The first record of redfieldiiform fish (Actinopterygii) from the Upper Triassic of Korea: Implications for paleobiology and paleobiogeography of Redfieldiiformes

Su-Hwan Kim [a], Yuong-Nam Lee [a,*], Jin-Young Park [a], Sungjin Lee [a], Hang-Jae Lee [b]

[a] *School of Earth and Environmental Sciences, Seoul National University, Seoul 08826, South Korea*
[b] *Geological Museum, Korea Institute of Geoscience and Mineral Resources, Daejeon 34123, South Korea*

ABSTRACT

A new genus and species of redfieldiiform fish, *Hiascoactinus boryeongensis* gen. et sp. nov., is described based on a nearly complete specimen from the Upper Triassic Amisan Formation of South Korea. *Hiascoactinus* is distinguished from other redfieldiiforms by having a barely ornamented dermal skull surface except for the snout region, two heteromorphic suborbitals arranged vertically behind the postorbital, a pistol-shaped suprascapular, and dorsal and anal fins with divided fin membranes between rays. The morphological features of the snout region and dorsal and anal fins of *Hiascoactinus* provide important clues to understand its feeding and swimming behavior. All previously proposed Asian redfieldiiform fossils are inaccurately classified, and consequently, *Hiascoactinus* is regarded as the only valid redfieldiiform taxon in Asia. *Hiascoactinus* is assigned to the basal group of redfieldiiforms primarily based on the presence of an antopercle. The basal phylogenetic position of *Hiascoactinus* indicates that basal redfieldiiforms dispersed from the southern Gondwanaland to the easternmost Laurasia through the terrestrial water system, and these two landmasses were connected during the Late Triassic.

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1. Introduction

A variety of actinopterygian fossils have been found in the Mesozoic and Cenozoic deposits of South Korea. Despite abundant fossil materials, however, only a few were reported in research articles. Most of the Mesozoic specimens were collected from the Lower Cretaceous Jinju Formation, and are all freshwater fish taxa, including teleosteans (Osteoglossiformes, Elopiformes, Albuliformes, and Ichthyodectiformes) and holosteans (Lepisosteiformes and Amiiformes) (Kim et al., 2014; Yabumoto and Yang, 2000; Yabumoto et al., 2006). Specimens from the Cenozoic deposits were collected from the Lower Miocene Bukpyeong Formation and the Middle Miocene Duho Formation. Abundant isolated pharyngeal teeth of cypriniforms were reported from the terrestrial Bukpyeong Formation (Lee, 2004; Lee et al., 2003). Although many marine fish fossils have been collected from the Duho Formation, no scientific documentation has been made thus far except for a single taxon of Pleuronectiformes and a perciform species, *Zaprora koreana* (Ko, 2016; Ko and Nam, 2016; Nam and Nazarkin, 2018).

Redfieldiiformes is an extinct clade of actinopterygians. Since its first discovery in a red sandstone layer of Connecticut River Valley, North America (Redfield, 1837), seventeen genera of redfieldiiforms have been reported from the Lower Triassic to Lower Jurassic terrestrial deposits of many continents including Australia, Africa, North America, and South America. There are also putative redfieldiiform taxa in Europe (Dzik and Sulej, 2007; Schaeffer and McDonald, 1978), but confirmation has not been made. The phylogenetic position of redfieldiiforms is still unclear although some studies suggest that they are basal actinopterygians (Gardiner and Schaeffer, 1989; Mickle, 2015; Poplin and Dutheil, 2005). Nevertheless, Redfieidiiformes represents a monophyletic group based on a number of diagnostic features such as a fusiform body covered with ganoid scales, a hatchet-shaped preopercle, a single plate-like branchiostegal ray, caudally positioned dorsal and anal fins, the fin rays of dorsal and anal fins exceeding the number of radials, and a hemi-heterocercal caudal fin (Schaeffer, 1984).

Here we report for the first time on a well-preserved actinopterygian fossil from the Upper Triassic Amisan Formation of South Korea. It has many diagnostic anatomical features of the clade Redfieldiiformes but morphologically differs from other redfieldiiform taxa, representing a new taxon which is named as *Hiascoactinus boryeongensis* gen. et sp. nov. The holotype of *H. boryeongensis* is described, and its paleontological and paleobiogeographic importance is discussed herein. This is the

* Corresponding author.
E-mail addresses: shwan0@snu.ac.kr (S.-H. Kim), ynlee@snu.ac.kr (Y.-N. Lee), dinotopia3@snu.ac.kr (J.-Y. Park), sungjinlee@snu.ac.kr (S. Lee), fossilis@kigam.re.kr (H.-J. Lee).

first fossil record of a redfieldiiform fish from the Korean Peninsula and possibly from Asia.

2. Geological setting

The Amisan Formation occurs in the lower part of the Nampo Group of the Chungnam Basin (Fig. 1). It overlies the Hajo Formation, which is composed mainly of conglomerates and is underlined by the Jogyeri Formation, which is composed of feldspar breccias and conglomerates (Suh et al., 1984). The Amisan Formation is up to 1000 m thick (Yang, 1999) and subdivided into three members. The lowest member shows a fining-upward sandstone-shale succession, and an alluvial fan environment was involved during the formation. The middle and upper members show coarsening-upward sandstone-dominated deposits from a fluvial-dominated lacustrine-delta environment (Egawa and Lee, 2009). A variety of fossils were discovered from the Amisan Formation, which includes abundant fossil plants (Kim, 1976; Kim, 1990, 2001, 2010, 2013; Kim et al., 2002; Kim and Roh, 2008; Kimura and Kim, 1984), bivalves (Kim et al., 2015), conchostracans (Kim and Lee, 2015), and insects (Nam and Kim, 2014; Nam et al., 2017). Some fossil fishes were also collected from this formation, but none of them has been studied scientifically. The *Dictyophyllum-Clathropteris* floral assemblage reported from the Nampo Group (including the Amisan Formation) indicates that the paleoenvironment of this area was a tropical to subtropical climate near the equator (Kimura and Kim, 1984). The paleomagnetic study supports this paleobotanical interpretation (Kim and Kim, 1998). The depositional age of the Amisan Formation was suggested as Late Triassic to Early Jurassic based on the *Dictyophyllum-Clathropteris* floral assemblage (Kimura and Kim, 1984). Conchostracan fossils suggest that a minimum depositional age is up to the Late Triassic (Kim and Lee, 2015).

3. Systematic paleontology

Osteichthyes Huxley, 1880
Actinopterygii Cope, 1887
Redfieldiiformes Berg, 1940
Hiascoactinus boryeongensis gen.et sp. nov.

