

# The biogeography of extant species of *Austroharpa* Finlay, 1931 (Mollusca: Harpidae) **Writing Sample – Not for Publication**

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## ABSTRACT

This article adds to the knowledge of extant species of *Austroharpa*, Finlay, 1931, by refining their respective geographic distribution and consolidating the available information on their biology.

New records are published for *A. learorum*, *A. wilsoni* and *A. exquisita* with a discussion on the status of some taxa and populations considering biogeographic data.

A comprehensive distribution map is proposed, based on selected records from Museums and private collections, as well as from literature.

Elements of description of the living animal are mentioned for all species except for *A. michearti*, with the publication of rare *in situ* photographs of *A. loisae* and *A. punctata*, and pictures *in vivo* of *A. learorum* and *A. wilsoni*.

The holotypes of every known recent species are illustrated together in color for the first time.

**Keywords:** Harpidae, Australia, Endemic species, Mollusca, New records, Biogeography, Distribution

## INTRODUCTION

The family Harpidae, Bronn 1849, has few extant genera (4)<sup>4</sup> and comprises of little more than sixty species with an incredibly wide distribution. Members of this family are living from intertidal zone down to several hundred meters in tropical, subtropical and temperate waters. The genera *Harpa* and *Oniscidia* contain several species with a large geographical range, while *Morum* and *Austroharpa* generally have a more limited distribution.

The genus *Austroharpa* was introduced by New Zealand paleontologist Harold J. Finlay in 1931 for the fossil species *Harpa pulligera* Tate, 1889, while only one living species was known at the time, *Austroharpa punctata* (Verco, 1896). Five more recent species have since been described, all endemic to southern temperate Australian waters: *A. exquisita* (Iredale, 1931), *A. wilsoni* Rehder, 1973, *A. loisae* Rehder, 1973, *A. learorum* Hart & Limpus, 1998 and *A. michearti* Lorenz, 2020.

Because of the relative scarcity of specimens available for study, small shell size and the difficulty to reach their remote habitat, the biology of *Austroharpa* is poorly known. On the other hand, this lack of availability and the fact that the genus belongs to the Harpidae, a family highly prized by collectors, gives the shells a high market value.

Very few research vessels have operated in deep waters off the lower west and south coasts of Western Australia, and most have concentrated on the economically important Northwest Shelf.<sup>5</sup> These voyages have generated considerable information on the fauna of this area, with the slope (350 to 500 m) having an entirely new faunal assemblage for Australia. Some expeditions have focused on central west coast waters, generally reaching as far south as Cape Leeuwin,<sup>6</sup> but also around Perth area.<sup>7</sup>

In 2005, a CSIRO benthic survey of the deep continental shelf and slope in Australia's southwestern region provided museum scientists with a rare opportunity to sample the fauna of this poorly studied area. Material from this survey has enabled a much better knowledge of the geographical range of *Austroharpa* species.

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<sup>4</sup> WoRMS accepts the genus *Harpa* Röding, 1798, *Austroharpa* Finlay, 1931 and *Morum* Röding, 1798 - MolluscaBase eds. (2020). MolluscaBase. Harpidae Bronn, 1849. Accessed through: World Register of Marine Species at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=196294> on 2021-09-05.

Following the work of Squires, 2018, the genus *Oniscidia* Mörch, 1852 is also accepted here.

<sup>5</sup> Campaigns Soelas, AIMS 2001, AIMS 2002, etc.

<sup>6</sup> Campaigns Sprightly 1976, Diamantina 1963-1964-1970-1972-1976, Flinders 1977-1980, RV Franklin 1996

<sup>7</sup> Campaigns Bluefin 1962-1965

## MATERIAL AND METHODS

### Systematics

For nomenclatural stability, we are using the taxonomy accepted by the World Register of Marine Species<sup>8</sup> and sorting the taxa chronologically by date of publication. Extinct species are mentioned as reference.

Kingdom: Animalia - Phylum: Mollusca - Class: Gastropoda - Subclass: Caenogastropoda - Order: Neogastropoda - Family: Harpidae Bronn, 1849 - Subfamily: Harpinae Bronn, 1849 - Genus: *Austroharpa* Finlay, 1931

Species: *A. pulligera* (Tate, 1889) †, *A. abbreviata* (Tate, 1889) †, *A. cassinoides* (Tate, 1889) †, *A. clathrata* (Tate, 1889) †, *A. spirata* (Tate, 1889) †, *A. sulcosa* (Tate, 1889) †, *A. tenuis* (Tate, 1889) †, *A. pachycheila* (Tate, 1894) †, *A. punctata* (Verco, 1896), *A. exquisita* (Iredale, 1931), *A. tatei* Finlay, 1931 †, *A. loisae* Rehder, 1973, *A. wilsoni* Rehder, 1973, *A. kendricki* Ludbrook, 1978 †, *A. spiralistriata* Ludbrook, 1978 †, *A. learorum* Hart & Limpus, 1998, *A. mikeharti* Lorenz, 2020.

### Record selection and use of data

Of a total of 226 specimen records found in museums databases, literature and private collections, 36 are disregarded based on missing geographic data and 3 on identification issues. Therefore 187 are selected to form the original distribution data used in this study.

We note that the volume of available data for each taxon decreases with time, the most recently described species showing the lowest number of known specimens.

When latitude and longitude were available for a specimen, the collection site coordinates were converted in decimal degrees, if necessary, to be pinpointed on a nautical chart using Google Earth Pro as layer.<sup>9</sup> For several specimens these coordinates were extrapolated from location data (distance from a landmark, detailed nautical directions or daymark) and/or depth (often converted in meters from fathoms or feet) using the 5 m bathymetry contours layer available on Seamap Australia.<sup>10</sup> The geolocation of each specimen on a three-dimensional basis was often deduced from the less-precise and/or geographic data.

All collection records and public data used in this study have been compiled from the following institutions:

AM: Australian Museum, 111 Smith St, Sydney NSW 2000, Australia

AMNH: American Museum of Natural History, 200 Central Park West, New York, NY 10024, USA

CSIRO: Building 101, Clunies Ross Street, Black Mountain ACT 2601, Australia

DMNS: Denver Museum of Nature and Science, 2001 Colorado Blvd, Denver, CO 80205, USA

FLMNH: Florida Museum of Natural History, 3215 Hull Rd, Gainesville, FL 32611, USA

IFSM: International Fossil Shell Museum, Kievitdwarstraat 17, Utrecht NL-3514 VC

MAGNT: Museum and Art Gallery of Northern Territory, 19 Conacher St, The Gardens NT 0820, Australia

MV: Museums Victoria, 11 Nicholson Street, Carlton, Victoria 3053, Australia

NBC: Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, Netherlands

NMNH/USNM: Smithsonian National Museum of Natural History, 10th St & Constitution Ave, DC 20560, Washington, USA

NMNS: National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan

NMV: Museums Victoria, PO Box 666, Melbourne VIC 3001, Australia

RBCM: Royal BC Museum, 675 Belleville Street, Victoria, Canada

RBINS: Rue Vautier 29, 1000 Bruxelles, Belgium

SAM: South Australian Museum, North Terrace, Adelaide SA 5000, Australia

SBMNH: Santa Barbara Museum of Natural History, 2559 Puesta del Sol Rd, Sta Barbara, CA 93105, USA

SMF: Senckenberg Museum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

TMAG: Tasmanian Museum and Art Gallery, Dunn Pl, Hobart TAS 7000, Tasmania

UF: University of Florida, University of Florida, 220 Bartram Hall, Gainesville, FL 32611, USA

