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ZOOTAXA

Scale ontogeny in the cardinalfish family Apogonidae

OFER GON

South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa. E-mail: o.gon@saiab.ac.za

Abstract

Following the discovery of spinoid scales in species of the cardinalfish genus *Siphamia*, a survey of 20 apogonid genera, using scanning electron microscopy, found that scale ontogeny in the Apogonidae usually proceeds along three phases, cycloid, spinoid and transforming ctenoid, that develop in that order. The transforming ctenoid scales of the Pempheridae, considered a sister group of the Apgogonidae by some authors, follow the same ontogenetic pattern. Transforming ctenoid scales are the ancestral scale type in the Apogonidae, making their spinoid and cycloid scales a secondary loss or reversal. Though sharing the transforming ctenoid scale type with the apogonids, the ontogeny of this scale type in several scorpionfishes (Scorpaenidae) does not have a spinoid phase. Recent molecular studies indicate that gobiids are related to apogonids, but the goby species examined in this study have peripheral ctenoid scales that lacked a spinoid phase in their ontogeny. The observations made in this study suggest that the peripheral ctenoid scale, the whole ctenoid scale and the crenate scale found in percomorph fishes were derived from a transforming ctenoid scale. Scale morphology and ontogeny could provide useful characters for resolving relationships between percomorph families.

Key words: crenate scales, ctenoid scales, cycloid scales, Gobiidae, Kurtidae, Pempheridae, peripheral ctenoid scales, Scorpaenidae, spinoid scales, transforming ctenoid scales

Introduction

Bony fishes are known to have three major types of scales, cycloid, spinoid and ctenoid, presumed to have evolved in this order (Johnson 1984, Roberts 1993). Although spinoid and ctenoid scales are different by definition, many authors have over the years applied the term 'ctenoid' to fish scales with spines or projections on the posterior field and/or on its margin. As a consequence, and despite the observation made by Johnson (1984) on their potential use in fish systematics, the immense diversity of spiny scales and the phylogenetic information hidden in them have been largely overlooked. In his extensive review of fish scale morphology Roberts (1993) recognized three main types of spiny scales: crenate, spinoid and ctenoid; the last scale type was further divided into peripheral, whole and transforming ctenoid scales, based on morphological characteristics of the ctenii and their position on the scale's posterior field.

The majority of taxa in the cardinalfish family Apogonidae have ctenoid scales, while a small number of species have cycloid ones. Spinoid scales were discovered recently in the genus *Siphamia* (Gon & Allen 2012), resulting in the unusual situation of three scale types, i.e. cycloid, spinoid and ctenoid, being present not only in a single fish family, but in a single genus within this family. Furthermore, the two *Siphamia* species with ctenoid scales actually had both true spines and true ctenii on their scales. The ensuing search for spinoid scales in other apogonid taxa led to a better understanding of scale development in this family.

Apogonid scales were then compared with scales of selected percomorph taxa in an attempt to clarify relationships to families that have been linked to apogonids in previous studies (e.g. Johnson 1993, Prokofiev 2006, Thacker & Roje 2009). The results suggest that the study of scale ontogeny could provide helpful clues for resolving higher level relationships within the Percomorpha.

Materials and methods

Scales were harvested from adult and, when available, juvenile preserved specimens from the Australian Museum (AMS), Sydney; the Australian National Fish Collection, Commonwealth Scientific and Industrial Research Organisation (CSIRO), Hobart; the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown; Port Elizabeth Museum, South Africa (PEM) and the Senckenberg Research Institute and Natural History Museum (SMF), Frankfurt. The material included 52 species belonging to 20 apogonid genera, as well as 22 species of nine other percomorph families, that were used as comparative material (Table 1). Specimen length is the standard length (SL).