3.1. Etymology

The generic name is derived from the Latin "hiásco" (divided) and the Greek "aktís" (ray), reference to the unique fin membrane of the dorsal and anal fins of the type specimen. The species epithet, "*boryeongensis*", refers to its type locality "Boryeong" City of South Korea.
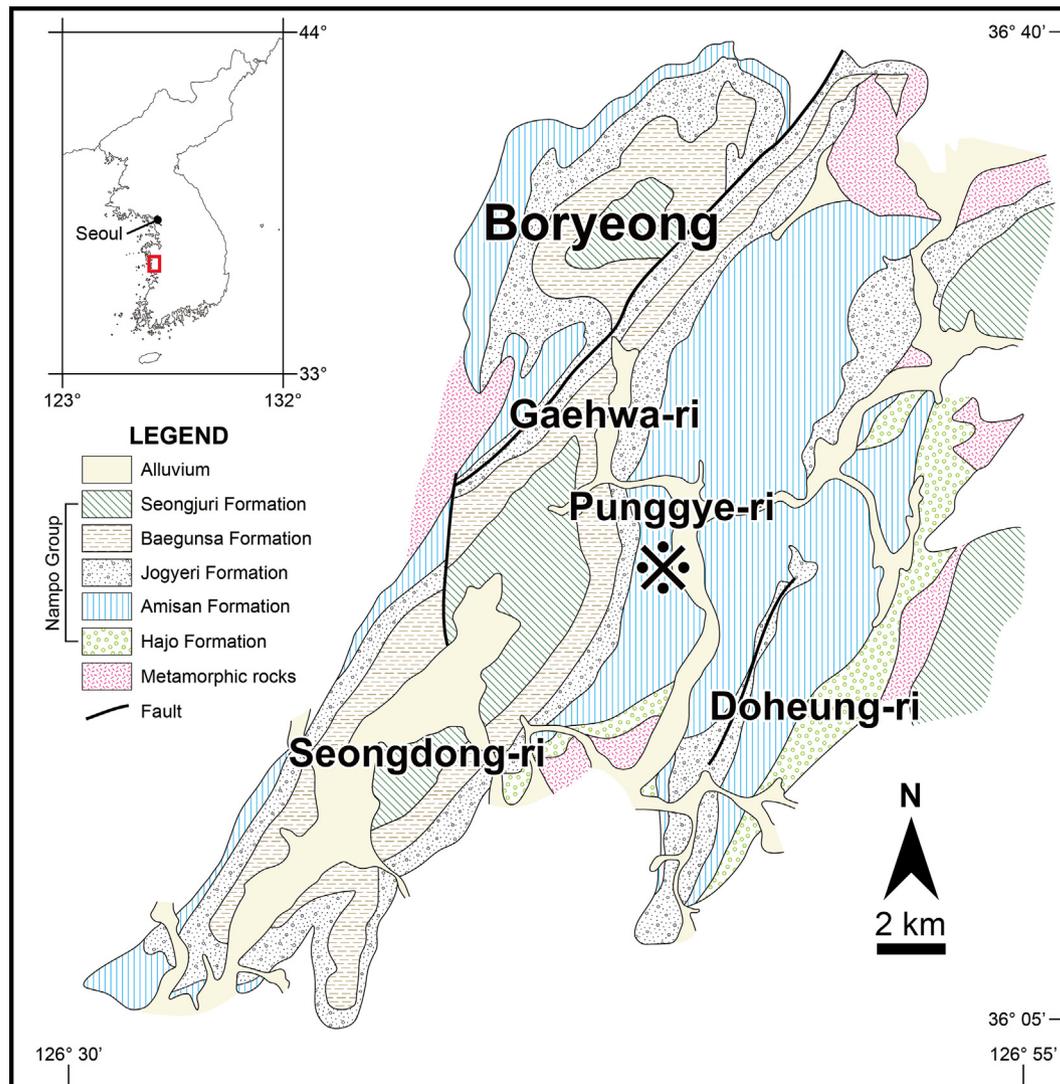

Fig. 1. Geological map of Boryeong area and the locality where the specimen was discovered. Modified from Yang, 1999.

3.2. Holotype

KIGAM 9A56, an almost complete specimen lacking the ventral region of the dermal skull elements, anterior abdominal region and the distal portion of a caudal fin (Fig. 2). The specimen is deposited at the Geological Museum of Korea Institute of Geoscience and Mineral Resources (KIGAM), Daejeon, South Korea.

3.3. Type locality and horizon

Amisan Formation, Upper Triassic, Punggye-ri, Misan-myeon, Boryeong City, South Chungcheong Province, South Korea (Fig. 1).

3.4. Diagnosis

A redfieldiiform fish with the following characteristics: snout tubercles, opercular series broad and oblique, large antopercle, smoothly curved anterodorsal margin of the maxilla, maxilla without posteroventral process, inclined ridge and pointed process on the caudal margin of the lateral line scales, well-developed anal fin originating anterior to the dorsal fin and ending posterior to it, and relatively fine segmented fin rays. Four autapomorphies are recognized with a potential one: a barely ornamented dermal skull surface except for the snout region, two suborbitals arranged vertically behind the postorbital, a pistol-shaped suprascapular, and incompletely closed fin membranes between rays of the dorsal and anal fins (potential character).

