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SHORT COMMUNICATION

An application of morphological analysis and DNA barcoding to identify *Ipnops* from the Clarion-Clipperton Zone (CCZ) as *I. meadi* Nielsen, 1966 with notes on other species of the genus (Aulopiformes: Ipnopidae)

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Abstract

Although *Ipnops* specimens are relatively common in the Clarion-Clipperton Fracture Zone (CCZ), an area targeted for potential future deep-sea mining, a reliable species identification has not yet been possible due to the lack of a captured specimen. In April 2012, an *Ipnops* specimen was caught for the first time from the eastern CCZ during an exploration cruise of the BGR. Species identification of this specimen was performed using a comparative application of morphological analysis and DNA barcoding and resulted in its clear assignment to *Ipnops meadi* Nielsen, 1966. Of the 23 compared morphological characters, 22 are inside the ranges available for *I. meadi*. Molecular analyses show a sequence distance of 0.76% divergence to an *Ipnops* specimen collected off Hawaii, close to the CCZ and also within the known geographical distribution range of *I. meadi*. The additional study of five specimens of *I. meadi* from the Arabian Sea has extended the previously known range of the following morphological characters of this species: gill rakers on anterior arch (17–21), head length (17.6–24.0 % SL), upper jaw length (10.7–14.0 % SL), maximum width of eye-plates (7.8–9.8 % SL), preanal length (58.8–79.0 % SL), and predorsal length (34.5–40.5 % SL). *Ipnops* specimens deriving from Australian waters could not be clearly assigned with confidence to one of the valid *Ipnops* species based on current morphological and molecular analyses. It seems possible that at least one previously undescribed *Ipnops* species occurs in Australian waters and further work is required on the genus to resolve uncertainties.

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Introduction

The Clarion Clipperton Fracture Zone (CCZ) is an area of great interest as it holds the largest known deposits of polymetallic nodules, which are rich in metals such as manganese, nickel, cobalt and copper and are being targeted for potential mining (Miller et al. 2018; Hein et al. 2020). Mining of polymetallic nodules has been prompted by the demand for metals necessary for high technology applications and renewable energy infrastructure (Hein et al. 2020). Despite the growing interest as mirrored in a substantial number of recent scientific expeditions, baseline information on the associated megafaunal communities and their ecology is still restricted and based largely on imagery studies (e.g. Harbour et al. 2020; Simon-Lledó et al. 2020; Drazen et al. 2021). Although the importance of these studies is unquestionable, there is a need for specimen collection and thus verified species identifications necessary for future management and conservation actions (Amon et al. 2016; Amon et al. 2017; Bribiesca-Contreras et al. 2022; Christodoulou et al. 2022).

It has been assumed in several studies, based on seabed imagery, that the relatively common *Ipnops* specimens in the CCZ could be assigned to the species *Ipnops meadi* Nielsen, 1966 (e.g. Amon et al. 2017; Drazen et al. 2021). Okiyama and Ida (2010) also assumed that the *Ipnops* specimen photographed by them in the Japan Trench, off Cape Erimo, was *I. meadi*. However, a reliable species identification has not yet been possible due to a lack of a captured specimen. During the BIONOD exploration cruise of the German Federal Institute for Geosciences and Natural Resources (BGR) in the Eastern Central Pacific Ocean, in April 2012, a specimen belonging to the genus *Ipnops* (Aulopiformes: Ipnopidae) was caught for the first time in the CCZ.

Fishes of the aulopiform family Ipnopidae number 33 species in six genera (Nelson et al. 2016; Fricke et al. 2022) and occur in tropical and temperate waters of the Atlantic, Indian and Pacific Oceans at depths between 476 and 6000 m (McEachran and Fechhelm 1998; Franco et al. 2009).

The species are mostly small and slender with a depressed head and flattened abdomen (Nielsen 1966). The mouth is large, reaching far behind the eye, the slightly protruding lower jaw has a fleshy tip, the teeth are small and needle-shaped, the gill slits are wide and the gill rakers are long (Paxton and Niem 1999; Bray 2017). They have a lateral line along the midline of the body, deciduous scales, a short-based dorsal fin located anterior to the anal fin and some species have elongated pectoral, pelvic and caudal rays (Bray 2017).

The species of the ipnopid genus *Ipnops* Günther, 1878 have dorsally directed, flat and degenerated eyes without a lens on the upper surface of the head covered by transparent frontals and parietals forming a thin bony membrane (Nielsen 1966). The genus *Ipnops* comprises the following four species (Fricke et al. 2022): *I. agassizii* Garman, 1899, *I. meadi* Nielsen, 1966, *I. murrayi* Günther, 1878 and *I. pristibrachium* (Fowler, 1943).

Although the horizontal and vertical distributions of these species in the world's oceans are not yet fully known, some differences do exist. *Ipnops agassizii* is distributed circumglobally in warmer temperate waters of the Atlantic, Indian and Pacific Oceans. In the Eastern Central Atlantic Ocean, this species occurs east of the mid-Atlantic Ridge between 5 and 6°N, as well as off Namibia, Mauritania and Cape Verde (Bannerman et al. 2015). Its known depth distribution ranges from 1392 to at least 2820 m (Nielsen 1966). *Ipnops meadi* is known to occur in the Indo-Pacific Ocean off Kenya, the Seychelles, the Maldives, Sri Lanka, northern and southern Japan, Indonesia (Sulawesi), the Magellan Rise near Hawaii in the Eastern Central Pacific Ocean and off Peru (Russell et al. 2020). This species was found at depths between 3310 and 4940 m (Nielsen 1966). *Ipnops murrayi* occurs in the Atlantic Ocean from the Bahamas to the Gulf of Mexico and Caribbean Sea. It has also been recorded from southeastern Brazil and Tristan da Cunha, whereas specimens from the Cape Verde Islands and Mauritania require verification (Moore and Polanco Fernandez 2019). Its known depth range is 1555–3475 m (Nielsen 1966). *Ipnops pristibrachium* is only known from off Sulawesi in the Western Central Pacific Ocean (Holleman et al. 2020) from a depth of 1525–1992 m (Nielsen 1966). This species was once considered a synonym of *I. agassizii* (Sulak 1990), but was recently considered as a valid species (Chen 2002; Fricke et al. 2022).