Scales were cleaned while immersed in water or alcohol using a small paint brush under a dissecting microscope. Spinoid and ctenoid scales were mounted on stubs, coated with gold dust and observed with a Tescan Vega TS 5136LM scanning electron microscope (SEM); cycloid scales were observed and photographed using an Olympus SZX Stereo light microscope (LM); both microscopes reside at the Electron Microscopy Unit of Rhodes University, Grahamstown, South Africa.

The inferences made in this paper are based on the observed similarities between the studied scales and comparison with existing literature, as well as the understanding that scale morphology and development represent but one aspect of the morphological evolution of the studied taxa.

TABLE 1. List of material examined (taxa arranged in alphabetical order by family, genus and species).

Family/Genus/Species	Museum Number	SL (mm)
Apistidae		
Apistus carinatus	SAIAB 87086	61.8
Apogonidae		
Apogon coccineus	SAIAB 3225	27.9
A. imberbis	SAIAB 65675	59.2
Apogonichthyoides taeniatus	SAIAB 3115	83.1
Archamia bleekeri	SAIAB 19448	55.8
Cercamia eremia	SAIAB 69075	34.25
Cheilodipterus intermedius	AMS I.33273-010	12.0
C. macrodon	SAIAB 34634	143.0
C. novemstriatus	SAIAB 69182	32.9
C. quinquelineatus	SAIAB 1891	63.5
Foa sp.	SAIAB 18422	52.0
Fowleria aurita	SAIAB 5819	32.0
F. isostigma	SAIAB 87545	84.2
F. variegata	SAIAB 87543	38.8
Fowleria sp.	AMS I.42791-033	14.8
Glossamia aprion	SAIAB 61838	100.0
Holapogon maximus	SAIAB 55280	154.0
Jaydia novaeguineae	SAIAB 96303	88.9
Neamia octospina	SAIAB 4521	25.2
Ostorhinchus aureus	SAIAB 3171	44.8
O. cookii	SAIAB uncatalogued	15.5
O. doederleini	AMS I.30881-019	11.0
O. nigripes	SAIAB 3081	46.6
Phaeoptyx conklini	SAIAB 60098	43.5
Pristiapogon kallopterus	SAIAB 9989	73.5

TABLE 1. (Continued)

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Rhabdamia nigrimentum	SAIAB 69337	37.1
Siphamia spp. (23)	Material listed in Gon & Allen (2012)	
Sphaeramia orbicularis	SAIAB 18436	32.4
Taeniamia pallida	SAIAB 96212	18.4-25.5
	SAIAB 96247	57.2
Verulux cypselurus	SAIAB 35483	38.85
Zapogon evermanni	SAIAB 7351	94.4
Unidentified	AMS I.41401-010	14.8
Cheilodactylidae		
Cheilodactylus pixii	SAIAB uncatalogued,	115.0
Eleotridae		
Eleotris mauritianus	SAIAB 64565	74.8
Epigonidae		
Florenciella lugubris	SAIAB 14088	97.5
Gobiidae		
Bathygobius cocosensis	SAIAB 56733	38.5
Caffrogobius saldanha	SAIAB uncatalogued	14.5 & 48.8
Coryogalops william	SAIAB uncatalogued	39.8
Gnatholepis anjerensis	SAIAB 2576	83.5
	SAIAB 1988	15.9
Kurtidae		
Kurtus gulliveri	SAIAB 70522	148.0
Pempheridae		
Parapriacanthus ransonneti	SAIAB 46199	39.9
Pempheris sp.	SAIAB 9521	46.6
Pempheris flavicycla	SAIAB 77805	119
Platycephalidae		
Cociella heemstrai	SAIAB 1508	85.0
Scorpaenidae		
Dendrochirus brachypterus	SAIAB 4163	77.0
	SAIAB 87001	35.8
Parascorpaena mossambica	SAIAB35158	12.8 & 14.6
Pterois mombasae	SAIAB 14532	71.5
	SAIAB 68969	14.9
Scorpaenodes guamensis	SAIAB 98510	14.0 & 43.5
Scorpaenopsis venosa	SAIAB 40271	17.9
Sebastapistes mauritana	SAIAB 14387	18.3
	SAIAB 53496	65.3
Sebastes capensis	SAIAB 75152	65.2