3.5. Description

KIGAM 9A56 is a well-preserved redfieldiiform fish (Fig. 2). As it is preserved on the shale surface as a fossil slab, only its right lateral side is visible. The specimen is nearly complete except for missing portions of its anteroventral region and distal caudal fin. The total length of the preserved fossil is 138 mm, and the greatest depth is 36 mm. Besides, some of its craniomandibular elements are also either missing or poorly preserved, in part because of its cranium being distorted (Fig. 3). Nevertheless, many of the major cranial and postcranial elements are observable although the vertebral column is entirely covered by scales. However, the heavily damaged surface of the anterior half and the tail
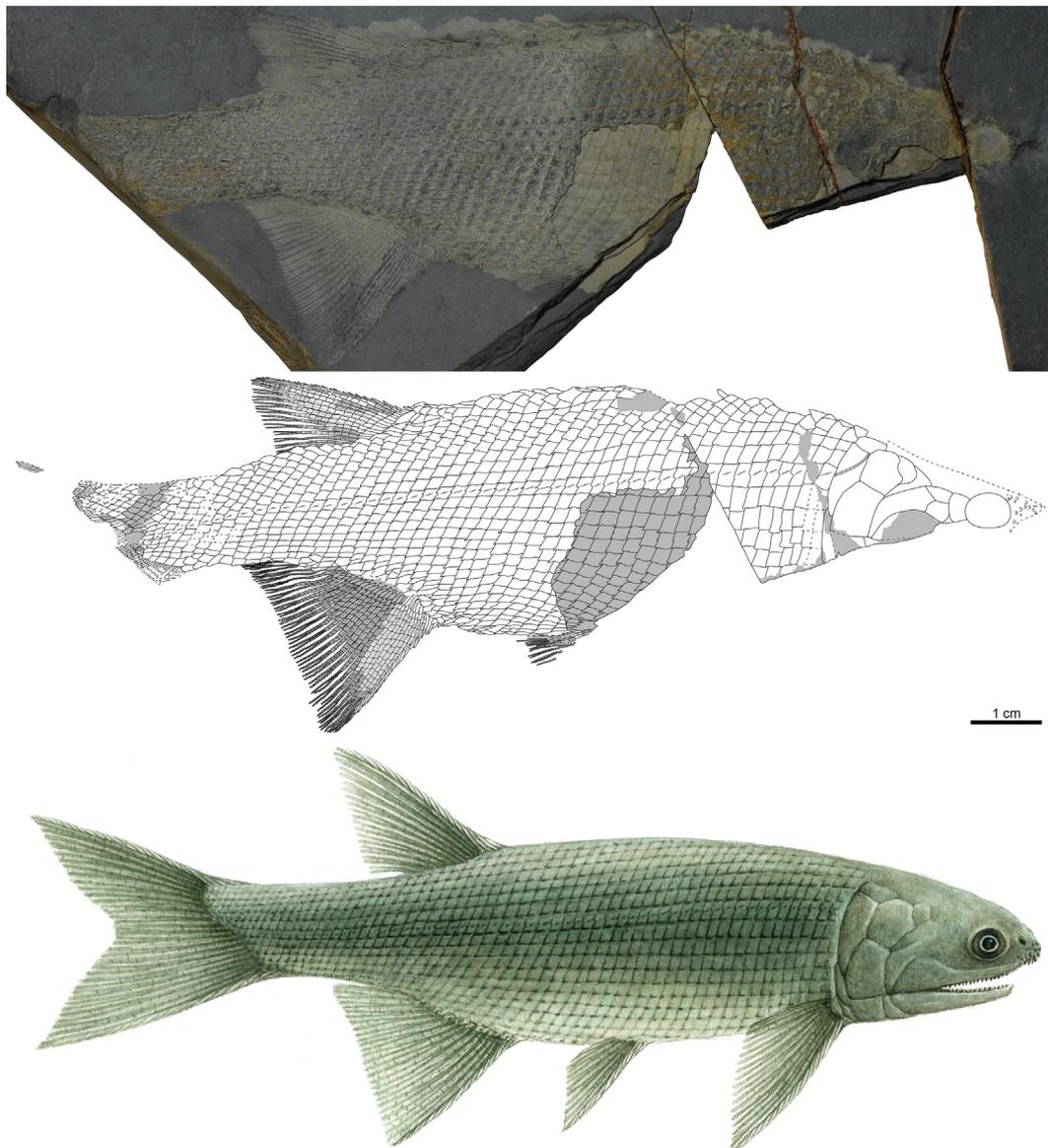
Fig. 2. Photograph, drawing, and reconstruction (by Cho Kwang Hyun) of the holotype specimen (KIGAM 9A56). Grey areas and dashed lines indicate broken portions and reconstructed portions, respectively.

region hinder the precise identification of several borders between individual bones.

3.5.1. Snout

In redfieldiiforms, the snout region usually consists of the adnasal, nasal, postrostral, rostral and 'premaxilla' (premaxillo-antorbital) (Schaeffer, 1984). In KIGAM 9A56, however, the borders between each component of the snout region and the exact location of the nostril are not recognizable because this region is slightly covered by the matrix (Fig. 3). Nevertheless, the general profile of the snout tapers anteriorly with a pointed tip as in other redfieldiiforms. The preserved snout bones constitute the anterior margin of the orbit (Fig. 3). The overall surface of snout bones is ornamented with randomly distributed large tubercles which are also characteristic of other redfieldiiforms (Hutchinson, 1973; Schaeffer, 1984).

3.5.2. Skull roof

During fossilization, the cranium of KIGAM 9A56 was obliquely compressed so that most of cranial elements on the right side is not visible (Fig. 3). Among the skull roof bones anterior to the suprascapular, the parietal and postparietal are entirely missing while some bones are partially preserved above the circumorbital bones, dermohyal, and opercular bones. Although the exact shapes of these bones are not discernable, they are likely to be dermosphenotic, dermopterotic and extrascapular based on the anatomy of other redfieldiiforms. The suprascapular is distinct in morphology being pistol-shaped (Fig. 3). It covers the entire dorsal margin of supracleithrum. Anteriorly, the suprascapular has a small and dorsoventrally shallow arm that extends to meet the extrascapular above the mid-length of opercle. The preserved skull roof bones of *Hiascoactinus* are unornamented (Fig. 3). It makes *Hiascoactinus* distinguishable from other redfieldiiforms that have ornamented skull roof bones with tubercles and rugae such as *Calaichthys*, *Redfieldius*, and *Lasalichthys* (Gouiric-Cavalli et al., 2017; Gibson, 2018; Schaeffer and McDonald, 1978).

3.5.3. Orbitals

The large orbit is oval and located anteriorly (Fig. 3). KIGAM 9A56 has a single postorbital, which forms the posterior margin of the orbit (Fig. 3). The postorbital is quite broad and deep, and the posterior margin of postorbital contacts two suborbitals. The fairly large suborbitals are vertically arranged and completely separate the anterior arm of preopercle from the postorbital (Fig. 3). Two suborbitals are different in shape from each other. The upper suborbital is trapezoidal and the lower one is subrectangular with round edges. The presence of the vertically arranged two suborbitals is one of the unique characters of *Hiascoactinus*. Most of the redfieldiiforms have a single suborbital except for *Hiascoactinus*, *Redfieldius* and *Calaichthys* that have multiple

suborbitals. However, *Redfieldius* has two horizontally arranged suborbitals between the postorbital and dermohyal above the preopercle. *Calaichthys* has three small rectangular suborbitals with a vertical arrangement (Gouiric-Cavalli et al., 2017; Schaeffer and McDonald, 1978).

3.5.4. Opercular region

The opercular series and dermohyal are unornamented and obliquely arranged in general (Fig. 3). The hatchet-shaped preopercle has an anterior arm which is nearly parallel to the long axis of the body and slightly broadens anteriorly (Fig. 3). The "hatchet-shaped" preopercle is prevalent in redfieldiiforms and many Paleozoic palaeoniscoids (Mickle, 2013; Schaeffer, 1984). The preopercle also contacts two suborbitals anteriorly as a wedge between them. It also extends posteriorly to the level of the anteroventral margin of subopercle and then, tapers towards its posteroventral end.