This work aims to present a detailed species identification of the first *Ipnops* specimen caught in the CCZ based on the integration of morphological characters and DNA barcodes.

Material and methods

Specimen sampling and processing

An *Ipnops* specimen was caught in the CCZ, Eastern Central Pacific Ocean, during the BIONOD cruise of BGR with RV *L'Atalante* on the 2nd of April 2012. The specimen was sampled from just (< 2 m) above the seafloor using an epibenthic sledge (station 06EBS) whilst trawling from 11°42.76′N, 116°40.35′W (4261 m depth) to 11°46.22′N, 116°41.13′W (4259 m depth). The catch location of the specimen is shown in Fig. 1.

Immediately after collection, the specimen was preserved in pre-cooled 96% ethanol and a tissue sample was taken for

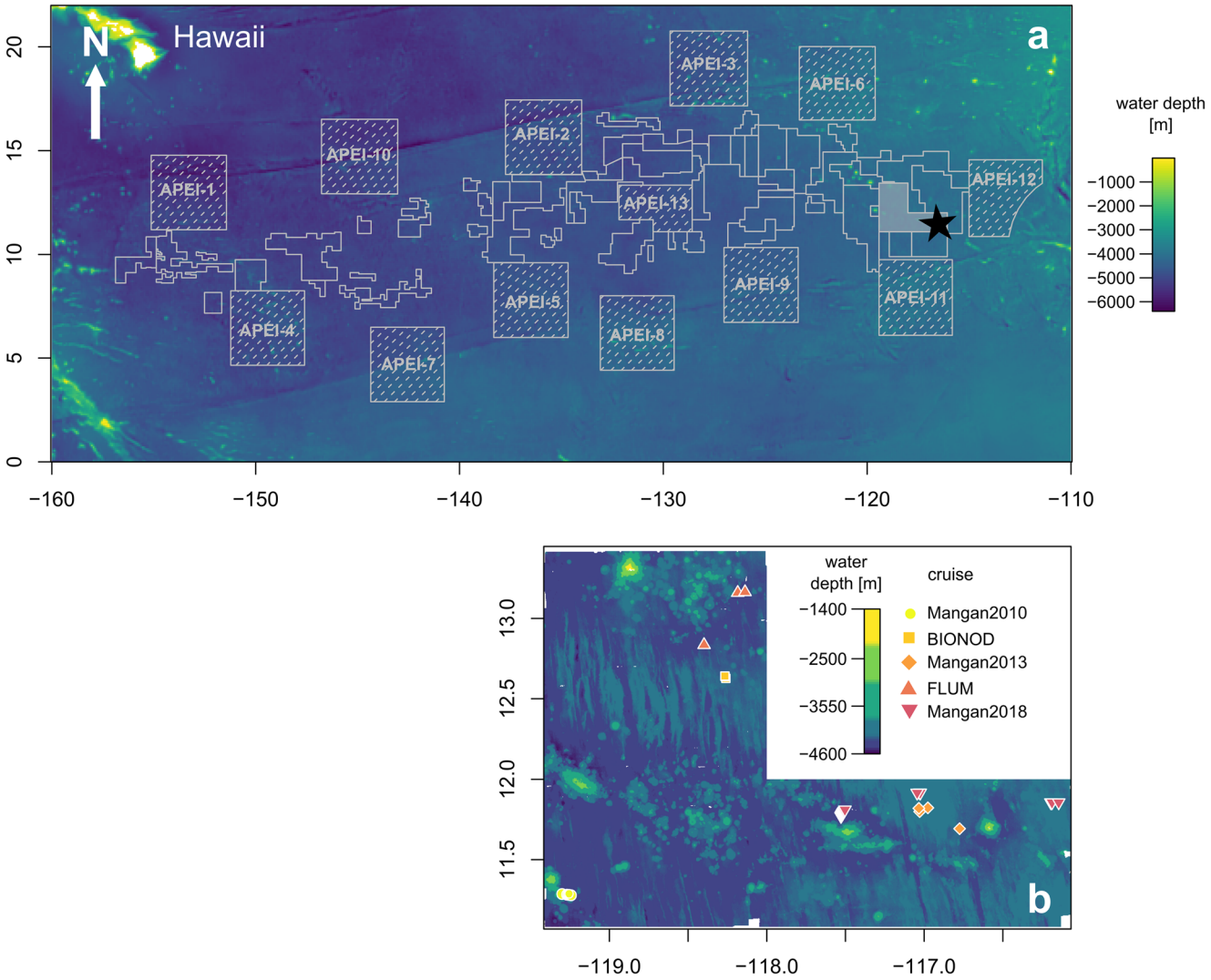

Fig. 1 **a** Bathymetric map (GEBCO 2014, International Seabed Authority 2020, 2021) showing the catch location (black star) of the specimen of *Ipnops meadi* Nielsen, 1966 obtained from the German Contract Area, CCZ (marked in grey), in the Eastern Central Pacific; **b** bathymetric map showing 42 locations in the German Contract Area at which *Ipnops* specimens were recorded based on available seafloor images

molecular analysis at Senckenberg's German Center for Marine Biodiversity Research (DZMB, Wilhelmshaven, Germany). About 8 years later, the specimen was transferred to the Zoological Museum Hamburg (ZMH), where it was deposited in the fish collection under catalogue number ZMH 25593.

Eighteen Australian specimens were collected from the RV *Investigator* with a beam trawl (4 m wide, 0.5 m high, mouth area 2 m^2) designed to sample fishes and invertebrates from flat to low relief seafloor habitats (Lewis 2010). The latitude and longitude data for the stations are for the start of the trawl and are listed in the "Morphological comparisons" section.

A small piece of muscle tissue (for DNA analysis) was extracted from Australian specimens collected in 2015 and 2017 and subsequently frozen, before whole fishes were fixed in 10% formaldehyde and deposited in the CSIRO Australian National Fish Collection (ANFC), Hobart. ANFC registration numbers are listed below in the "Morphological comparisons" section and in Table 2.