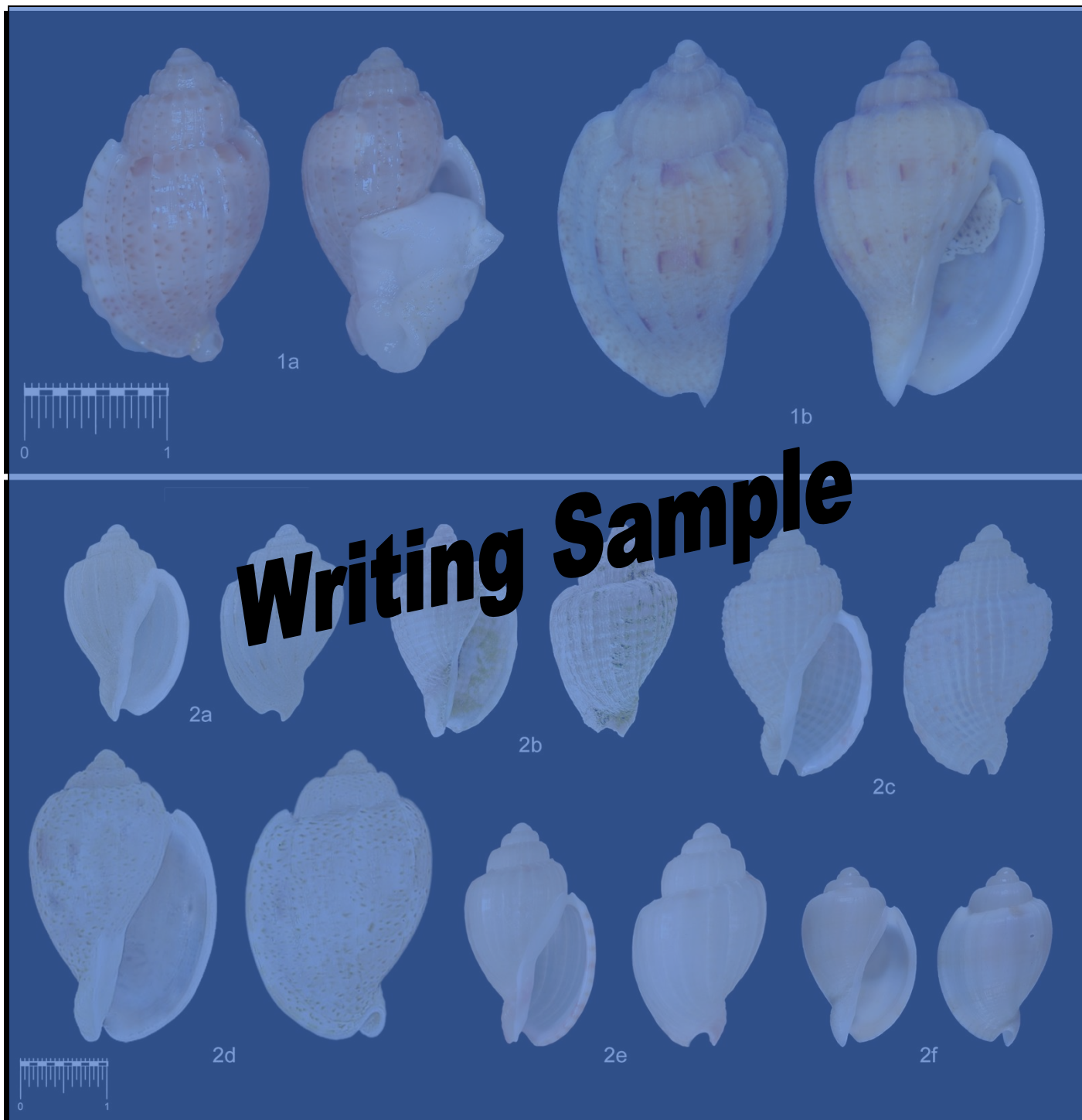
UWBM: University of Washington Burke Museum, 4300 15th Ave NE, Seattle, WA 98105, USA

WAM: Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia

<sup>8</sup> MolluscaBase eds. (2020). MolluscaBase. *Austroharpa Finlay, 1931*. Accessed through: World Register of Marine Species at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=403782> on 2020-10-19

<sup>9</sup> Google Earth Pro, Version 7.3.3.7786, downloaded July 21st, 2020 for Mac OS X (10.14.6)

<sup>10</sup> Seamap, Australian 5m bathymetry contours, accessed august 2020 at <https://seamapaustralia.org>



**Figure 1: Specimens *in vivo* and holotypes**

1a: *A. wilsoni*, *in vivo*, photo CSIRO, 2005.

1b: *A. learorum*, *in vivo*, photo courtesy of R. Walker, 2019 with the permission of F. Lorenz.

2a: *A. learorum*, holotype, SAM D18987, photo courtesy of A. L. Crowther.

2b: *A. exquisita*, holotype, AM C57752, photo courtesy of the Australian Museum.

2c: *A. loisae*, holotype, WAM S13978, photo courtesy of the Western Australian Museum.

2d: *A. punctata*, holotype, SAM D13516, image reconstructed from Rehder, 1973.

2e: *A. wilsoni*, holotype, WAM S13979, photo courtesy of the Western Australian Museum.

2f: *A. miharti*, holotype, WAM S29971, photo courtesy of F. Lorenz.

## List of selected records

*Austroharpa punctata* (Verco, 1896) -> **SA:** 42 - NBC (208169); 95, 101 - AM (C.19272, C.209816); 153, 156, 157, 158, 161, 162, 163, 164 - Coltro, M. Colln.; 170 - Cotton & Godfrey in lit. (1932); 84 - DMNS (28370); 99 - FLMNH (447863); 171 - Guyonneau, S. Colln.; 177, 181 - Hawke, A. Colln.; 121, 122, 123 - Lorenz, F. in lit. (2020); 80 - MAGNT (P009806); 79, 83 - NBC (208168, 208170); 50 - NMNH (846593); 85 - NMV (F66433); 169 - RBCM (979-09455); 183, 184 - RBINS (145421, 145422); 129, 130, 131, 132, 133, 135 - Rehder, H. A. in lit. (1973); 77, 128, 134 - SAM (D46842, D460, D13516); 81, 82, 98 - SBMNH (150191, 150190, 150189); 89 - SMF (322063); 100 - UF (447863); 49, 51 - USNM (706971, 846593); 87, 88 - UWBM (55347, 55106). **VIC:** 119 - SAM (D46841); 120 - NMV (F83038); 167 - Baker, J. L. in lit. (2011). **WA:** 72 - AM (C245526); 155 - Coltro, M. Colln.; 174, 175, 176 - Guyonneau, S. Colln.; 67 - IFSM (33257); 124, 125, 126, 127 - Lorenz, F. in lit. (2020); 55 - NBC (208176); 66 - UWBM (55105); 64, 70 - Walker, R. Colln.

*Austroharpa exquisita* (Iredale, 1931) -> **NSW:** 10, 14, 15, 16, 17, 18, 19, 20, 25, 46, 48, 97, 103, 106, 107, 110, 111 - AM (C.383765, C.383762, C.383759, C.383764, C.383761, C.383756, C.383758, C.383757, C.62064, C.383755, C.245532, C.209226, C.383753, C.57752, C.170679, C.73509, C.383754); 173 - Guyonneau S. Colln.; 180 - Hawke, A. Colln.; 108 - NMNH (675036); 105 - NMV (F18000); 137, 138, 139, 140, 141, 142 - Rehder, H. A. in lit. (1973); 41 - SAM (D46832); 102, 109, 185, 187 - TMAG (E23965, E33673); 104 - USNM (634267). **QLD:** 1, 12, 13 - AM (C.383766, C.383767, C.383763); 3, 8 - AMNH (276279, 232338); 7 - FLMNH (448542); 179 - Hawke, A. Colln.; 9 - MAGNT (P045934); 5 - NMV (F66433); 1 - NMNS; 136 - Rehder, H. A. in lit. (1973); 6 - SAM (D46844). **TAS:** 146 - R. Colln.; 147 - IFSM (46726, 46725); 142 - AM (C.87157); 117 - AMNH (173676); 168 - Gabriel, C. J. in lit. (1972); 174, 175 - NMV (F66433, F66434); 143, 144, 145 - Rehder, H. A. in lit. (1973); 115 - SBMNH (150193). **WA:** 11, 22, 29, 33, 35, 47, 147, 148, 149, 150, 151 - WAM (S11571, S15969, S15333, S15971, S13978, S15966, 12963, 15672, 3470, 15872, 15772); 65 - AMNH (277115); 154, 159, 160 - Coltro, M. Colln.; 58 - FLMNH (448524); 172 - Guyonneau, S. Colln.; 182 - Hawke, A. Colln.; 56, 63 - IFSM (46726, 46725); 57, 59 - NBC (208167, 208172); 92 - NMNH (846555); 54 - SAM (D46840); 60 - SBMNH (150193); 38, 39, 44, 53, 68 - UWBM (54911, 54910, 55104, 55107, 55348); 90 - Walker, R. Colln.