The D-shaped antopercle is fairly large (Fig. 3). The antopercle is also present in many other redifieldiiforms such as *Atopocephala*, *Schizurichthys*, *Ischnolepis*, *Brookvalia*, *Phlyctaenichthys* and *Helichthys* (Hutchinson, 1973; Schaeffer, 1984). However, the ratio of antopercle to opercle in *Hiascoactinus* is the largest among redfieldiiforms. The rectangular opercle is smaller than the subopercle (Fig. 3). The anterodorsal margin of opercle is concave posteriorly due to the intrusion of antopercle. The subopercle is rectangular and slightly curved ventrally (Fig. 3). The surface of subopercle at the middle is laterally convex.

The large dermohyal is boomerang-shaped being strongly recurved (Fig. 3). The anterior tip of dermohyal is dorsal to the posterior end of upper suborbital completely covering the preopercle. This results in the separation of the preopercle from the dermopterotic. This character is also known in *Helichthys* and *Lasalichthys* (Gibson, 2018; Hutchinson, 1978; Schaeffer, 1967).

A single fragmentary branchiostegal ray is preserved (Fig. 3). It is plate-like and located ventral to the subopercle and posterior to the dentary. In other redfieldiiforms, only *Daedalichthys* has two branchiostegal rays on each side which are vertically arranged, and the rest have a single branchiostegal ray (Hutchinson, 1973; Schaeffer, 1984). This is different from Paleozoic palaeoniscoids which have numerous branchiostegal rays (Mickle, 2013). The upper branchiostegal ray of *Daedalichthys* contacts the preopercle anteriorly, and its anterior margin is above the posteroventral margin of preopercle. In other taxa, the dorsal margin of a branchiostegal ray is leveled or below the posteroventral margin of preopercle except for *Dictyopyge* and *Pacorichthys* whose branchiostegal rays extend slightly above this margin (Lombardo, 2013; Schaeffer and McDonald, 1978). However, there is no redfieldiiform taxon with two branchiostegal rays, both of which are below the level of preopercle. In this regard, it seems to be reasonable to assume that *Hiascoactinus* has a single branchiostegal ray on each side since the dorsal margin of branchiostegal ray does not
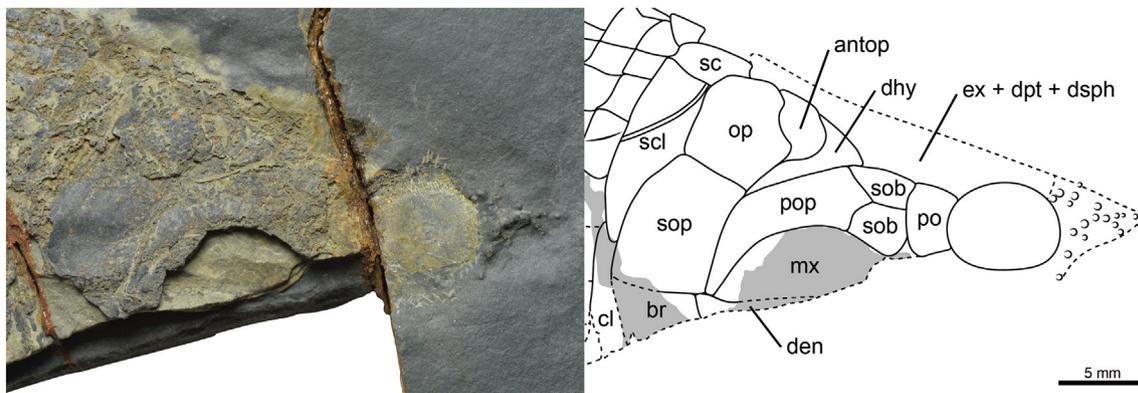
Fig. 3. Photograph and drawing of cranial elements of *Hiascoactinus boryeongensis* gen. et sp. nov. Grey areas and dash lines indicate broken portions and reconstructed portions, respectively. Abbreviations: antop, antopercle; br, branchiostegal ray; cl, cleithrum; den, dentary; dhy, dermohyal; dpt, dermopterotic; dsph, dermosphenotic; ex, extrascapular; mx, maxilla; op, opercle; po, postorbital; pop, preopercle; sc, suprascapular; scl, supracleithrum; sob, suborbital; sop, subopercle.

dorsally extend to the posteroventral margin of preopercle in *Hiascoactinus*.

3.5.5. Jaws

Due to poor preservation, only the posterior tip of dentary is preserved with the border of the maxilla with the preopercle although the outline of maxilla is recognizable (Fig. 3). The maxilla is deep in the middle with a convex dorsal margin and smoothly tapers anteriorly and posteriorly (Fig. 3). Anteriorly tapered maxillae with a smooth curve are also known in other redfieldiiforms such as *Calaichthys* and *Ischnolepis* (Gouiric-Cavalli et al., 2017; Hutchinson, 1973). However, the maxillae of many redfieldiiforms have a distinct recession on the dorsal margin where they contact with the circumorbital bones. *Hiascoactinus* lacks a posteroventral process on its maxilla as in *Atopocephala*, *Ischnolepis*, and *Phlyctaenichthys* (Schaeffer, 1984). On the other hand, Paleozoic palaeoniscoids have prominent posteroventral processes on the maxillae (Mickle, 2013). There are no teeth preserved on the maxilla or dentary in KIGAM 9A56 (Fig. 3).