Image transect data

Occurrence data of *Ipnops* in the German Contract Area in the CCZ were collected using photographic images obtained with towed camera systems. Images were obtained from transects during the cruises BIONOD on RV *L'Atalante* (March 29–May 10, 2012), MANGAN14 on R/V *Kilo Moana* (April 15–June 03, 2014), FLUM on RV *Sonne* (May 03–June 16, 2015), and MANGAN18 on RV *Sonne* (April 05–May 29, 2018). All transects were annotated using the annotation platform BIIGLE (Langenkämper et al. 2017) as set up on the server of the Senckenberg Nature Research Society. A total

of 42 occurrences of *Ipnops* specimens were recorded using these photographic images (for locations, see Fig. 1). Three selected photographs of *Ipnops* specimens obtained with towed camera systems are available in Online Resource 1.

Morphological analyses

Meristic counts (Table 1) were made on the left-hand side of the specimens according to Hubbs and Lagler (1958) with a modification concerning the urostyle that was not included in the vertebral counts according to Nielsen (1966). Vertebrae; the rays of dorsal, anal and caudal fins; and other osteological elements were examined from radiographs using an X-ray imaging system (Faxitron LX-60). Digital radiographs of Australian specimens were created using an Inspex 20i 70kVp Microfocus source with LTX-1717 X-ray Detector (Kodex Inc.). External morphometric measurements were taken by vernier caliper to one tenth of a millimetre following Hubbs and Lagler (1958) with the exception that the symphysis of the upper jaw was used as the anteriormost part instead of the protruding lower jaw as in Nielsen (1966). All morphometric characters are provided as a percentage of the standard length. Images of the specimen were taken with a Digital BK Plus imaging system (Dun, Inc.), equipped with a Canon EOS 5DS DSRL camera with a 100-mm macro lens. Image stacking was performed using Zerene Stacker v.1.04 (Zerene Systems LLC.).

Morphological comparisons

We have compared the *Ipnops* specimen from the CCZ with all four currently known *Ipnops* species based on their morphological characters provided by Nielsen (1966) and Franco et al. (2009). Furthermore, the following additional material was analysed for morphological comparisons: *I. meadi*: ZMH 25834, 4 specimens, 84–112 mm SL, Northwestern Indian Ocean, Arabian Sea, 14°30′N, 64°38′E, RV *Meteor*, cruise 33/1, station 647, otter trawl, 3940 m depth, 11 October 1995. ZMH 25835, 1 specimen, 113 mm SL, Northwestern Indian Ocean, Arabian Sea, 14°26′N, 64°32′E, RV *Meteor*, cruise 33/1, station 649, otter trawl, 3953 m depth, 12 October 1995. *Ipnops* sp. 1 (Eastern Indian Ocean, Great Australian Bight, South Australia, all collected by RV *Investigator*): CSIRO H 7906-01, 1 specimen, 130 mm SL, 34°04.44′S, 129°10.92′E, IN2015_C01/064, 2649–2803 m depth, 13 November 2015. CSIRO H 7920-04, 1 specimen, 137 mm SL, 35°49.10′S, 134°06.54′E, IN2015_C02/141, 2852–2800 m depth, 05 December 2015. CSIRO H 7933-03, 1 specimen, 129 mm SL, 35°00.56′S, 130°19.02′E, IN2015_C02/227, 2848–2831 m depth, 11 December 2015. CSIRO H 8091-05, 1 specimen, 125 mm SL, 35°48.89′S, 132°01.27′E, IN2017_C01/175, 3930–4250 m depth, 15 April 2017. CSIRO H 8092-01, 1 specimen, 114 mm SL, CSIRO H 8092-08, 1 specimen, 56 mm SL, and CSIRO H 8092-11, 1 specimen, 131 mm SL, 35°42.95′S, 131°39.38′E, IN2017_C01/178, 3817–3950 m depth, 16 April 2017. CSIRO H 8096-04, 1 specimen, 133 mm SL, 34°26.84′S, 129°31.90′E, IN2017_C01/197, 3235–3350 m depth, 21 April 2017. CSIRO H 8097-03, 1 specimen, 120 mm SL and CSIRO H 8097-05, 1 specimen, 106 mm SL, 34°32.92′S, 129°36.12′E, IN2017_C01/198, 3389–3540 m depth, 21 April 2017.

Ipnops sp. 2 (Southwestern Pacific Ocean, Eastern Australia, all collected by RV *Investigator*): CSIRO H 8114-01, 1 specimen, 140 mm SL (largest of 2 specimens in lot), NE of Flinders Island, Bass Strait, Tasmania, 39°27.72′S, 149°16.56′E, IN2017_V03/022, 2760–2692 m depth, 22 May 2017. CSIRO H 8118-03, 1 specimen, 140 mm SL, E of Bermagui, New South Wales, 36°21.30′S, 150°38.64′E, IN2017_V03/044, 2821–2687 m depth, 27 May 2017. CSIRO H 8119-01, 1 specimen, 138 mm SL, SE of Jervis Bay, New South Wales, 35°19.98′S, 151°15.48′E, IN2017_V03/056, 2650–2636 m depth, 29 May 2017. CSIRO H 8120-04, 1 specimen, 136 mm SL (largest of 3 specimens in lot), E of Newcastle, New South Wales, 32°58.10′S, 152°57.12′E, IN2017_V03/067, 2704–2902 m depth, 31 May 2017. CSIRO H 8127-01, 1 specimen, 128 mm SL, Central Eastern Commonwealth Marine Reserve, New South Wales, 30°05.86′S, 153°53.92′E, IN2017_V03/086, 2429–2518 m depth, 05 June 2017. CSIRO H 8128-01, 1 specimen, 114 mm SL, E of Byron Bay, New South Wales, 28°40.59′S, 154°12.20′E, IN2017_V03/090, 2587–2562 m depth, 07 June 2017. CSIRO H 8131-01, 1 specimen, c. 136 mm SL (genetic data only as specimen not found at CSIRO), E of Moreton Bay, Queensland, 26°56.75′S, 153°56.70′E, IN2017_V03/101, 2520–2576 m depth, 09 June 2017. CSIRO H 8138-02, 1 specimen, 96 mm SL, Coral Sea Commonwealth Marine Reserve, Queensland, 23°45.06′S, 154°38.34′E, IN2017_V03/122, 2369–2329 m depth, 13 June 2017.