Results and discussion

Scale development in the Apogonidae. Spinoid and ctenoid scales differ from each other in that in the former the spines are continuous with the body of the scale whereas ctenii are "discrete spines ... formed as separate ossifications" (Roberts 1993). The scale of *Siphamia cephalotes* (Fig. 1a) is unusual because it has spines as well as

transforming ctenii. In fact, it is two scales types, spinoid and transforming ctenoid, merged into one. A comparison of this scale with scales removed from adult specimens representing several apogonid genera did not reveal much more than what is already known, i.e. that most apogonids have transforming ctenoid scales. However, common to all the ctenoid scales used in this comparison is a sinusoidal line of what seems to be an old row of ctenii at the base of the ctenii field, except that they are fully integrated with the body of the scale, like the spines in *S. cephalotes* (Fig. 1b–i). Because scales grow outward from their focus, this row of apparent spines must have developed before the transforming ctenii. To verify this inference, another comparison was made with developing scales taken from small juveniles (Fig. 2), which confirmed that this is indeed the case. Moreover, this finding also has an ontogenetic implication, demonstrated by the ontogeny of the scales of *Taeniamia pallida*. In this species, scales of specimens smaller than 18 mm SL are cycloid (Fig. 3a), spines on the scales emerge at about 18.5 mm SL (Fig. 3b) and the first row of transforming ctenii appears at about 25 mm SL (Fig. 3c). In a 57.2-mm adult female the spines and some of the ctenii were truncated (Fig. 3d), possibly as a consequence of progressive resorption (Hughes 1981, Roberts 1993). Consequently, apogonid ctenoid scales exhibit three developmental phases, cycloid, spinoid and transforming ctenoid that develop in this order during scale ontogeny.

Fraser (1972) considered ctenoid scales an ancestral percoid state that is also present in the Apogonidae. The phylogenetic analysis of Rodman-Bergman (2004) from morphological data, using pseudamine genera (with cycloid or no scales) as outgroups, recovered the genera *Lachneratus* and *Cercamia* as a sister group of a clade containing the remaining apogonid genera. *Lachneratus* has cycloid scales (Fraser & Struhsakder 1991) and *Cercamia* has weakly ctenoid ones (Randall & Smith 1988). Thacker & Roje's (2009) molecular phylogeny of the Apogonidae recovered a basal clade consisting of *Zoramia fragilis* and *Pterapogon kauderni*, both with ctenoid scales, and *Rhabdamia cypselura* with cycloid scales inserted between them. Cowman & Bellwood (2011) had *Pseudamia* (cycloid scales), *Siphamia* (all three types of scales) and *Rhabdamia* (at least cycloid and ctenoid scales), as the three basal taxa of the family. In the most recent molecular study, Mabuchi *et al*. (2014) recovered *Amioides* (ctenoid scales) and *Pseudamia*, as the two basal taxa of the family. These examples agree with Fraser's (1972) hypothesis, at least theoretically, because the sister groups they recovered all contained species with ctenoid scales, and the most parsimonious explanation for the presence of cycloid scales is the secondary loss of the ctenii.