*Austroharpa wilsoni* Rehder, 1973 -> **WA:** 21, 23, 26, 27, 28, 30, 31, 34, 36, 37, 43, 52, 61, 75 - WAM (S15331, S15963, S13979, S15956, S15959, S15330, S15957, S15970, S15332, S15961, S15960, S15968, S11569, S15958); 166 - Brough, B. in lit. (1973); 24 - Walker, R. Colln.; 62 - CSIRO (24209008); 32 - FLMNH (448541); 165 - Lorenz, F. in Litt (2020); 40, 45, 152 - USNM (846556, 703250, 703249); 76 - UWBM (54909).

*Austroharpa learorum* Hart & Limpus, 1998 -> **WA:** 69, 74, 86 - AM (C.245525, C.245531, C.245530); 178 - Hawke, A. Colln.; 78 - SAM (D18987); 91 - UWBM (55465); 71, 73 - Walker, R. Colln.; 93, 94 - WAM (S11769, S11570).

*Austroharpa mikelharti* Lorenz, 2020 -> **WA:** 96 - WAM (S29971)

RECORDS MAPS

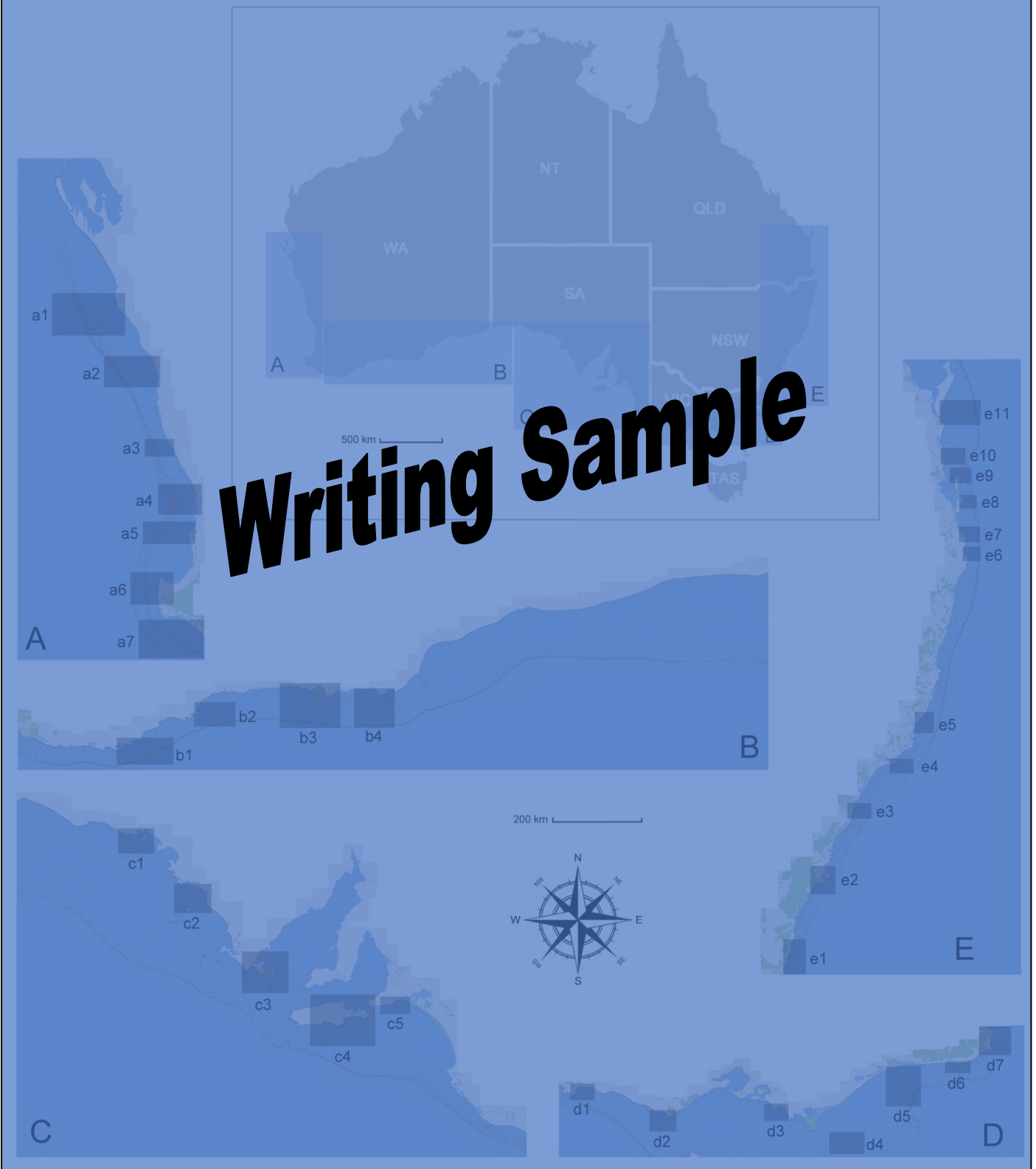


Figure 2: General Chart, sections and zone cuts





Figure 3: West area records - Kalbarri, Perth, Augusta, Albany - sections A & B



Figure 4: Southwest area records - Bremer Bay, Esperance, Ceduna, Port Lincoln - sections B & C