Comparison of the main characters is given in Table 1, where differences between the *Ipnops* specimen from the CCZ and the other *Ipnops* material are indicated in bold.

DNA extraction, amplification and sequencing

Total genomic DNA from the *Ipnops* specimen from the CCZ was extracted at the DZMB using the Qiagen DNeasy Blood and Tissue Kit following the manufacturers' protocol. A 657-bp fragment of the mitochondrial (mt) cytochrome oxidase sub-unit I (COI) gene was amplified by polymerase chain reaction (PCR). Amplifications were performed using AccuStart PCR SuperMix (ThermoFisher Scientific) in a 25-μL volume containing 12.5 μL AccuStart PCR SuperMix, 9.5 μL ddH_2O, 0.5 μL of each primer (10 pmol μL^{-1}) and 2 μL of DNA template. For the COI amplification, a primer cocktail (C_FishF1t1-C_FishR1t1) including FishF2_t1 (5′-TGTAAAACGACGGCCAGTCGACTAATCATAAAGATATCGGCAC), FishR2_t1 (5′-CAGGAAACAGCT ATGACACTTCAGGGTGACCGAAGAAT

Table 1 Counts and measurements of the specimen of *Ipnops meadi* from the CCZ (ZMH 25593) in comparison with estimated morphological characters of the four species of the genus *Ipnops* given in Nielsen (1966) and Franco et al. (2009) and *Ipnops* sp. 1 and 2 from Australian waters

	Ipnops meadi Eastern Central Pacific Ocean, CCZ This study	*Ipnops meadi* Western Indian Ocean to Eastern Central Pacific Nielsen (1966)	*Ipnops meadi* Northwestern Indian Ocean, Arabian Sea This study	*Ipnops murrayi* Western and Southern Atlantic Ocean Nielsen (1966)	*Ipnops murrayi* Southwestern Atlantic Ocean, off Brazil Franco et al. (2009)	*Ipnops agassizii* Western Indian Ocean to Eastern Central Pacific Nielsen (1966)	*Ipnops pristibrachium* Western Central Pacific Ocean, off Sulawesi Nielsen (1966)	*Ipnops* sp. 1 Southeastern Indian Ocean, Great Australian Bight This study	*Ipnops* sp. 2 Southwestern Pacific Ocean, East Australia This study
N	1	21	5	11	13	12	3	10	7
Standard length (SL, mm)[1]	124	50–121	84–113	60–131	66–116	81–134	115–137	56–137	96–140
Meristic characters									
Dorsal-fin rays	9	**8–9**	**8–9**	**9–10**	**9–10**	**9–11**	**9–10**	**8–9**	**8–9**
Caudal-fin rays[2]	17	**17–19**	19	**17–19**	-	19	19–20	19	19
Anal-fin rays	13	**11–13**	11–12	**13–15**	**13–15**	15–19	15–16	**13–16**	**13–15**
Pectoral-fin rays	15	**14–16**	**14–15**	**13–15**	**13–15**	**13–16**	**14–15**	**15–16**	**14–16**
Pelvic-fin rays	8	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**
Gill rakers on anterior arch	18	**17–20**	19–21	20–23	21–22	20–24	22–23	23–27	22
Precaudal vertebrae	18	**16–18**	16–17	**17–19**	**-**	**18–19**	**-**	**18–20**	**20–22**
Caudal vertebrae[3]	37	**35–39**	**36–39**	**35–40**	-	38–41	-	38–42	**37–39**
Total vertebrae[3]	55	**51–55**	**52–55**	**54–58**	56–57	57–61	57–59	57–60	58–60
Anterior D-ray over vertebra no.	18	**16–18**	17	**17–18**	**-**	**18–20**	**18–19**	**18–19**	19–20
Anterior A-ray under vertebra no.	36	**33–36**	**34–36**	**35–38**	**-**	**35–40**	37–38	37–39	37–39
Lateral line scales	51	**49–53**	**51–53**	53–57	53–58	55–58	56–57	56–59[4]	57–60[4]
Presence of otoliths	Yes	No	No (four spec.); **yes** (one spec.)	**Yes**	**-**	**Yes**	**Yes**	**Yes**	**Yes**
Morphometric characters (%SL)									
Head length[1]	18.5	19.5–24.0	**17.6–19.8**	**18.5–22.0**	**17.9–20.3**	**18.0–21.0**	**18.5**	**18.5–24.0**	18.9–21.1
Body depth at anterior D	7.7	**6.0–7.8**	6.0–7.1	**6.7–7.9**	5.4–7.4	5.9–7.5	**7.3–7.8**	**5.5–7.7**	6.9–7.6
Upper jaw length	10.8	11.0–14.0	**10.7–12.5**	11.5–13.5	–	11.0–13.0	11.0–11.5	10.7–13.0	**10.6–12.9**
Maximum width of eye-plates	7.5	8.1–9.8	7.8–8.3	9.1–10.0	8.3–9.5	8.4–9.9	8.2–8.7	9.4–11.2	10.4–11.2
Preanal length[1]	67.6	**64.0–79.0**	58.8–66.4	**65.0–68.0**	62.4–67.5	61.0–67.0	63.0–66.0	63.7–67.1	64.7–66.8
Predorsal length[1]	36.9	**35.0–40.5**	34.5–36.7	34.0–36.0	30.7–36.8	33.5–36.0	34.0–36.0	**34.8–39.6**	**35.7–39.2**
Length of dorsal fin base	7.4	**7.1–9.0**	7.9–8.8	8.6–9.6	8.3–13.1	8.3–11.0	9.4–10.0	**6.1–9.0**	7.7–8.8
Length of anal fin base	14.4	**12.0–15.5**	**13.9–15.5**	17.0–20.0	16.9–19.7	17.5–26.5	20.0	15.4–20.3	18.2–20.3
Anterior anal fin to caudal base	32.2	**30.0–35.0**	**30.4–33.9**	**31.5–36.0**	-	33.0–41.0	34.5–38.5	32.3–36.8	33.7–36.5
Length of upper pectoral ray	Long	**Long**	**Long**	Short	-	Short	Short	Short	Short