Scale ontogeny as an indicator of relationship. To find out if transforming ctenoid scales are indeed ancestral for the apogonids, and if scale development can provide useful information for elucidating the placement of the Apogonidae within the Percomorpha, apogonid scales were compared with those of pempherids, kurtids and gobiids. Scales of the investigated *Pempheris* species are very similar to apogonid scales: they are transforming ctenoid scales that, like those of apogonids, have a basal row of spines preceding the series of ctenii, and both become truncated with growth. They also exhibit the same sequence of scale development as the apogonids (Figs. 4a–b). Both cycloid and ctenoid scales have been found in adult pempherids (Randal *et al*. 2013), but not spinoid ones. *Kurtus gulliveri* has miniscule cycloid scales (Fig. 4c) that have no features comparable to the former two groups. Given the ancestral position of transforming ctenoid scales within the percomorph group (Fraser 1972) and their developmental pattern described above (Figs. 3, 4a–b), there are three equally parsimonious topologies that explain the possible relationship between these scales: (1) the apogonid and pempherid scales are sisters, sharing the transforming ctenii and the same scale development pattern; (2) the kurtid cycloid scale is sister to the apogonid transforming ctenoid scale; and (3) the kurtid cycloid scale is sister to the pempherid transforming ctenoid scale. Each topology requires two evolutionary steps, i.e. the loss of spines and ctenii in the kurtid scale. These three hypothetical arrangements support Fraser's (1972) hypothesis that a [transforming] ctenoid scale is ancestral in the Apogonidae. Moreover, it also means that in the Apogonidae, and probably in the Pempheridae, scale phylogeny advanced in the opposite direction to scale ontogeny. Roberts (1993) interpreted this as "changes in ontogenetic trajectories that result in the retention of plesiomorphic terminal character states", while Gon & Allen (2012) found it to be evidence of paedomorphy. The gobiid species examined have peripheral ctenoid scales (Fig. 4d–f) that are dissimilar to apogonid and pempherid transforming ctenoid scales (Figs. 1, 3, 4a–b). In addition, the goby scales showed no indication of an intermediate spinoid phase in their posterior field (Figs. 4d–f).

