major burrowing animals in the heavy mud of the mangrove forest floor (Berry, 1963). The debris builds up around the burrow and forms a distinctive feature of the mangrove landscape. The mounds often include mangrove trees and other vegetation, the roots of which stabilize the soil. At some locations these mounds approach 2 m in height and 8-10 m in circumference, at other locations they may be smaller. Numerous invertebrates use these mounds and Berry (1963) and Macnae (1968) have listed fauna associated with the lobster mounds which include the grapsoid crabs in the genera *Graspus* and *Sesarma* and the alphaeid pistol shrimp in the genus *Alpheus*, as well as goboid fishes (e.g. *Periophthalmus*).

Appendix

Alphabetical list of binomials and their taxonomic authorities that appear in the text and in table 1

Alpheus microrhynchus De Man, Anabas scandens (Daldorff) [= Anabas testudineus], Anabas testudineus (Bloch), Bandicota indica Hodgson, Bitia hydroides (Gray), Bungarus fasciatus (Schneider), Bungarus multicinctus Blyth, Cantoria annulata (Jong), Cantoria violacea Girard, Caranx ire Cuvier, Carcharhinus caustus (Whitley), Cerberus microlepis Boulenger, Cerberus rynchops (Schneider), Chelodina rugosa Ogilby, Claris teysmanni Bleeker, Crocodylus porosus Schneider, Cylindrophis ruffus (Laurenti), Dotillopsis brevitarsis De Man, Enhydris albomaculata (Dumeril and Bibron), Enhydris alternans (Reuss), Enhydris bennettii (Gray), Enhydris bocourti (Jan), Enhydris chinensis (Gray), Enhydris doriae (Peters), Enhydris dussumieri (Dumeril and Bibron), Enhydris enhydris (Schneider), Enhydris indica (Gray), Enhydris innominata (Bourret), Enhydris jagorii (Peters), Enhydris longicauda (Bourret), Enhydris maculosa (Blanford), Enhydris matannensis (Boulenger), Enhydris pahangensis Tweedie, Enhydris pakistanica Mertens, Enhydris plumbea (Boie), Enhydris polylepis (Fisher), Enhydris punctata (Gray), Enhydris sieboldii (Schegel), Enhydris smithi (Boulenger), Erpeton tentaculatus Lacepede, Erythroculter aoki Jordan and Synyder (= Muraenichthys aoki), Fluta alba (Zouiev) (= Monopterus alba), Fordonia leucobalia (Schlegel), Gerarda prevostiana (Eydoux and Gervais), Haliaeutus leucogaster (Gmelin), Haliaster indus (Boddaert), Heurnia ventromaculata Jong, Homalopsis buccata (Linnaeus), Limnonectes limnocharis (Boie), Macropodus opercularis (Linnaeus), Macropodus viridiauratus Lacepede, Megalops cyprinoids (Broussonet), Microhyla pulchra Gray (= Kaloula pulchra (Gray)), Milyus migrans (Boddaert), Monopterus alba (Zouiev), Myron richardsonii Gray, Naja naja (Linnaeus), Polypedates leucomystax (Boie), Puntius bionotatus (Valenciennes), Rana limnocharis (Boie), Rasbora sumatrana (Bleeker), Sarmiatium germaini (Grapsidae), Scylla serrata (Forsskål), Synodus evermanni Jordan and Bollman, Systomus orphoides (Valenciennes), Thalassina anomala (Herbst), Tilapia mossambica (Peters), Trichopterus trichopterus (Pallas), Trichopsis vittata (Cuvier), Varanus indicus (Daudin), Xenopeltis unicolor (Reinwardt), Xenorhynchus asiaticus Latham.

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