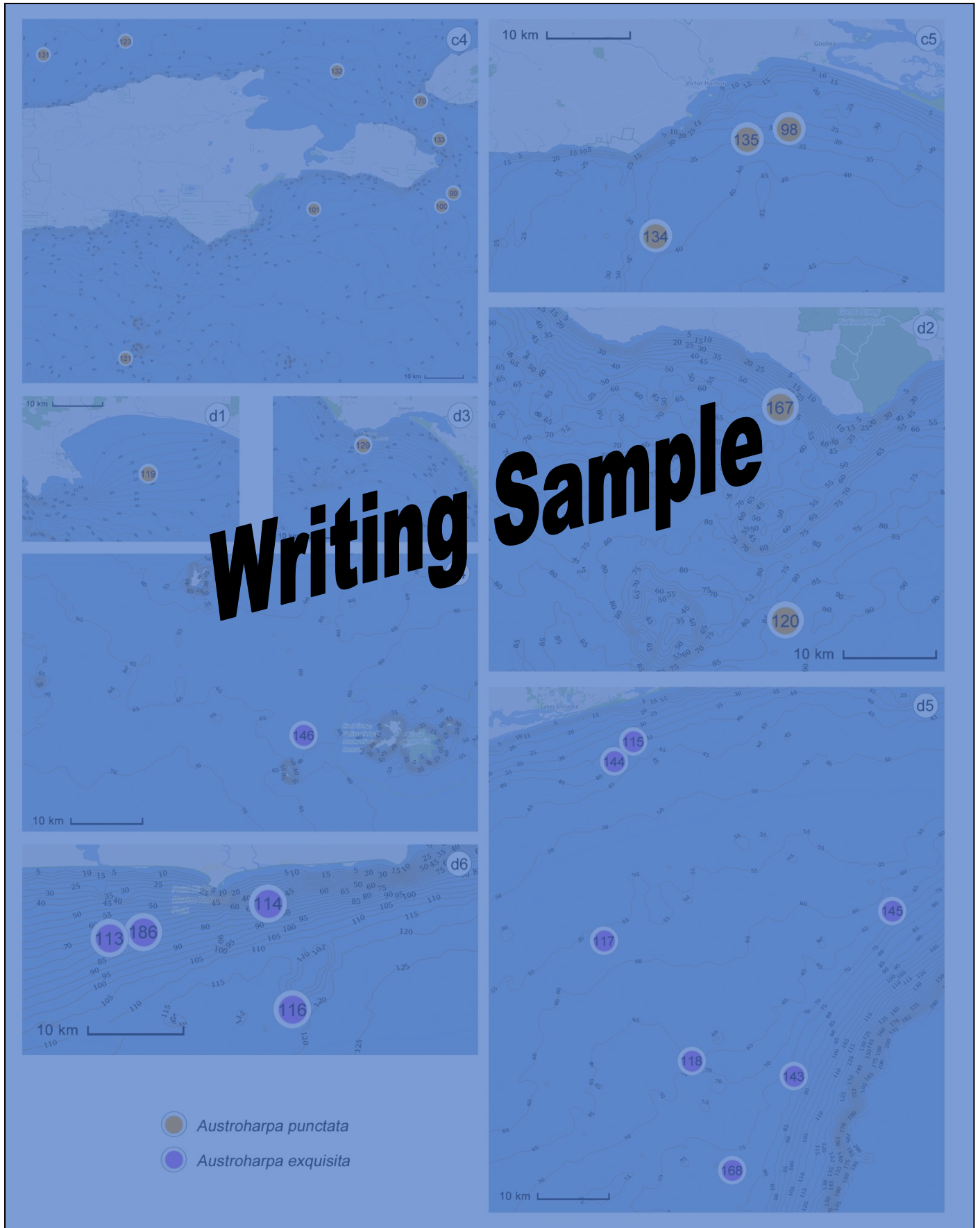


Figure 5: Southeast area records - Kangaroo Island, Adelaide, Lakes Entrance - sections C & D



Figure 6: East area records - Eden, Sydney, Port Macquarie, Brisbane - sections D & E

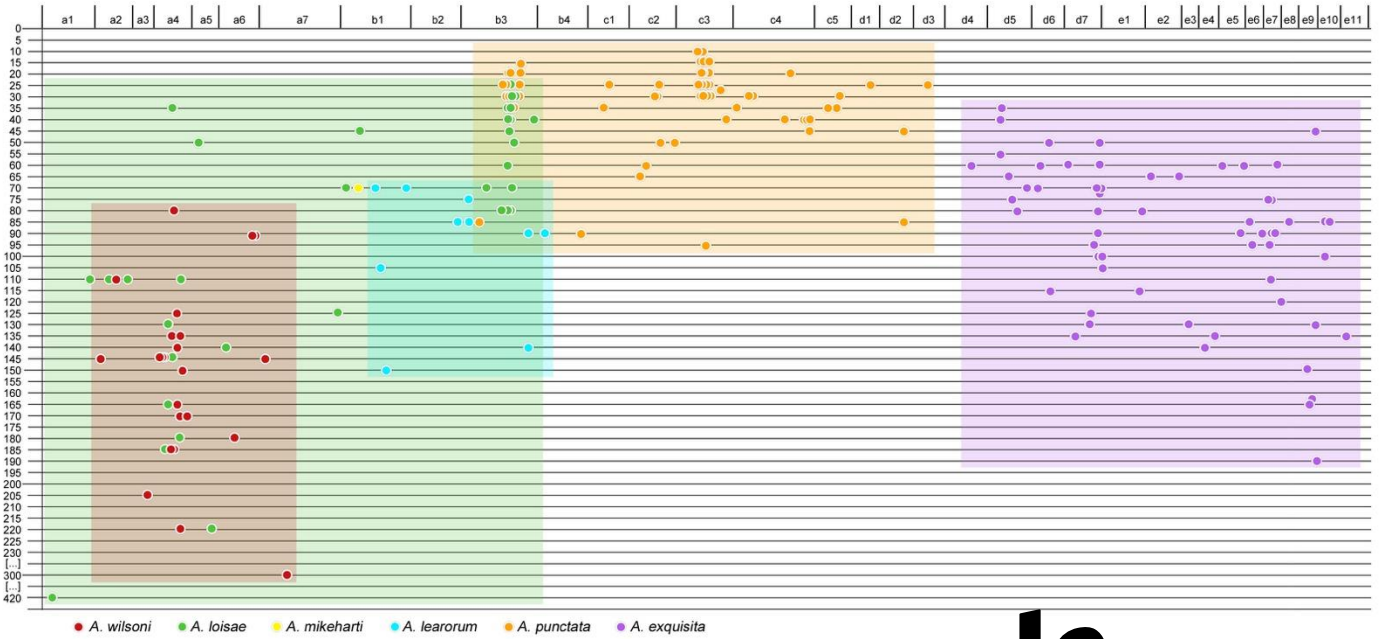


Figure 7: Table of depth records - y = depth in meters / x = zone cuts in cross section

**Writing Sample**

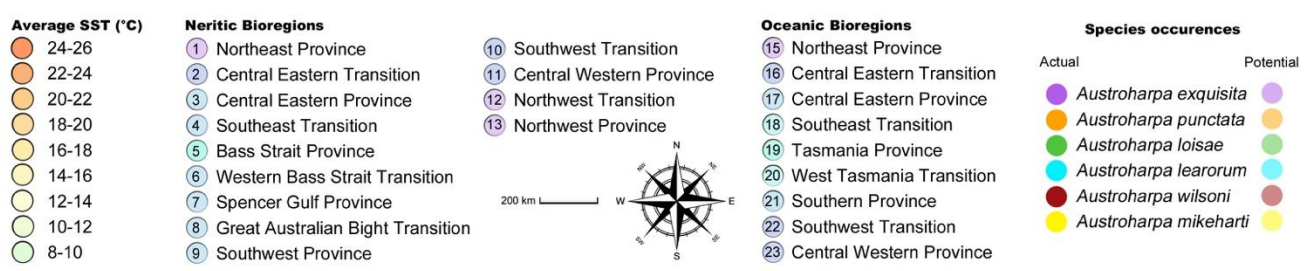
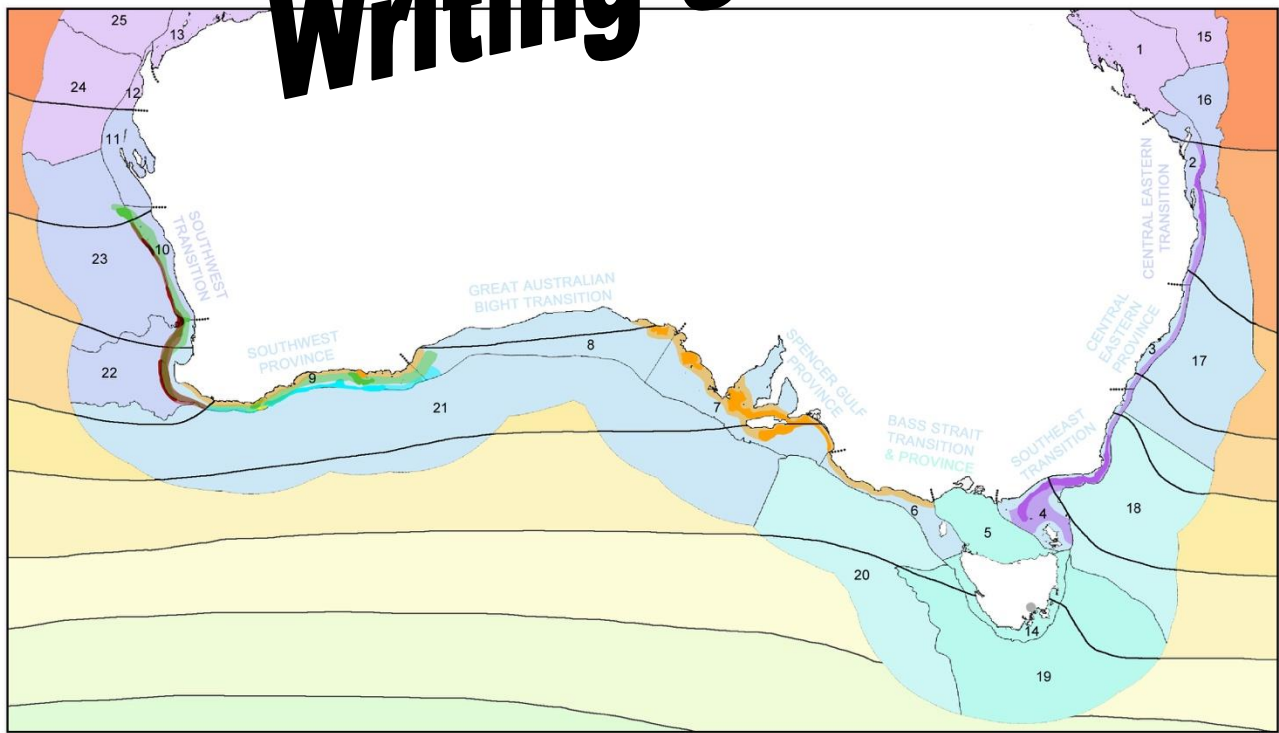