Matching or overlapping of the *Ipnops* species with the *Ipnops* specimen from the CCZ are indicated in bold; [1] symphysis of the upper jaw used as the anteriormost part instead of the protruding lower jaw according to Nielsen (1966); [2] only principal rays according to Hubbs and Lagler (1958); [3] urostyle not included in the vertebral counts according to Nielsen (1966); [4] approximate counts based on scale pockets due to lack of scales; "-" data not available

CAGAA), VF2_t1 (5′-TGTAAAACGACGGCCAGTCA ACCAACC ACAAAGACATTGGCAC) and FR1d_t1 (5′-CAGGAAACAGCTATGACACCTCAGGGTGTCCG AARAAYCA RAA) (Ivanova et al. 2007) tailed with M13F and M13R-pUC was used. The amplification conditions consisted of an initial denaturation step of 3 min at 94°C, 35 cycles of 30 s at 94°C, 60 s at 47°C and 1 min at 72°C, followed by a final extension step of 5 min at 72°C. All PCR products were purified using ExoSap-IT (ThermoFisher Scientific). Amplified fragments were sequenced in both directions at Macrogen Europe Laboratory (Amsterdam, The Netherlands). Forward and reverse sequences were assembled and edited using Geneious v.9.1.7 (https://www.geneious.com; Kearse et al. 2012).

DNAs from muscle samples from the Australian specimens were extracted using the Wizard® SV Genomic DNA Purification system (Promega, Australia) with starting material of 0.25g. Tissue extractions were undertaken using SV mini-columns following the manufacturer's instructions (including an overnight digestion at 55°C) and the addition of 20μL Proteinase K (20mg/mL, Promega). DNAs were individually precipitated in 160μL nuclease-free water. DNA was quantified on a Nanodrop 8000 UV-Vis Spectrophotometer (Thermo Scientific, USA) and aliquoted into 96-well plates. The DNA samples were sent at room temperature to the Ramaciotti Centre for Genomics (UNSW Sydney, Australia) where a portion of the COI was amplified (using FishF1&F2 and FishR2 primers (Ward et al. 2005) and an annealing temperature of 54°C). Bi-directional cycle sequencing was then undertaken using the abovementioned PCR primers and BigDye® Terminator v3.1 Cycle sequencing kit (Life Technologies, USA) on the PCR products, with cycle sequenced products run on an ABI3730XL Autosequencer (Applied Biosystems, USA) at Ramaciotti. Raw forward and reverse sequences were de novo assembled in Geneious v8.1.9 (https://www.geneious.com). Remaining archival DNA is stored at −80°C at the CSIRO Marine Laboratories in Hobart.

Processing of COI sequences

The obtained COI sequences were compared with the GenBank nucleotide database using BLASTN (Altschul et al. 1990). Our dataset consists of the new *Ipnops* sequence, the 18 sequences from the ANFC and four additional *Ipnops* sequences from either BOLD or GenBank. The COI sequences were aligned using MAFFT v7.308 under G-INS-I algorithm (Katoh et al. 2002). Sequence divergences were estimated as uncorrected *p*-distances using MEGA7 (Table 2). A neighbour-joining tree was constructed in MEGA7 using a *p*-distance substitution model, treating gaps and missing data with "pairwise deletion" and by running 1000 bootstrap replicates (Fig. 3).

Specimen metadata and sequences were uploaded to the Barcode of Life Data System. Additionally GenBank Accession numbers were acquired and are listed in Table 2, which are available for all recorded specimen sequences except for one specimen from the Caribbean Sea.

Results and discussion

Morphological description of the specimen

Counts and measurements of the collected CCZ specimen (ZMH 25593) are provided in Table 1. The specimen belongs to the genus *Ipnops* according to the characters given by Nielsen (1966). The morphological description of the specimen is as follows:

Body long and slender, its abdominal part flattened. Anus under ventral fins, just anterior to dorsal fin. Scales relatively large, body and sides of the head scaled (Fig. 2). Scales absent on fins, except for the caudal fin, whose base is partly covered by scales.

Head depressed dorsoventrally; its width greater than its height. Eye-plates on the upper surface of the head, dorsally directed, flat and without a lens; eyes covered with a thin and transparent bony membrane formed by frontals and parietals. Otoliths present (Fig. 2).

Mouth large. Lower jaw slightly protruding with relatively large pores. Anterior three pores smaller than the distance between pores, posterior three pores equal to or larger than the distance between pores. Upper jaw accounts for approximately 58 % of the head length. Gill slits long. 18 long and relatively thin gill rakers on the anterior arch, three on the upper branch, one on the angle and 14 on the lower branch.

Dorsal fin short-based (7.4 % SL) and located in front of anal fin. Anterior ray of dorsal fin placed over the 18th vertebra (Table 1) and much closer to snout than to the base of caudal fin (predorsal length 36.9 % SL). Origin of anal fin placed below the 36th vertebra and closer to caudal base than to the anus (preanal length 67.6 % SL). Pelvic fin base far anterior of dorsal fin. Dorsal ray of pectoral fin relatively long.

Teeth on jaws fine and numerous, only a few small pointed teeth on vomer and palatine. A lateral line present along the midline of the body (Fig. 2). Head, neck, chest, mouth and gill cavity are dark-brown after 10 years of preservation in 96% ethanol. Body yellow-brown, fins lighter.

Integrative taxonomic identification of *Ipnops meadi* Nielsen, 1966

ZMH 25593 differs clearly from *I. murrayi* in the following characteristics: fewer gill rakers (18 vs. 20–23) and lateral line scales (51 vs. 53–58), shorter upper jaw length (10.8 vs. 11.5–13.5), shorter maximum width of eye-plates (7.5 vs. 8.3–10.0), shorter length of dorsal (7.4 vs. 8.3–13.1) and anal fin bases (14.4 vs. 16.9–20.0), longer predorsal length (36.9 vs. 30.7–36.8), and longer upper pectoral rays (Table 1).