The pempherids, kurtids and gobiids have been proposed as relatives of the Apogonidae by several morphological and molecular phylogenetic studies, briefly reviewed by Thacker (2009), Thacker & Roje (2009) and Betancur *et al*. (2013). Recent molecular phylogenies of Near *et al*. (2012, 2013) also retrieved the Apogonidae in a clade with kurtids and gobiids. However, Near *et al*. (2012) and the latest and most comprehensive molecular phylogenetic
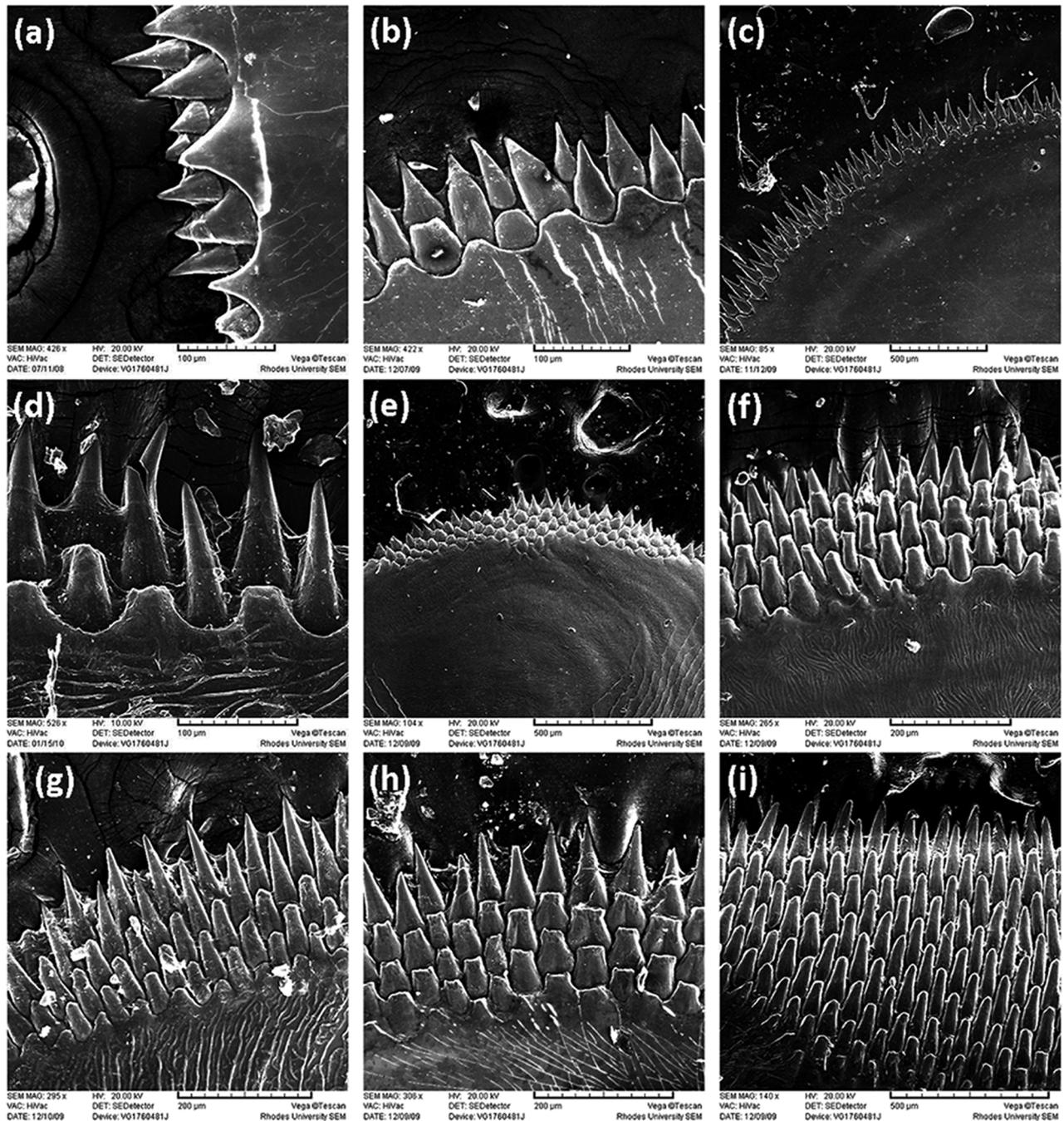
FIGURE 1. SEM images of adult transforming ctenoid scales of species representing selected apogonid genera: (a) *Siphamia cephalotes* CSIRO B3505, 35.5 mm. (b) *Apogon coccineus* SAIAB 3325, 27.9 mm. (c) *Pristiapogon kallopterus* SAIAB 9989, 73.5 mm. (d) *Jaydia novaeguineae* SAIAB 96303, 88.9 mm. (e) *Cheilodipterus novemstriatus* SAIAB 69182, 32.9 mm. (f) *Foa* sp. SAIAB 18422, 52.0 mm. (g) *Fowleria variegata* SAIAB 87543, 38.8 mm. (h) *Phaeoptyx conklini* SAIAB 60098, 43.5 mm. (i) *Holapogon maximus* SAIAB 55280, 154.0 mm.

study of the Apogonidae by Mabuchi *et al*. (2014) excluded the Pempheridae from their analyses. Thacker (2009, 2014), Thacker & Roje (2009) recovered the Apogonidae and Pempheridae as sister taxa, classified them in the suborder Apogonoidei, and grouped this suborder with the Kurtoidei (Kurtidae alone) and the Gobioidei in the order Gobiiformes. Betancur *et al*. (2013) and Near *et al*. (2013: fig. S1C) retrieved a well-supported sister relationship between the Apogonidae and the Kurtidae, but excluded the Pempheridae from the Gobiiformes of Thacker (2009) and Thacker & Roje (2009). Thacker *et al*. (2015) obtained a similar result, but with poorly supported sister group relationship between the apogonids and kurtids. These classifications contrast with Wiley &

Johnson (2010), who kept these families as part of a restricted, non-monophyletic Perciformes they considered *incertae sedis* within their Division Percomorphacea (= Percomorpha sensu Johnson & Patterson 1993). The Gobiiformes of Datovo *et al*. (2014) did not include the Apogonidae and the Pempheridae, based on a morphological study of branchial musculature.