3.5.6. Pectoral girdle

The supracleithrum of *Hiascoactinus* is dorsoventrally deep and bears a prominent sensory canal (Fig. 3). This sensory canal contacts posteriorly with the first lateral line scale and runs obliquely upwards to the anterodorsal edge of supracleithrum with a slight curve. Only the upper portion of cleithrum is preserved. It is narrow and rod-shaped. It also dorsally extends to a third of the length of subopercle.
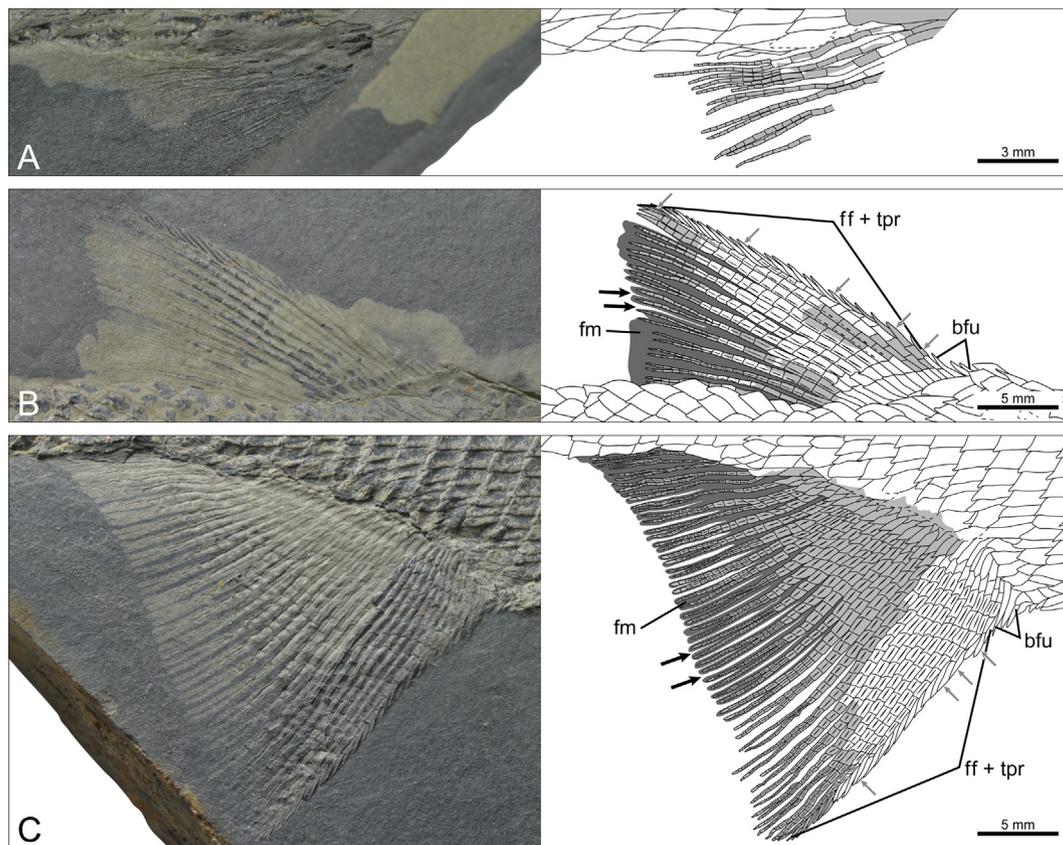
3.5.7. Pelvic fin

The pelvic fin of *Hiascoactinus* is located at the mid-length of the ventral margin of its body where it is deepest dorsoventrally (Fig. 4A).

The anterior portion of the pelvic fin is not preserved, but seven lepidotrichia are preserved. They are very thin in comparison with the rays of the dorsal or anal fin. All rays of the preserved pelvic fin are evenly segmented and distally bifurcated. The branched regions of rays are more finely segmented, and the posterior margin of a pelvic fin has an uneven margin.

3.5.8. Dorsal and anal fins

The dorsal and anal fins of *Hiascoactinus* are well preserved with clearly visible fin membranes (Fig. 4B–C). These fins are set back far posteriorly on the dorsal and ventral margins of the body, respectively (Fig. 2). The anterior and posterior ends of each of the two fins are not completely aligned, and the dorsal fin is smaller than the anal one. The lepidotrichia of dorsal and anal fins are finely segmented. Each segment has a central ridge and tends to become shorter distally. The preserved fin membranes of dorsal and anal fins are light brown in color, and do not completely fill the gap between each principal ray and branched ray. The membranes follow the contour of these rays, and since the pattern of the notches is regular in shape, we consider this as a natural character rather than a taphonomic one. The notches between principal rays of anal fin deeply extend beyond the node of ray, but those of the dorsal fin are obscured due to the overlapping of the fin membranes of each principal ray. Judging from the finely segmented lepidotrichia and segregated fin membrane of *Hiascoactinus*, it seems likely that this taxon had highly flowing fins. Fin membranes have never been reported in other redfieldiiforms before, but it is not certain whether they are truly absent in these taxa. Due to completely covered scales, it is not possible to confirm whether the number of lepidotrichia of dorsal and anal fins is higher than that of radials.

Fig. 4. Pelvic, dorsal and anal fins of the holotype specimen (KIGAM 9A56) of *Hiascoactinus boryeongensis* gen. et sp. nov. A, Photograph and drawing of the pelvic fin; B, Photograph and drawing of the dorsal fin; C, Photograph and drawing of the anal fin. Grey areas and dash lines indicate broken portions and reconstructed portions, respectively. Note gap of divided fin membranes between each principal ray and branched ray (marked by black arrows). Abbreviations: bfu, basal fulcra; ff, fringing fulcra; fm, fin membrane; tpr, tips of procurrent rays (grey arrows).

The dorsal fin originates above the 34th vertical scale row and is right triangle-shaped with a nearly straight posterior margin (Fig. 4B). It is comprised of five procurrent rays and 11 principal rays. Each procurrent ray has a tip that looks similar to a fringing fulcrum. All principal rays are bifurcated distally, and there is no central ridge on each segment of the bifurcated portions of rays. Three basal fulcra precede the procurrent rays. Posterior to the basal fulcra, there are well-developed fringing fulcra with tips of procurrent rays along the anterior margin of a dorsal fin.

The prominently large anal fin of *Hiascoactinus* originates below the 24th vertical scale row and is similar to that of *Redfieldius* in that they have a relatively large-angled ventral edge and a nearly straight posterior margin (Fig. 4C). In most of the other redfieldiiforms, however, anal fins have a posterior margin which is either concave or perpendicular to the longitudinal axis of their body (Brough, 1931; Hutchinson, 1973; Schaeffer, 1967). The base of the anal fin of *Hiascoactinus* is longer than that of the dorsal fin, and it originates anterior to the dorsal fin and ends posterior to this fin. The anal fin consists of four robust procurrent rays and 29 principal rays. As in the dorsal fin, the anal fin has three basal fulcra, a series of well-developed fringing fulcra with tips of procurrent rays and distally bifurcated principal rays, but there is a prominent central ridge on each segment of the branched portions of principal rays.

3.5.9. Caudal fin

The hemi-heterocercal caudal fin has a posteriorly expanded scaly dorsal lobe (Fig. 5). Most of the caudal fin, except for the base, is missing. It forms an S-shaped border with the margin of caudal peduncle. Although the shape of the caudal fin of *Hiascoactinus* is uncertain, it could be assumed to be similar to caudal fins of other redfieldiiforms that are generally forked and equilobate (Brough, 1931; Hutchinson, 1973; Schaeffer, 1967). The caudal fin has approximately 11 rays in the epaxial position posterior to the basal fulcra whose number is uncertain. The preserved rays are finely segmented, but the exact number of lepidotrichia is not countable.

3.5.10. Squamation

The whole trunk of *Hiascoactinus* is covered with slightly thick ganoid scales (Fig. 6). As a whole, scales are rhomboid to parallelogram in shape. The posterior margins of scales are straight except for those of lateral line scales. The scales that are closer to the lateral line or skull tend to be dorsoventrally deeper than others. The scales near the dorsal midline are also relatively deep although they are not close to the lateral line. The lateral line is covered with 50 scales, and they have an oblique central ridge on the surface. On the posterior margin of each scale, a prominent process is directed downward. It seems that the lateral line canal, underlying the lateral line scales, is connected to the sensory canal on the supracleithrum (Fig. 3). In general, the scales slightly overlap the anterior portion of the ones that are right posterior to them. The anterior margin of the scales on a small region in the anterior flank has

an inconspicuous process which can be observed by their impressions (Fig. 6). These peg-and-socket structures make tight articulations of squamation by fitting into the grooves of the adjoining scales. There are no scutes on any part of the body.