Figure 8: Species actual and potential occurrences zones with IMCRA Bioregions and Average Sea Surface Temperature

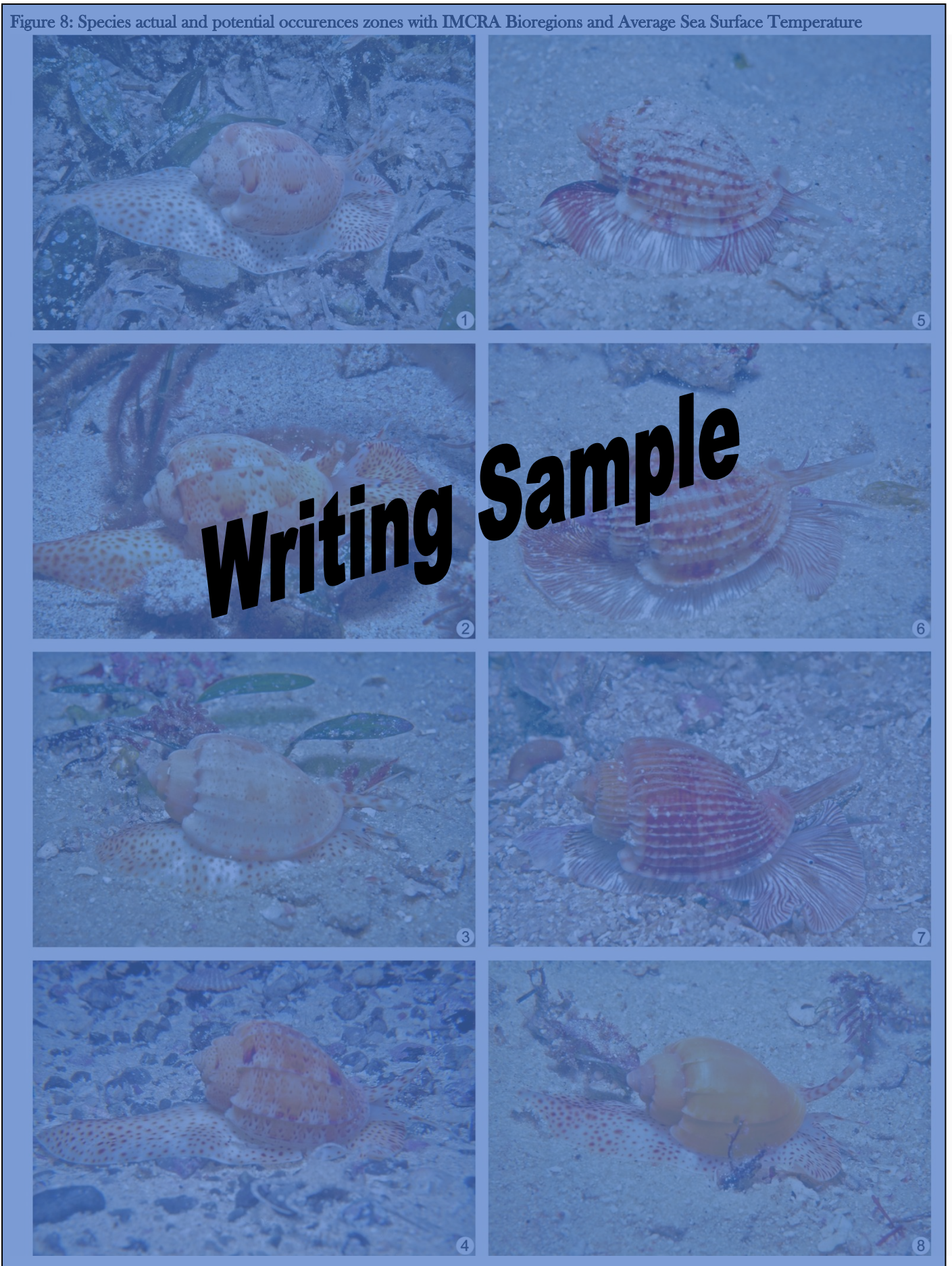


Figure 9: Living specimens *in situ*



1: *A. punctata*, Port Lincoln / 2: *A. punctata*, Port Lincoln / 3: *A. punctata*, Esperance / 4: *A. punctata*, Esperance / 5: *A. loisae*, Esperance / 6: *A. loisae*, Esperance / 7: *A. loisae*, Esperance / 8: *A. punctata*, Esperance  
All photos by Peter Clarkson - Scans of original color slides courtesy of Richard Clarkson.

## RESULTS & DISCUSSION

### *Austroharpa wilsoni* Rehder, 1973

#### Distribution:

This species was described from several dead shells collected during deep water dredging trips off the central Western Australian coast in 1965. Rehder stated that *A. wilsoni* occurred between Cape Leeuwin and Dongara, in depths between 60 and 120 fathoms (110 to 220 m). Subsequent examination of the specimens in the Western Australian Museum by Barry Wilson, after whom Rehder named the species, broadened the geographic range from Cape Leeuwin to Geraldton, with depth of between 140 and 200 meters (Wilson, 1994).

The present study confirms the distribution of *A. wilsoni* from an area situated SW of Geraldton to SW of Cape Leeuwin, at average depth ranges between 100 and 200 meters.

#### Description:

The original mention of the animal was reported in Rehder, 1973 from Barry Wilson who described the first live specimen dredged in 1972 offshore Cape Naturaliste.<sup>11</sup> The collection of a second live specimen of *A. wilsoni* during the 2005 CSIRO cruise off Cape Mentelle gave the opportunity to observe and photograph the specimen onboard (Fig. 1-1a) and to complete the description of the soft parts as well as the unaltered test.

Background color of the animal off white to pale yellow. Metapodium thick and fleshy, surface almost smooth except for some scattered small verrucosities. Small, scattered orange-brown spots often circled by a small lemon-yellow halo present throughout the body, less scarce on the sides. Tentacles translucent lemon-yellow with the same type of spotting. Siphon is also spotted and distinctly annulate. Sole plain translucent off white. Penis large and off white.

Shell light salmon-pink and translucent, letting show some of the internal structure. The shell consists of two orange-pink spiral bands on the last whorl, the one on the shoulder showing some large reddish-brown blotches between one of the lamellae, the two on the body separated by a central, slightly clearer spiral line. A reddish-brown spot is present on each of the two spots all along the edges of the lamellae, that are diffused and more triangular in shape. The distance between the lamellae is small.

For other detailed conchological characters, see Rehder, 1973, pp. 267-268.

#### Habitat:

*A. wilsoni* is a deepwater species known from the continental slope where it prefers a cold, dark environment (average temperature 14-16°C). On muddy / sandy bottom usually with coarse shell debris, living amongst sponges (e.g. *Agelas* sp., *Halichondria* sp.) and bryozoa (e.g. *Laminopora* sp., *Adeonellopsis* sp.), together with decapods - on which it possibly feeds - (e.g. *Lahaina* sp., *Cyrtomaia* sp.), polychaetes (e.g. *Aonidella* sp., *Euphione* sp.), ophiurans (e.g. *Ophiacantha* sp., *Ophiomyxa* sp.), seastars (e.g. *Henricia* sp., *Luidia* sp.), benthic fishes (e.g. *Phenacoscopus* sp., *Allenichthys* sp.), elasmobranchs (e.g. *Bathytoshia* sp., *Asymbolus* sp.) and other molluscs (e.g. *Turritella* sp., *Sassia* sp.).