Table 2 Nucleotide mean distance (*p*-distance) of cytochrome oxidase sub-unit I (COI) between *Ipnops meadi* from CCZ (ZMH25593) and 22 *Ipnops* (Aulopiformes, Ipnopidae) sequences based on COI records from BOLD and GenBank with a minimum sequence length of 500bp

GenBank accession	BOLD process IDs	Specimen registration	Species	Distance (%)	Catch region	Catch location
ON526742	CCZ5459-22	ZMH 25593	*Ipnops meadi*	-	Eastern Central Pacific Ocean	CCZ
AP004198	----------	CBM-ZFT99-144	*Ipnops* cf. *meadi*	0.765	Estern Central Pacific Ocean	Off Hawaii, close to CCZ
MG856891	----------	DPND 4000	*Ipnops murrayi*	13.52	Western Central Atlantic Ocean	Gulf of Mexico
----------	MFLE040-12	ECO-CH LP 6060	*Ipnops murrayi*	13.52	Western Central Atlantic Ocean	Caribbean Sea, off Haiti
MT323649	----------	DPND 1345	*Ipnops murrayi*	13.67	Western Central Atlantic Ocean	Gulf of Mexico
ON749772	FOAP384-18	CSIRO H 8096-04	*Ipnops* sp. 1	13.65	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749764	FOAP396-18	CSIRO H 8097-03	*Ipnops* sp. 1	14.24	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749769	FOAP011-16	CSIRO H 7906-01	*Ipnops* sp. 1	14.09	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749776	FOAP397-18	CSIRO H 8097-05	*Ipnops* sp. 1	14.40	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749763	FOAP354-18	CSIRO H 8092-01	*Ipnops* sp. 1	14.24	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749771	FOAP394-18	CSIRO H 8092-08	*Ipnops* sp. 1	14.40	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749773	FOAP132-16	CSIRO H 7933-03	*Ipnops* sp. 1	14.38	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749768	FOAP154-16	CSIRO H 7920-04	*Ipnops* sp. 1	14.42	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749762	FOAP383-18	CSIRO H 8091-05	*Ipnops* sp. 1	14.09	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749775	FOAP395-18	CSIRO H 8092-11	*Ipnops* sp. 1	13.94	Southeastern Indian Ocean	South Australia, Great Australian Bight
ON749770	FOAO2513-20	CSIRO H 8114-01	*Ipnops* sp. 2	14.85	Southwestern Pacific Ocean	East Australia, off Tasmania
ON749779	FOAO1085-18	CSIRO H 8138-02	*Ipnops* sp. 2	14.85	Southwestern Pacific Ocean	East Australia, off Queensland
ON749766	FOAO2535-20	CSIRO H 8131-01	*Ipnops* sp. 2	14.09	Southwestern Pacific Ocean	East Australia, off Queensland
ON749778	FOAO2528-20	CSIRO H 8128-01	*Ipnops* sp. 2	14.85	Southwestern Pacific Ocean	East Australia, off New South Wales
ON749765	FOAO2521-20	CSIRO H 8120-04	*Ipnops* sp. 2	14.70	Southwestern Pacific Ocean	East Australia, off New South Wales
ON749774	FOAO2526-20	CSIRO H 8127-01	*Ipnops* sp. 2	15.16	Southwestern Pacific Ocean	East Australia, off New South Wales
ON749777	FOAO2516-20	CSIRO H 8118-03	*Ipnops* sp. 2	14.55	Southwestern Pacific Ocean	East Australia, off New South Wales
ON749767	FOAO2518-20	CSIRO H 8119-01	*Ipnops* sp. 2	14.85	Southwestern Pacific Ocean	East Australia, off New South Wales