4. Discussion

4.1. Paleobiology of Hiascoactinus and other redfieldiiforms

The tubercular ornamentations are present on the snout region of *Hiascoactinus* (Fig. 3). This feature is also known in *Redfieldius*, *Helichthys*, *Lasalichthys*, *Dictyopyge* and *Cionichthys* (Gibson, 2018; Hutchinson, 1978; Schaeffer, 1967; Schaeffer and McDonald, 1978). Schaeffer (1967) first hypothesized that a well-developed fleshy upper lip was attached on top of this structure. He further suggested that the redfieldiiforms with snout ornamentations could scoop river or lake detritus by using the upper lip as bottom feeders. However, since many modern fishes having an upper lip are supported by unornamented premaxillae (Girgis, 1952; Mousavi-Sabet and Eagderi, 2016), the presence of a fleshy lip cannot be inferred by the presence of snout ornamentations. Moreover, modern bottom feeders have specialized premaxillary and maxillary structures in such a way that their premaxillae slide forward as the maxillae orient anteroventrally (Girgis, 1952), creating a tube-like extension of the mouth during feeding. In redfieldiiforms, on the other hand, premaxillo-antorbitals and maxillae are fixed to other cranial elements so they were not capable of this kind of upper jaw movement. Judging from the morphological profiles of premaxillo-antorbital and maxilla, redfieldiiforms probably had a large gape well-suited for overtaking prey. This is also supported by the presence of small pointed teeth along the jaw in many redfieldiiforms, which is not appropriate for scooping sediments.

In some modern fishes (e.g., salmoniforms, gonorhynchiforms, perciforms, and especially cypriniforms), similar well-developed tubercles are present on the snout region as well as the entire body. These breeding tubercles, also called nuptial tubercles, are present on mature males, and usually more developed in males than females. These tubercles enable the fish to maintain body contact between individuals during spawning or are used to defend the nest and territory. However, unlike odontodes, the breeding tubercles consist of keratinized or non-keratinized epidermal cells. This structure also begins developing before the spawning season, and are shed or gradually shrunk in size after spawning (Wiley and Collette, 1970). Morphologically, they are quite different from tubercles of redfieldiiforms, but it is not certain whether the snout tubercles of redfieldiiforms similarly had a function or not. Future research for morphological differences between redfieldiiform cranial ornamentations may provide insights into this notion. However, since only a handful of redfieldiiform specimens are currently known, this hypothesis is difficult to assess for now.
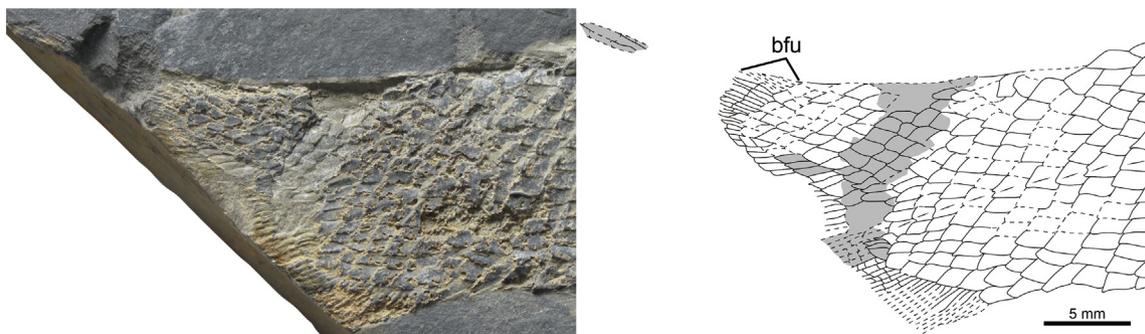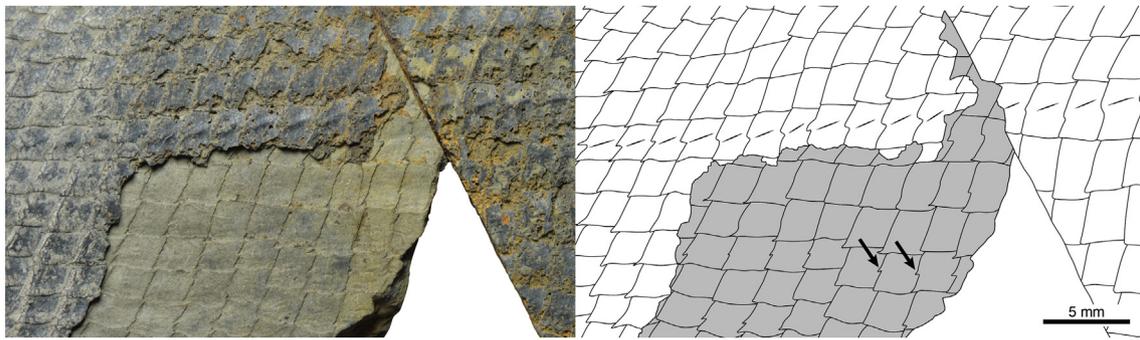

Fig. 5. Photograph and drawing of the caudal fin of the holotype specimen (KIGAM 9A56). Grey areas and dashed lines indicate broken portions and reconstructed portions, respectively. Abbreviations: bfu, basal fulcra.

Fig. 6. Photograph and drawing of squamation of the holotype specimen (KIGAM 9A56). Grey areas indicate broken portions. Note peg-and-socket structures on the anterior margin in the anterior flank (marked by arrows).