### *Austroharpa learorum* Hart & Limpus, 1998

#### Distribution:

The original description of *A. learorum* contained no accurate locality data other than Central Great Australian Bight, which is not precise enough to be included in the present list of records (Hart & Limpus, 1998). The single dead specimen collected from the vessel Bluefin in 1962 provided the first accurate account of *A. learorum* (CSIRO Colln.) southeast of Albany. This established the westward distribution which was confirmed by the 2005 CSIRO campaign with two other dead specimens collected south of Bald Island. The eastward known distribution of the species was previously offshore Cape Le Grand with a dead specimen trawled by commercial fishermen in 1997 (SAM Colln.). In 2019, a living specimen was collected using ROV<sup>12</sup> in the middle of the range and a dead specimen near the Recherche archipelago (Walker, R. pers. com. and Lorenz, 2020).

The known distribution of *A. learorum* therefore extends from SSE of Bald Island to S of Salisbury Island, at a depth range between 70 and 150 meters.

<sup>11</sup> Specimen S15968 preserved in the collection of the Western Australian Museum.

<sup>12</sup> Remotely Operated Vehicle

**Description:**

To the knowledge of the authors, only two specimens collected alive have been observed so far, unfortunately not with the animal extended, but some of the soft parts are visible on a photograph made by Ray Walker (fig. 1-1b).

Background color of the foot light beige, off white on the edges of the metapodium, with scattered tiny coffee-brown spots becoming larger and diffuse on the center. Anterior end tapered and slightly rounded, sole off white.

Shell beige to orange-yellow, opaque. Color pattern of the last whorl red-brown to orange, made up of random diffuse ripples spirally oriented between the ribs, spot-like on the edge of the ribs. Three diffuse spiral bands are suggested by dark segments on the edge of the ribs, which are sometimes preceded by a reddish-brown blotch, particularly for the central band and on the shoulder. The antepenultimate whorl is marked with very light orange ripples and the shoulder shows darker blotches irregularly spaced. For other morphological characters of the shell, see Hart & Limpus, 1998 and Lorenz, 2020.

**Habitat:**

*A. learorum* is known from moderately deep waters on the edge of the continental slope, with average temperature of 15-16°C. Live specimens were found on silty sand substrate among sponges (e.g. *Sarcotragus* sp., *Asteropus* sp., *Hippospongia* sp.). Dead specimens were collected either on soft or hard substrates.

***Austroharpa loisae* Rehder, 1973****Distribution:**

In the original description, Rehder mentions only the western records from dredging in moderately deep waters from 70 to 103 fathoms (128 to 188 m) in a range between WSW of Cape Naturaliste to NW of Rottneest Island. The northern range has been extended to offshore Kalbarri with a dead specimen trawled at about 420 meters by the CSIRO in 2005. Other populations occur at shallower depths in the Albany and Esperance areas. There appears to be a correlation between the recorded depths and the water temperature: the northern part of the distribution range has warmer sea surface temperatures (up to an average 22°C) and deeper collection records (100, 200 m and more). Shallow-water records (30 to 80 m) of the southern part of the range has colder sea surface temperatures (up to an average 18°C). Although the geographical range seems to be fragmented because of the rarity of the species, a recent record south of Windy Harbour at 130 meters (R. Walker specimens) shows a morphological difference suggests that *A. loisae* forms a continuous population with a local adaptation to depth in line with its temperature preference. The known distribution of *A. loisae* extends from NW of Cape Naturaliste in deep waters to SE of Esperance in shallow waters.

**Description:**

To the author's knowledge, the only living deep-water specimen observed was collected off Dongara in 1970 during a cruise of the Diamantina. No description of the animal was made. However, several photographs have been taken of shallow-water specimens from Esperance area by Peter Clarkson in their living habitat. Three of them are illustrated in figure 9.

The background color of the animal is off-white with large irregular patches of pearl white. The propodium is widely arcuate on the front with lateral lobes that expand symmetrically and make the anterior part a lot larger than the metapodium. The neck between the two parts of the foot narrows the general shape of the sole, which off-white in color. The foot is striate with dark reddish-brown radial lines, some of them making arborescences near the edge. Eye stalks are translucent off-white with reddish-brown longitudinal lines. Eyes black circled by a small white blotch. The siphon is off-white with dash-like brownish longitudinal spots less numerous close to the tip, so the anterior part has less pattern than the base.

The shell color ranges from off-white to greyish-yellow with a random pattern of red-brown or pink-purple ripples and small blotches, variable in color and density. On the last whorl there are two clearer spiral bands which are more or less visible depending on the pattern, one on the shoulder with dark patches of reddish-brown and one on the lower central part of the shell. The color of the protoconch and the first couple of teleoconch whorls is variable, from pale pink to grey-orange or purple.

For other detailed conchological characteristics, see Rehder, 1973, p. 265.

**Habitat:**

*A. loisae* is known from a large bathymetric and geographic range. The average temperature for the species is between 15 and 19°C and the depth between 30 and 400 meters, which suggests an adaptation to different habitats, behaviors and diets along the range of the population. The northern deep-water animals share the characteristic continental slope biotope with *A. wilsoni*, while the southern shallow-water animals live in a biotope similar to the western population of *A. punctata*.

It should be noted that, if *A. loisae* shows a wide biogeographic spectrum for the genus, this distribution is still quite narrow for a gastropod and corresponds to a typical case of endemism. This narrow specific distribution range is directly correlated with the non-planktotrophic mode of development of the larvae (Bouchet, 2002), hence the paucispiral protoconch found in each known extant species of *Austroharpa*.



## *Austroharpa punctata* (Verco, 1896)

### Distribution:

When Verco described a peculiar and interesting new species of *Harpa* in 1896 from a few dead specimens off South Australia, the only known locality was a small area south of Adelaide, between the east end of Kangaroo Island and Newland Head. In 1973, Rehder broadened the range to the northwest up to Nuyts Archipelago and confirming its eastward limit at Encounter Bay (Spencer Gulf bioregion). The first author found a few scattered records from Victoria, however it was not possible to verify them. Making an extension of the range to the southeast is doubtful, considering that the Victorian records are located in a different bioregion (Western Bass Strait). The locality of Cape Jaffa mentioned in Lorenz, 2020 from collection records could not be confirmed by other records. However, the habitat continuity from Encounter Bay to the south of Long Bay, and the fact that Cape Jaffa is the southeastern limit of the Spencer Gulf province suggests this area should be included in the known distribution range.

In 1998, Hart & Limpus mention an extension westward to Esperance but the continuity across the Great Australian Bight (GAB) has never been confirmed (Lorenz, 2020 and pers. obs.) because of the absence of specimens from this region. For similar depths, the water temperatures in the GAB transition are higher than in the other bioregions where *A. punctata* occurs. The possibility of a continuous population could theoretically be proven by observation of specimens in deeper waters along the continental slope, however no such specimen is known yet. Unlike *A. loisae*, *A. punctata* appears to be restricted to a specific shallow-water biotope (see the habitat section below). The existence of two separate populations is also supported by a difference in morphological characters (see description below). The western population is confirmed by several records near Esperance, however the authors have chosen not to include the records near Albany and in the area in between mentioned by Lorenz, 2020. The specimens from Albany are said to be *ex pisces* and no intermediate records exist in the WA museum's databases.

The non-planktotrophic mode of development, and the most plausible reproduction scenario being that *Austroharpa* spp. lay benthic eggs from which hatch crawling young (Hughes, 1990 for *Morum*), make the GAB gap a strong ecological barrier that possibly appeared during the Holocene. Indicators suggest a continuous rise of the sea surface temperatures since the Medieval times (Wyrwol et al., 2009), that could have placed the coastal region between Calgana, WA to Yalata, SA in a sea temperature range too high to support viable populations of *A. punctata*. An initial continuous suitable habitat for the species could have been split in two a few centuries ago and two biologically separated genetic pools may have formed, supported by a mode of reproduction that favors congregation over dispersion. This hypothesis should be tested by future DNA analysis, as well as benthic research campaigns in the GAB region.

As of now, the known distribution of *A. punctata* extends from the Nuyts Archipelago, SA to Cape Jaffa, SA for the eastern population, and from Observatory Island, WA to Morro Bay, WA for the western population, at an average depth range between 10 and 60 meters.