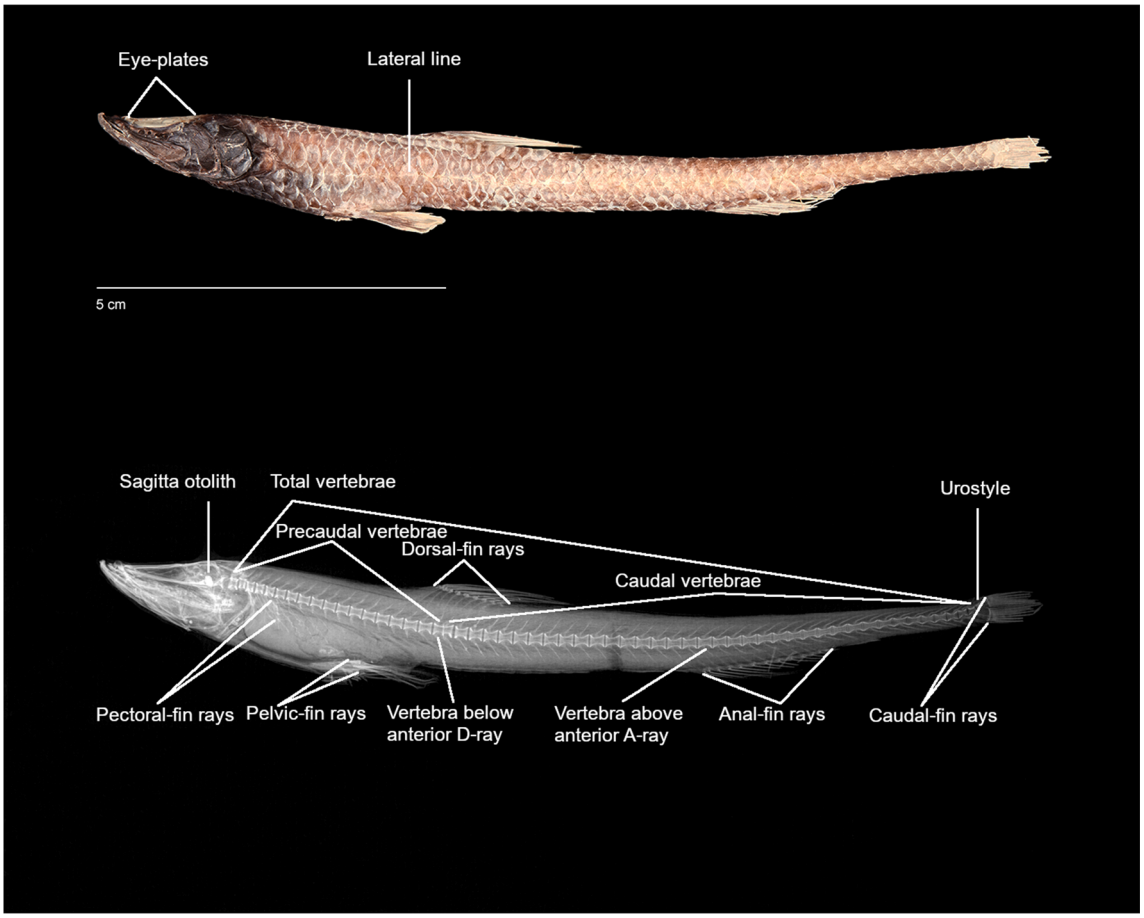

Fig. 2 *Ipnops meadi*, ZMH 25593, 124 mm SL, captured in the CCZ by epibenthic sledge during the BIONOD cruise of BGR on the 2nd of April 2012 (trawling from 11°42.76′N, 116°40.35′W to 11°46.22′N, 116°41.13′W; black star in Fig. 1). Top: picture of preserved specimen; bottom: radiograph of preserved specimen. Important meristic characters for species identification have been labelled (also see Table 1)

ZMH 25593 is clearly distinguished from its other two congeners, *I. agassizii* and *I. pristibrachium*, by a number of key characters. In total, out of 23 characters compared, ZMH 25593 differs in 15 characters from *I. agassizii* and in 14 characters from *I. pristibrachium* (for details, see Table 1). Therefore, an assignment of ZMH 25593 to these species can be excluded.

The characteristics of the *Ipnops* specimen from the CCZ agree well with the counts and measurements given by Nielsen (1966) for *I. meadi* from the Western Indian Ocean to the Eastern Central Pacific Ocean and of *I. meadi* from the Arabian Sea (Table 1). All counts fall within the minimum and maximum values of all 13 meristic characters of the 26 analysed specimens of *I. meadi*. Nine out of ten measurements are also within the ranges available for *I. meadi* (Table 1). Only the maximum width of eye-plates is slightly smaller than the known ranges for *I. meadi*. This difference can perhaps be attributed to the relatively small number of *I. meadi* specimens (only 26) which have been morphologically analysed in detail to date and to the fact that ZMH 25593 is the largest specimen of *I. meadi* studied so far.

The additional study of five specimens of *I. meadi* from the Arabian Sea (ZMH 25834 and ZMH 25835) has somewhat extended the range of the following characters compared to Nielsen (1966): gill rakers on anterior arch (17–21), head length (17.6–24.0 % SL), upper jaw length (10.7–14.0 % SL), maximum width of eye-plates (7.8–9.8 % SL), preanal length (58.8–79.0 % SL), and predorsal length (34.5–40.5 % SL).

It should also be mentioned here that Nielsen (1966) stated the absence of otoliths as a feature of *I. meadi* in contrast to all other *Ipnops* species. Marshall and Staiger (1975) reported that this could be the result of long preservation periods in formaldehyde rather than an actual character of the species. J. G. Nielsen himself confirmed this later (Franco et al. 2009). This explains the presence of otoliths in ZMH 25593, as this specimen was not preserved in formaldehyde.

It should be noted here that based on our study, we cannot confirm the current view that *I. pristibrachium* is a valid species (Chen 2002, Fricke et al. 2022), because almost all of its characters are within the range of *I. agassizii* (Table 1). In this aspect, we rather follow Nielsen (1966) that *I. pristibrachium* should be considered a synonym of *I. agassizii*.

ZMH 25593 is also clearly distinguishable from the Australian *Ipnops* specimens not yet assigned to a species. It differs in 12 characters from *Ipnops* sp. 1 from the Great