Another possible function of the snout tubercles in redfieldiiforms can be found in tooth-like tubercles, also called odontodes, which are structurally comparable to teeth and present on dermal bones of various fossil and extant fishes (Chen et al., 2016; De Chambrier and Montoya-Burgos, 2008; Kovalchuk and Ferraris, 2016; Mickle, 2017; Ono, 1980; Sabaj et al., 1999; Schaefer and Buitrago-Suárez, 2002; Sire et al., 1998). These tubercles are used in feeding (teeth), epidermal protection (denticles), and also sometimes function as mechanosensory receptors in extant fishes (Fraser et al., 2010; Ono, 1980; Schaefer and Buitrago-Suárez, 2002). In some modern siluriform taxa (e.g., loricariids), well-developed odontodes are present on the snout region as well as the postcranium. These odontodes are conical in shape, which are morphologically quite similar to the snout tubercles of some redfieldiiforms (Gibson, 2018; Hutchinson, 1978; Schaeffer, 1967; Schaeffer and McDonald, 1978). The odontodes of many siluriforms are associated with barbels that are useful in sensing currents, and perhaps even detecting odors (Burgess, 1989). Although it was hypothesized that odontodes could have a hydrodynamic function in fishes with a wider distribution of this structure (Sire and Huysseune, 1996; Sire et al., 1998), the tubercles in redfieldiiforms are restricted to the snout, which casts doubt on this scenario for this group. Moreover, many kinds of sensory structures are present on the cranioventral region of the snout in various fish clades such as ampullae of Lorenzini in Chondrichthyes, *Erpetoichthys calabaricus* (Polypteridae), lungfish (Dipnoi), and barbels in catfish (Siluriformes) and sturgeons (Acipenseridae). Since the tubercles on redfieldiiforms are similar in shape as those of siluriforms, and are concentrated on the cranioventral region of the snout, it seems that the function of these structures is best explained as sensory organs. It is also possible that barbel-like-structures were associated with these structures, like in some modern siluriform taxa. Future histological studies on tubercles of redfieldiiforms may shed light on their exact function.

The dorsal and anal fins of fishes play an important role in maintaining balance and regulating direction during feeding or fleeing from predators (Pavlov et al., 2017). Many actinopterygian fishes erect these fins during turning maneuvers (Lauder and Drucker, 2004; Pavlov et al., 2017; Standen and Lauder, 2005). This maximizes the surface area of the dorsal and anal fins, creating a large lateral jet, followed by yawing of the body (Standen and Lauder, 2005). However, it seems that *Hiascoactinus* was not capable of effectively adjusting the shape of the median fins because the dorsal and anal fin membranes of *Hiascoactinus* are not fully connected between rays (Fig. 4B–C). These fin rays are also finely segmented, which made the fins flexible. Consequently, dorsal and anal fins of *Hiascoactinus* might have been inefficient in turning maneuvers, making it hard to pursue active prey. Instead, *Hiascoactinus* was probably a slow swimming predator which hunts inactive or sluggish prey such as various arthropods whose fossils were reported from the Amisan Formation as well (Kim and Lee, 2015; Nam and Kim, 2014). A similar morphology can be observed in only one living example, the Crowntail Betta, which is a domestic breed of *Betta splendens*. In contrast, other actinopterygians have median fin rays that are mostly filled with fin membranes. Since there are no studies about the unusual morphology of dorsal and anal fins like in *Hiascoactinus* and *B. splendens*, further studies are required to figure out the function of this unique structure.

4.2. A revised taxonomy of previously proposed redfieldiiform fishes from Asia

Previous Asian redfieldiiform records include Chinese and Siberian fossils (Ivanov and Klets, 2007; Liu, 1958). In China, *Sinkiangichthys longipectoralis* was erected based on a single specimen from the Lower Triassic deposits of Xinjiang Province in 1950s (Liu, 1958). This was the first report of a redfieldiiform fish from Asia. Liu (1958) claimed that *Sinkiangichthys* differs from other redfieldiiforms by having long pectoral fins. The pectoral fins of *Sinkiangichthys* are surely long relative to its body length. However, other redfieldiiform genera (e.g., *Redfieldius*, *Dictyopyge*, and *Cionichthys*) also tend to have relatively long pectoral fins compared to body size (Schaeffer, 1967; Schaeffer and McDonald, 1978). For this reason, this character cannot be stated as a diagnostic trait for this taxon. The plate-like branchiostegal ray and presence of fringing fulcra on all fins are synapomorphies of the clade Redfieldiiformes (Schaeffer, 1984). In *Sinkiangichthys*, however, there is no branchiostegal ray, and the pectoral fin does not have the fringing fulcra along the anterior margin of the first fin ray. Moreover, due to poor preservation, other synapomorphies of the clade Redfieldiiformes cannot be properly observed in the holotype of *Sinkiangichthys*. Therefore, it seems reasonable to conclude that *Sinkiangichthys longipectoralis* (specimen V. 949) has no proper diagnostic features as a valid taxon, thereby it should be reassigned as a *nomen dubium* or reclassified as an indeterminate actinopterygian (Actinopterygii indet.). Besides, Hutchinson (1973) stated that the characters that Liu (1958) used to assign *Sinkiangichthys* to Redfieldiiformes (e.g., anteriorly positioned orbits; anteriorly low maxilla with a high postorbital region; presence of heterocercal tail) can also be observed in other basal actinopterygian clades (e.g., Paleonisciformes, Perleidiformes), questioning its redfieldiiform affinity.