### Description:

The base color of the foot is a translucent, greyish white and marbled with opaque blotches of white. Numerous small to very small spots of rusty orange are spread throughout the body, with dark brown dots in the center of the biggest spots. The propodium shows the same pattern, with the spots being more elongate on the anterior part, almost forming small longitudinal dashes in some specimens. Tentacles are off-white and translucent with scattered elongate rusty-orange dots on the base below the black eyes. Two to three elongate orange blotches on the narrow end of the tentacle make it appear annulate. The tubular siphon is almost as long as the tentacles, spotted with the same pattern as the body.

The shell usually shows the exact same range of colors as the body, with variations of the orange color gradient from one specimen to another, but always with a combination of white, orange and brown. The patterns of the shell and the body match and form a visual continuity that can become mimetic on bottoms made of sand and gravels / broken shells. Unusual shells can show an overexpression of the triangular blotches, forming graphic lines that supplant the usual punctate appearance (see Poppe, 1999, Pl. 29-4). Some specimens show a regular body and a shell almost plain in color like the one photographed by P. Clarkson (fig. 9-8, formerly illustrated in Poppe, 1999). For more details about the shell, see Rehder, 1973, pp. 265-266.

The conchological differences between the two known populations of *A. punctata* are conspicuous when several specimens from each locality are observed together (see Lorenz, 2020). The eastern specimens (nominate population) are on average larger, heavier and broader with a pattern showing more contrast and graphic elements, and a narrower range of base color from pink to light orange. The western population produces shells on average smaller, lighter, narrower with a less contrasted and plainer pattern showing a wide range of base color from light pink to dark orange, yellow or red.

### Habitat:

Despite being separated by a distance of almost 1000 km, the two known populations of *A. punctata* share a similar shallow water environment. The species is found on soft bottoms composed of fine sand, coarse sand or fine sand mixed with shell debris and

gravels. The proximity of seagrass beds or patches is an important characteristic of the habitat (e.g. *Halophila* spp., *Posidonia* spp.). The macrobenthic fauna and flora have all the usual characteristics of South Australian seagrass meadows with a high level of biodiversity (Gaylar et al., 2013). The average temperature for the species is between 16 and 18°C, but this could raise to over 20°C due to the seasonal effects of the warm Leeuwin current.

### *Austroharpa exquisita* (Iredale, 1931)

#### **Distribution:**

Records of the species have been made on a very extended coastal line from Queensland to Tasmania, which represents about 2000 km of the Southeast coast of Australia, and an extremely large distribution for the genus. However, a gap in the records exists in between the zones at offshore Byron Bay and the Southeast of Port Macquarie, NSW, which also corresponds to a change in the neritic environments of the Central Eastern bioregions. The records from Port Macquarie to Sydney are scarce and sourced either from literature (Rehder, 1973 - 137, 138, 139) or from the old specimen references of the Australian Museum (1935 to 1978 - 25, 46, 48). To the authors knowledge, there is no verified record of *A. exquisita* in this area since the late 1970's despite the increased interest of commercial fishermen in bycatch. The approximate location data found with five specimens from private and museum collections - that have been excluded from the list of records - could also lead to a misinterpretation of the actual distribution of the species, with mentions like "Offshore Sydney" or "Trawled Central Coast NSW". Therefore, records coming from the central coastal area of NSW should be examined with caution.

This could also suggest that the geographical gap between records is potentially larger than expected, and that two distinct populations are separated by the Central Eastern bioregion. The depth records for the specimens collected in Queensland and northern New South Wales are on average between 70 and 140 meters for a SST at 22-24°C, when those collected in Victoria and southern New South Wales are on average between 60 and 110 meters for a SST at 18-20°C. The slight difference between average depths is not enough to compensate the difference between temperatures, which means that the northern population lives in warmer waters than the southern population.

The known distribution of *A. exquisita* extends from SSE Fraser Island, QLD to E Cape Byron, NSW for the northern population and from E. Jervis Bay, NSW to SE Wilsons Promontory, VIC for the southern population. The latest is nominate, includes the type locality in Twofold Bay and could possibly extends up to SE Port Macquarie.

#### **Description:**

The first and only notes published about the soft parts of this species were made by Rehder (1973), from a specimen collected at the type locality and preserved in alcohol, which he described the pattern as "an animal of which the propodium and head and anterior part of the metapodium show a pattern of spots which are densest at the posterior end."

Considering the conchological similarities and the probable common ancestral line between *A. exquisita* and *A. loisae*, a similar pattern on the soft parts could have been expected. However, the latter species shows conspicuous zebra lines instead of dots. The pattern described by Rehder for *A. exquisita* is much more like *A. punctata*, however the quality of the soft parts preserved in ethanol for a long time tends to be too poor to draw definitive conclusions.

For this species, more living material is needed to complete an accurate description of the animal.

#### **Habitat:**

Specimens of the southern population have been collected on coarse sand with shell debris or on muddy sand. Specimens of the northern population have mostly been collected on fine sand mixed with small to medium shell and coral debris.

### *Austroharpa mikharti* Lorenz, 2020

#### **Distribution:**

As of now, the closest biogeographic clues that can be discussed are related to the behavior of the predator fish from which all the known specimens have been collected.

The Blue Morwong, *Nemadactylus valenciennesi* (Whitley, 1937), is known to be an opportunistic molluscivore and can reach a maximum size of one meter and live 20 years (Coulson et al., 2010). This species is endemic to temperate waters of southern Australia. Adults live at a depth range of 40 to 240 meters (May & Maxwell, 1986), sharing a common distribution with all the known species of recent *Austroharpa*. It is a substantial catch for commercial fisheries as well as recreational fisherman. *Nemadactylus* species mostly inhabit rocky reefs but show a changing distribution pattern depending on the age and seasonal parameters (Coulson et al., 2010).

Apart from *A. mikeharti*, similar *ex pisces* records exist for *Austroharpa punctata* in the same locality, *A. punctata* and *A. exquisita* eastward, and possibly *A. learorum* in a close range (Lorenz, 2020 and pers. obs.). We note that the depth of catch is most often deeper than the average living depth range of the corresponding *Austroharpa* species in almost all of the *ex pisces* records. This possibly indicates that the predator fishes fed on *Austroharpa* in shallower waters than the fishing grounds where they were caught. *A. mikeharti* is known only from the type locality given in Lorenz, 2020: approximately 50 kilometers off the southeast of Albany, fish caught at 60 to 80 meters.

**Description:**

No living specimen have been found, Lorenz's extensive description of the shell (Lorenz, 2020, pp. 3-4) being the best information currently available on the morphology of the species.

The paucity of information on this latest described taxon and the specific distinction based on conchological characters from only *ex pisces* specimens is a source of contention in the private shell collector's community (pers. obs.). Finding shells in a better state of preservation or the observation of living specimens with similar shell characteristics would be the only means to accurately confirm the specific status in the future, and that for now Lorenz' species should be considered as a form of *A. punctata*.

However, the comparisons proposed by Lorenz (ibid) among *A. wilsoni*, *A. learorum*, and *A. punctata* are relevant but not conclusive. The first author found conchological similarities to fossil *Purpurina* species *A. valistriata* Ludbrook, 1978. The general shape of *A. mikeharti*, its length to width ratio, the low elevation of the shoulder, and more importantly the spiral striae on the last whorl (which are not living but present on the whole shell) are more consistent with this extinct taxon than with other recent species. The spiral striae, which is an ancestral characteristic adequately used by Ludbrook to name *A. sp. mikeharti* but found in other closely related species. This could confirm the validity of the taxon *A. mikeharti* and a possible lineage in between the two species.