Mapping two scale characters, the presence/absence of spines and ctenii, on the phylogeny of the Gobiomorpharia of Betancur *et al*. (2013: fig. 3, the Pempheridae excluded), the sister group relationship between the Apogonidae and Kurtidae (the Kurtiiformes) forces the loss of spines and ctenii by the Kurtidae (assuming an ancestor with ctenoid scales), or their gain by the apogonidae (assuming an ancestor with cycloid scales), i.e. two evolutionary steps. The gobiiformes would then lose spines, or acquire ctenii directly from a cycloid state, bringing the total number of steps to three or four. It is more parsimonious to group the goby scales with those of the kurtids, as it would require only two evolutionary steps, i.e. a loss of spines by the ancestor of these two groups followed by a loss of ctenii for the Kurtidae. One obtains the same result with the phylogeny of Thacker (2009) and Thacker & Roje (2009). Roberts (1993) found scales with transforming ctenii in the Rhyacichthyidae, a basal gobioid family (Thacker 2009, Datovo *et al.* 2014, Thacker *et al*. 2015) that Betancur *et al*. (2013) and Near *et al*. (2013) did not include in their analyses. This indicates that the goby ancestor may have had transforming ctenoid scales, lending support to the hypothesis of transforming ctenoid scales being ancestral for the Gobiomorpharia as well as the Apogonidae. Moreover, it suggests that the evolution of gobiid scales proceeded to reduce the ctenii field in the scales of these fishes. This is in agreement with Wiley & Johnson (2010) who counted transforming ctenoid scales among the synapomorphies of their Percomorphacea implying, as did Fraser (1972) and Roberts (1993), that the presence of spinoid and cycloid scales in this group represents secondary loss. The pseudo-cycloid scales found in two platycephalid species and interpreted by Hughes (1981) as failure to continue producing ctenii in scales where they initially existed, is evidence that secondary loss of ctenii can happen.
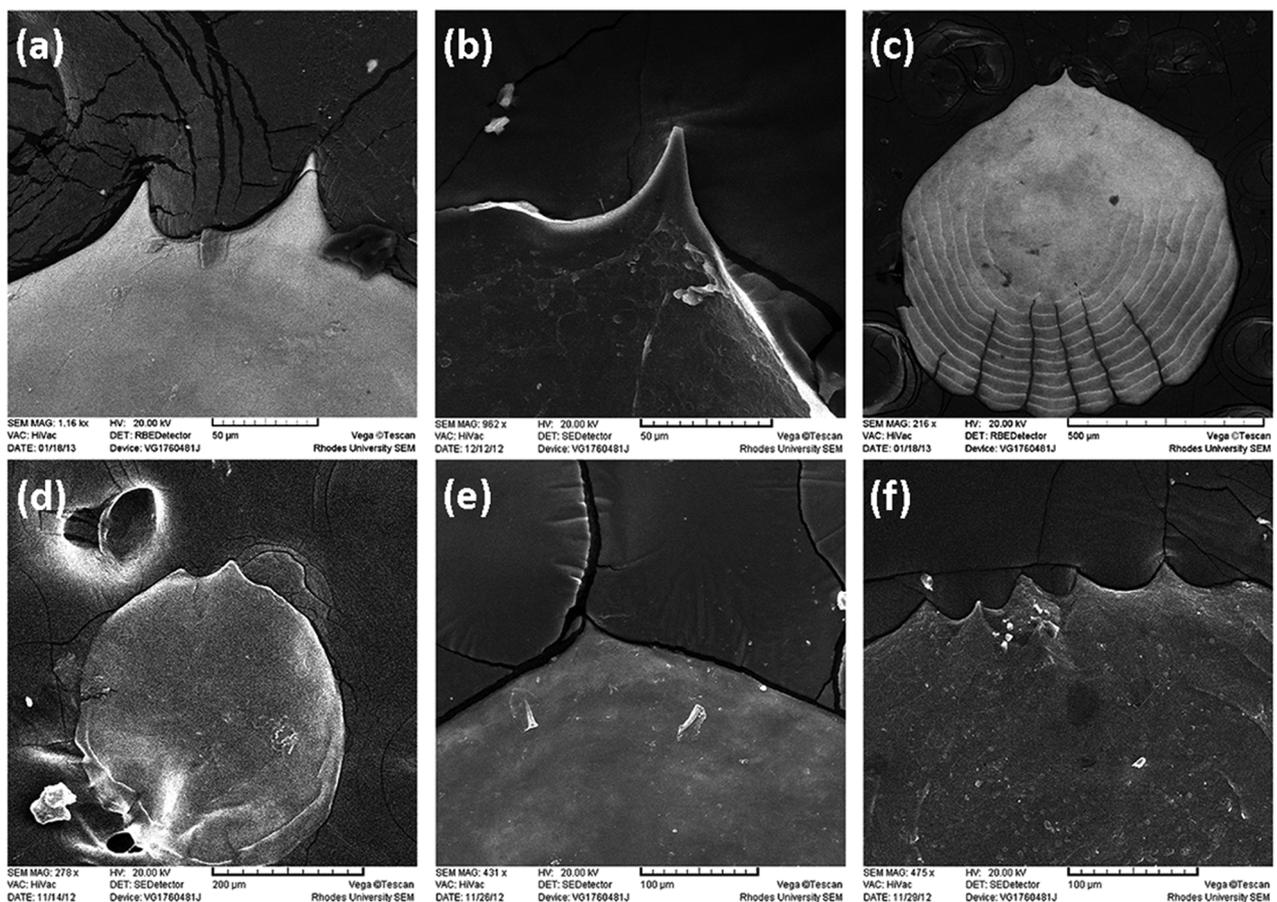