Discovery of numerous teeth and scales of redfieldiiform fishes was made in Russia (Ivanov and Klets, 2007). All materials were collected from the Lower Triassic Pribrezhnaya Formation and the Middle Triassic Morzhovaya Formation, which are exposed at the Cape of Tsvetkov and Chernokhrebetnaya River, the eastern part of Taymyr Peninsula, Krasnoyarsk Krai (Ivanov and Klets, 2007). However, the authors did not provide any figures or detailed descriptions of the specimens to support their claim. Their classification of these materials is also doubtful because it is nearly impossible to classify isolated teeth and scale elements as redfieldiiforms although histology of scales could be used in classifying fossil fishes (Brough, 1936). Moreover, both Pribrezhnaya and Morzhovaya formations are considered marine deposits (Ivanov and Klets, 2007). Since all known redfieldiiforms are freshwater taxa (Schaeffer, 1984), it is highly unlikely that the Russian specimens are redfieldiiform remains.
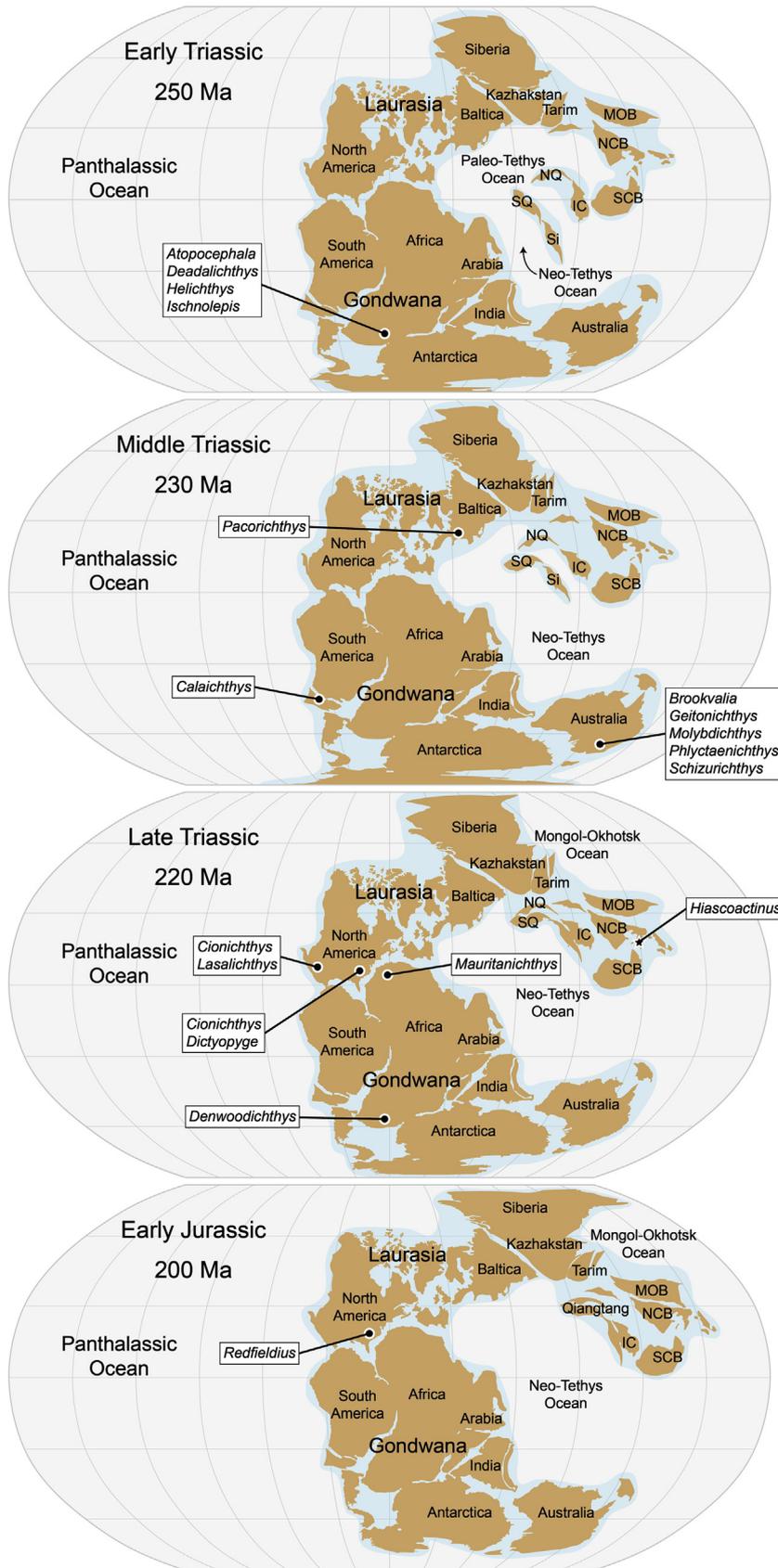
Fig. 7. Map of the redfieldiiform localities on Pangea during the 250 to 200 Ma (modified from Gouiric-Cavalli et al., 2017; Huang et al., 2018; Lee et al., 2011). Abbreviations: IC, Indochina; MOB, Mongolian; NCB, North China; NQ, North Qiangtang; SCB, South China; Si, Sibumasu; SQ, South Qiangtang.

Hiascoactinus is assigned to the clade Redfieldiiformes by having a hatchet-shaped preopercle, a subopercle larger than the opercle, a single plate-like branchiostegal ray, and caudally positioned dorsal and anal fins in near opposition to each other. Therefore, it seems that all previously proposed redfieldiiform materials from Asia are inaccurately classified, and consequently, *Hiascoactinus boryeongensis* is regarded here as the only valid redfieldiiform taxon in Asia.

4.3. Paleobiogeographic implications

Hutchinson (1973) subdivided Redfieldiiformes into the Brookvaliidae and Redfieldiidae. In this paper, he also assigned a genus *Schizurichthys* to the Schizurichthyidae. In fact, the first cladistic analysis of redfieldiiforms was conducted in 1978 (Hutchinson, 1978) and later, Schaeffer (1984) proposed a novel cladogram for redfieldiiforms by incorporating additional taxa. The presence of antopercle is a common character of basal redfieldiiforms including *Schizurichthys*, *Atopocephala*, *Ischnolepis*, *Brookvalia*, *Phlyctaenichthys*, and *Helichthys* (Hutchinson, 1973; Schaeffer, 1984). All of these taxa are from the Early Triassic of South Africa and Middle Triassic of South Australia, which are located on the southern end of Gondwana (Fig. 7) (Gibson, 2018; Gouiric-Cavalli et al., 2017; Brinkmann et al., 2010; Hutchinson, 1973; Murray, 2000). *Hiascoactinus* also has a well-developed antopercle (Fig. 3), implying it is a basal redfieldiiform. Furthermore, snout tubercles are present in *Hiascoactinus* (Fig. 3), which is a character that is also seen in *Helichthys*. Therefore, *Hiascoactinus* is most likely to be closer to the basal group of redfieldiiforms, especially *Helichthys*. If Schaeffer's hypothesis is correct (Schaeffer, 1984), redfieldiiforms would have been originated from the southern end of Gondwana. However, it is difficult to assume that the ancestors of *Hiascoactinus* had crossed the Paleo-Tethys Ocean from Australia to Asia since redfieldiiforms are exclusively freshwater fishes.

During the Late Carboniferous, the collision between the Tarim Craton and Kazakhstan-Yili Block formed the easternmost region of Laurasia (Han et al., 2011; Yang et al., 2018). This was then followed by the collision between the South and North China Cratons during the Triassic period (Yin and Nie, 1996), forming a coherent East Asian continent that had become part of Pangea by 220 Ma (Zhao et al., 2018). This tectonic event was due to the Indosinian Orogeny, which merged the massifs which form the current Korean Peninsula (Cluzel et al., 1991). These two events would have established the foundation of the dispersion of redfieldiiforms, from the southern end of Gondwana to eastern Laurasia through terrestrial water systems.

The Amisan Formation is distributed in the Kyonggi Massif, which is a part of the South China Craton. The discovery of *Hiascoactinus* thus provides definite paleontological evidence that Pangea was a continuous land from Gondwana to the easternmost end of East Asia during the Late Triassic. This also suggests that there would have been subsequent evolution of terrestrial water systems throughout East Asia, since the dispersal of freshwater fishes is generally triggered by floods, or connecting and changing of channels (Silva and Stewart, 2017; Sommer et al., 2014). The fossil occurrence of redfieldiiforms suggests that they originated in the southern regions of Gondwana in the Early Triassic and dispersed into the Baltica region of Laurasia in the Middle Triassic. They achieved the highest diversity and the maximum distribution in the Late Triassic but since then, they became restricted in North America and extinct in the Early Jurassic (Fig. 7) (Gibson, 2018; Gouiric-Cavalli et al., 2017).

Acknowledgments

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