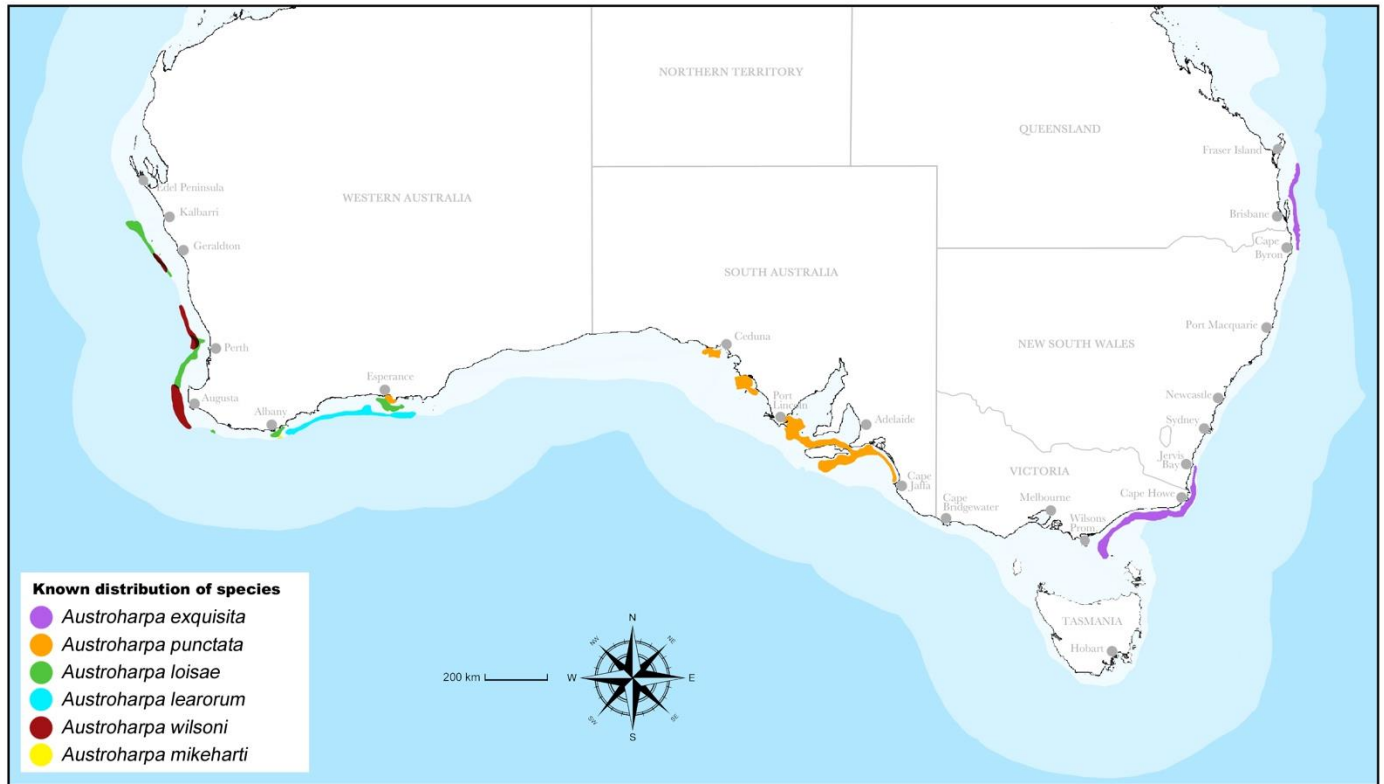


Figure 10: Known distribution of *Austroharpa* populations by species

## CONCLUSION

As of today, the known geographical range of *Austroharpa* species occurring in neritic bioregions of Australia is as follows:

*A. loisae* occurs in the Southwest Province and the Southwest Transition from Albany, WA to Esperance, WA.

*A. wilsoni* occurs in the Southwest Province and the Southwest Transition from Geraldton, WA to Cape Leeuwin, WA.

*A. mikeharti* occurs in the Southwest Province from Albany, WA to Esperance, WA.

*A. learorum* occurs in the Southwest Province from Albany Island, WA to Salisbury Island (Recherche Archipelago), WA.

*A. punctata* western pop. occurs in the Southwest Province from Observatory Island, WA to Mondrain Island, WA.

*A. punctata* eastern pop. occurs in the GAB Trans. and the Spencer Gulf Prov. from Nuyts Archipelago, SA to Cape Jaffa, SA.

*A. exquisita* southern pop. occurs in the Southeast Transition from Wilsons Promontory, VIC to Jervis Bay, NSW.

*A. exquisita* northern pop. occurs in the Central Eastern Transition from Fraser Island, QLD to Cape Byron, NSW.

The populations of *A. loisae* (deep water) and *A. wilsoni* overlap in the Southwest Transition.

The populations of *A. loisae* (shallow water) and *A. punctata* (western pop.) overlap on the eastern part of the Southwest Province.

There is a geographical gap in between the western and eastern populations of *A. punctata*, as well as in between the southern and northern populations of *A. exquisita*, however more anatomical and conchological studies are needed to investigate the taxonomical need of a subspecific status. DNA studies would be the only mean to separate possibly different genetic pools on a specific level.

All the species of *Austroharpa* being much sought after by collectors, it is necessary to add a note on their conservation concern. These predatory gastropods have a restricted to very restricted distribution range, show direct larval development with a low abundance, and get a high to very high market value. The sum of these factors relates to a high vulnerability of all *Austroharpa* taxa, with populations potentially sensible to destruction of habitat (commercial fisheries, pollution) and overfishing (for populations with moderately difficult accessibility).

However, the deficient data for most species make the real risk assesment difficult to build. Before the present article, several studies gave partial information on some species, including Baker, 2011, O'Hara & Barmby, 2000 and Ponder & Grayson, 1998. Following the ratings of the latter authors, *A. learorum* and *A. wilsoni* are placed in category A vulnerable with a very restricted range, *A. punctata*, *A. loisae* and *A. exquisita* are placed in category B vulnerable with a restricted range, and *A. mikeharti* is not rated due to a lack of data.



Since the beginning of the 20th century, it is common knowledge that the data available for the extant species of the genus *Austroharpa* is scarce. Yet, it is still possible to rely on the work of museum custodians, private collections and research organizations to compile scattered information and get an overall view of the molluscan biogeography. The case of *Austroharpa* species is very particular because of the historical interest that the collectors have for their shells: even if the findings are rare, the majority of them are notoriously documented, adding each time a new valuable entry for the malacological knowledge.

The 226 records examined for this article have been backed up with the direct or virtual observation of more than 120 specimens in private collections, which are not included in the original data but have been very helpful for general discussion. The overall conclusion that comes from this work is that more field studies are needed to understand the biology and behavior of these animals, and that further investigation must be made to link the recent living populations with the fossil records.

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## ABBREVIATIONS

NSW: New South Wales; SA: South Australia; WA: Western Australia; QLD: Queensland; VIC: Victoria; TAS: Tasmania.

AM: Australian Museum, William Hall Street, Sydney, NSW 1500, Australia

AMNH: American Museum of Natural History, 200 Central Park West, New York, NY 10024, USA

CSIRO: Commonwealth Scientific and Industrial Research Organisation, Black Mountain ACT 2601, Australia

DMNS: Denver Museum of Nature and Science, 2001 Colorado Blvd, Denver, CO 80205, USA

FLMNH: Florida Museum of Natural History, 3215 Hull Rd, Gainesville, FL 32611, USA

IFSM: International Fossil Shell Museum, Kievitdwarstraat 17, Utrecht NL-3514 VC

MAGNT: Museum and Art Gallery of Northern Territory, 19 Conacher St, The Gardens NT 0820, Australia

MV: Museums Victoria, 11 Nicholson Street, Carlton, Victoria 3053, Australia

NBC: Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, Netherlands

NMNH/USNM: Smithsonian National Museum of Natural History, 10th St & Constitution Ave, DC 20560, Washington, USA

NMNS: National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan

NMV: Museums Victoria, PO Box 666, Melbourne VIC 3001, Australia

RBCM: Royal BC Museum, 675 Belleville Street, Victoria, Canada

RBINS: Rue Vautier 29, 1000 Bruxelles, Belgium

SAM: South Australian Museum, North Terrace, Adelaide SA 5000, Australia

SBMNH: Santa Barbara Museum of Natural History, 2559 Puesta del Sol Rd, Sta Barbara, CA 93105, USA

SMF: Senckenberg Museum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

TMAG: Tasmanian Museum and Art Gallery, Dunn Pl, Hobart TAS 7000, Tasmania

UF: University of Florida, University of Florida, 220 Bartram Hall, Gainesville, FL 32611, USA

UWBM: University of Washington Burke Museum, 4300 15th Ave NE, Seattle, WA 98105, USA

WAM: Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia

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