FIGURE 2. SEM images of juvenile spinoid scales of species representing selected apogonid genera: (a) *Ostorhinchus doederleini* AMS I.30881-019, 11.0 mm. (b) *Cheilodipterus intermedius* AMS I.33273-010, 12 mm. (c) Unidentified apogonid AMS I.41401-010, 14.8 mm. (d) *Fowleria* sp. AMS I.42791-033, 14.8 mm. (e) *Taeniamia pallida* SAIAB 96212, 18.4 mm. (f) *Ostorhinchus cookii* 15.5 mm.
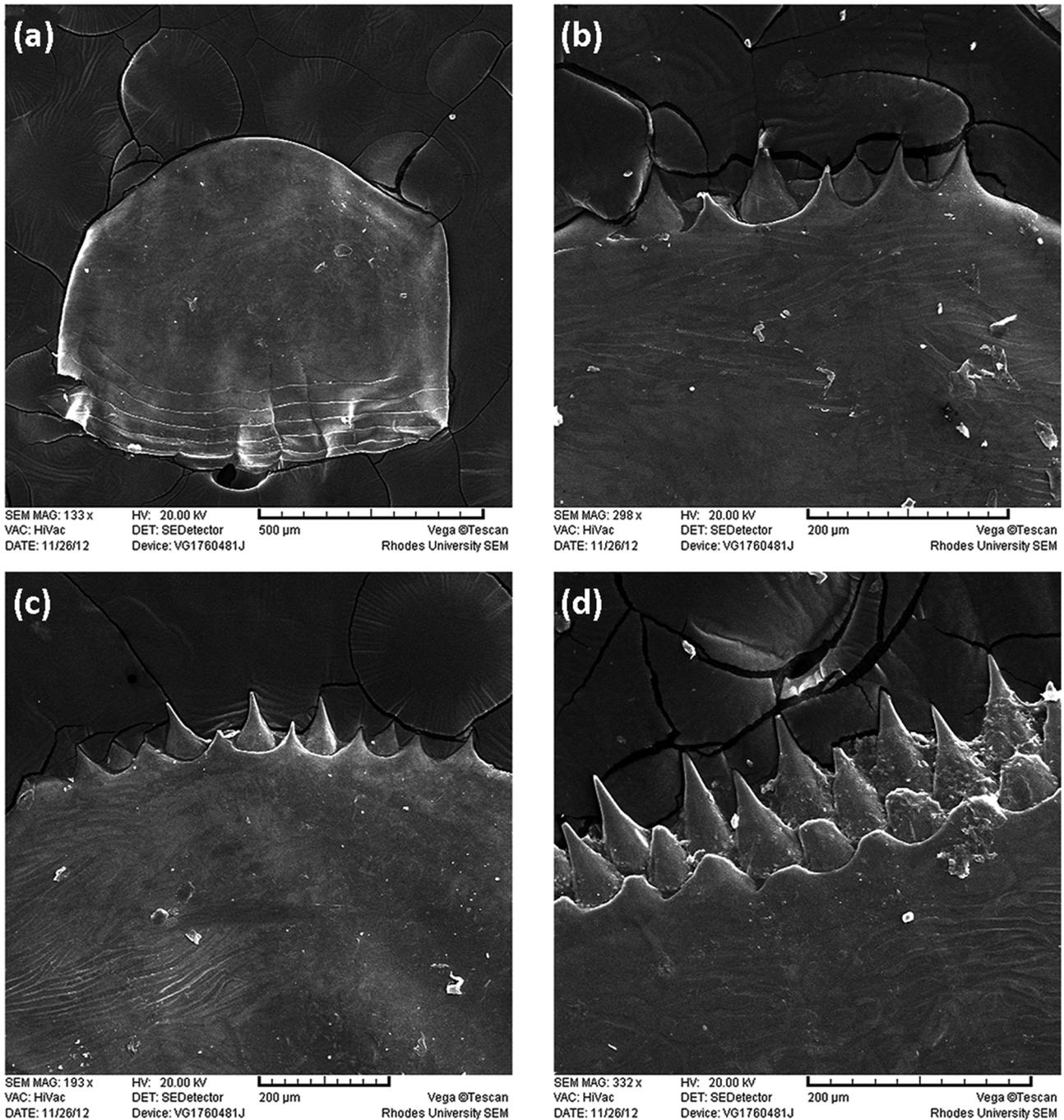
FIGURE 3. Ontogeny of transforming ctenoid scales in *Taeniamia pallida*. (a) Cycloid stage (SAIAB 96212, 18.4 mm). (b) & (c) Spinoid and early ctenoid stage showing baseline of spines and first row of ctenii with no truncation (SAIAB 96212, 20 & 25.5 mm, respectively). (d) adult scale with spines and first row of ctenii truncated (SAIAB 96247, 57.2 mm).