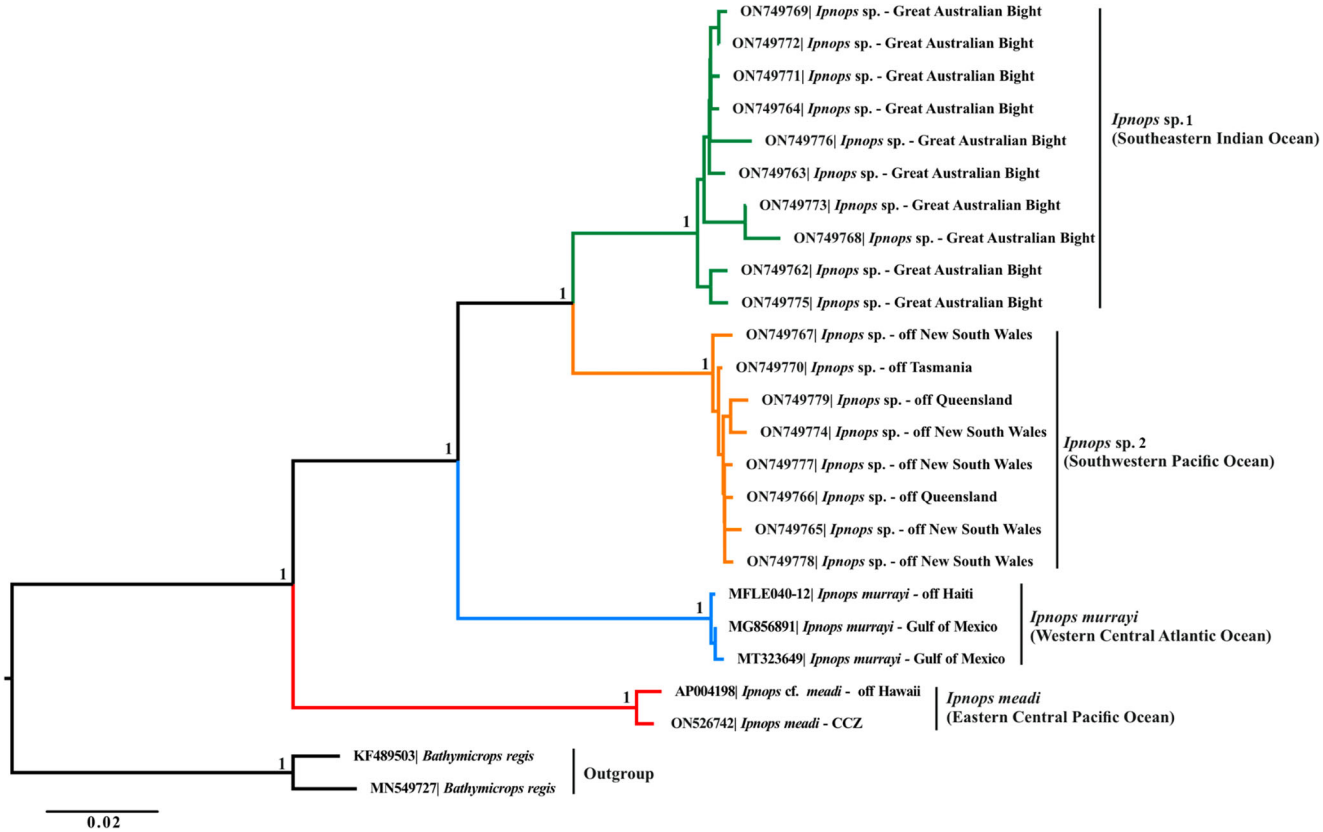

Fig. 3 Neighbour-joining tree of *p*-distance of *Ipnops* Günther, 1878 based on COI sequences. Numbers on nodes indicate neighbour-joining bootstrap values. Only values above 95% are shown

Australian Bight and in 14 characters from *Ipnops* sp. 2 from East Australia (for details, see Table 1).

The results of the molecular analyses agree well with the morphological analyses. The COI sequence (ON526742) of *I. meadi* collected from the CCZ is very similar (*p*-distance: 0.76%, Table 2; Fig. 3) to a COI sequence of an *Ipnops* specimen, identified as *Ipnops* cf. *meadi* from the Eastern Central Pacific Ocean (off Hawaii). Both specimens are within the known distribution area of *I. meadi* and in close proximity to each other (Table 2). This is the first time a verified COI sequence is available for this species.

Much higher mean genetic distances were found when compared with *I. murrayi* (13.52–13.67%) from the Western Central Atlantic Ocean, *Ipnops* sp. 1 from the Great Australian Bight (GAB) (13.65–14.42%) and *Ipnops* sp. 2 from East Australia (14.09–15.16%).

However, the *Ipnops* specimens from Australian waters could not be clearly assigned to one of the valid *Ipnops* species based on the molecular and morphological analyses. The morphological data for the two genetic lineages of Australian *Ipnops* do not unambiguously align with any one species of *Ipnops* from available data. The GAB samples match Atlantic samples identified as '*I. murrayi*' using the BOLD identification tool (not depicted in the tree as not publicly available). Nielsen (1966) discussed two specimens from the Western Indian Ocean that did not conform to any *Ipnops* species. He postulated that due to the specimens having characters in common with all three species of *Ipnops* that they could be hybrids and even raised the possibility of the species being subspecies (Nielsen 1966). Large COI sequence divergences (>5%) between multiple Australian forms points to further molecular and morphological investigations being necessary to resolve any possibly undescribed *Ipnops* species.

Final discussion and conclusion

Abyssal communities in the CCZ will be affected by potential future deep-sea mining activities. In order to evaluate the potential impact of nodule removal, contractors are required to comprehensively assess the biodiversity in their contract areas prior to any mining activity. The demersal fish fauna is an important component of the abyssal communities. Most of the records of reported fish species are based on images collected by remotely operated vehicles (ROV), towed cameras or baited camera landers (e.g. Harbour et al. 2020; Drazen et al. 2021; Leitner et al. 2021). None of these devices is able to collect specimens for accurate species identification. Baited traps used to collect scavengers (primarily amphipods) do potentially collect some fishes (mostly species of Macrouridae, Ophidiidae and Zoarcidae; Drazen et al. 2021), but *Ipnops* has not been attracted

by these devices so far. *Ipnops* is the most common fish genus observed in transects in the CCZ according to presently available abyssal imagery (Drazen et al. 2021). The distinctive reflection of light from its unique plate-like eyes (Online Resource 1) present in dorsal position makes the genus *Ipnops* easy to identify and detect. However, for species identification, voucher specimens are required. With this contribution, we report on the first collection of an *Ipnops* specimen from the CCZ. We have been able to match the morphological features with a DNA barcode retrieved from the COI gene. We can now confirm that the specimen reported from Hawaii also belongs to *I. meadi* and can exclude *I. murray*, *I. agassizii* and *I. pristibrachium* as potential species. The correct identification of the species present in the CCZ is crucial for the assessment of the potential impact of mining. In the present case, the confirmed range of distribution of *I. meadi* from the Indian Ocean to the Eastern Pacific Ocean makes it unlikely that deep-sea mining will threaten the species at a global scale, but it is reasonable to assume that they will be affected in mining areas, perhaps reducing their local standing stocks. However, this identification of a single voucher specimen does not necessarily conclude the existence of only one *Ipnops* species in the area. Very little is known on genetic diversity and connectivity of demersal fish populations at large geographic scales. This contribution is a first step in understanding distributional ranges in the abyss by matching taxonomy with morphological and genetic information for a common fish species in a potential mining area.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling have been obtained by the authors from the competent authorities and are mentioned in the Acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability The molecular datasets generated and/or analysed during the current study and other publicly available datasets are accessible in the BOLDSYSTEMS repository, www.boldsystems.org. Newly generated and already in BOLD existing nucleotide sequences were also deposited in the GenBank repository, www.ncbi.nlm.nih.gov/genbank, with accession numbers included in this published article.

Author contribution RT and PMA conceived and designed research. RT and JJP conducted the morphological analyses. MC and SAA carried out the molecular analyses. KU contributed the image annotation data. TW provided photographs of the collected specimen. RT wrote the original draft of the manuscript. AV has critically gone through the manuscript and provided suggestions. All authors read and approved the manuscript.

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