The finding in this study of two different scale ontogenetic pathways alone, albeit in two apparently different ctenoid scale types (tranforming and peripheral), could indicate relationships. Whether or not these ontogenetic pathways evolved independently more than once in different lineages remains to be discovered. With this in mind, a cursory search in several scorpaenid species (Table 1) revealed only direct development from an initial cycloid to the terminal transforming ctenoid state. Scans of skin-cuts from 12.8 and 14.6 mm specimens of *Parascorpaena mossambica* show scales with budding and developed ctenii (Fig. 5a, b, respectively), but no true spines. Scales with a row of fully formed ctenii were present in a 17.9 mm specimen of *Scorpaenopsis venosa* with no evidence of spines below it (Fig. 5d1, 2), and this was also the case in scales of *Dendrochirus brachypterus* (Fig. 5e, f) and *Scorpaenodes guamensis* (Fig. 5g1, 2). These scorpaenids, as well as the apogonids and the pempherids, all have

transforming ctenii in their developed scales, but scale ontogeny in the scorpaenids is different. The absence of the spinoid phase in the scale ontogeny of the gobiids and scorpaenids examined further supports the possibility that the loss of this stage may have happened more than once during percomorph evolution. However, a better understanding of the phylogenetic relationships between the different types of ctenoid scales is necessary to confirm it.
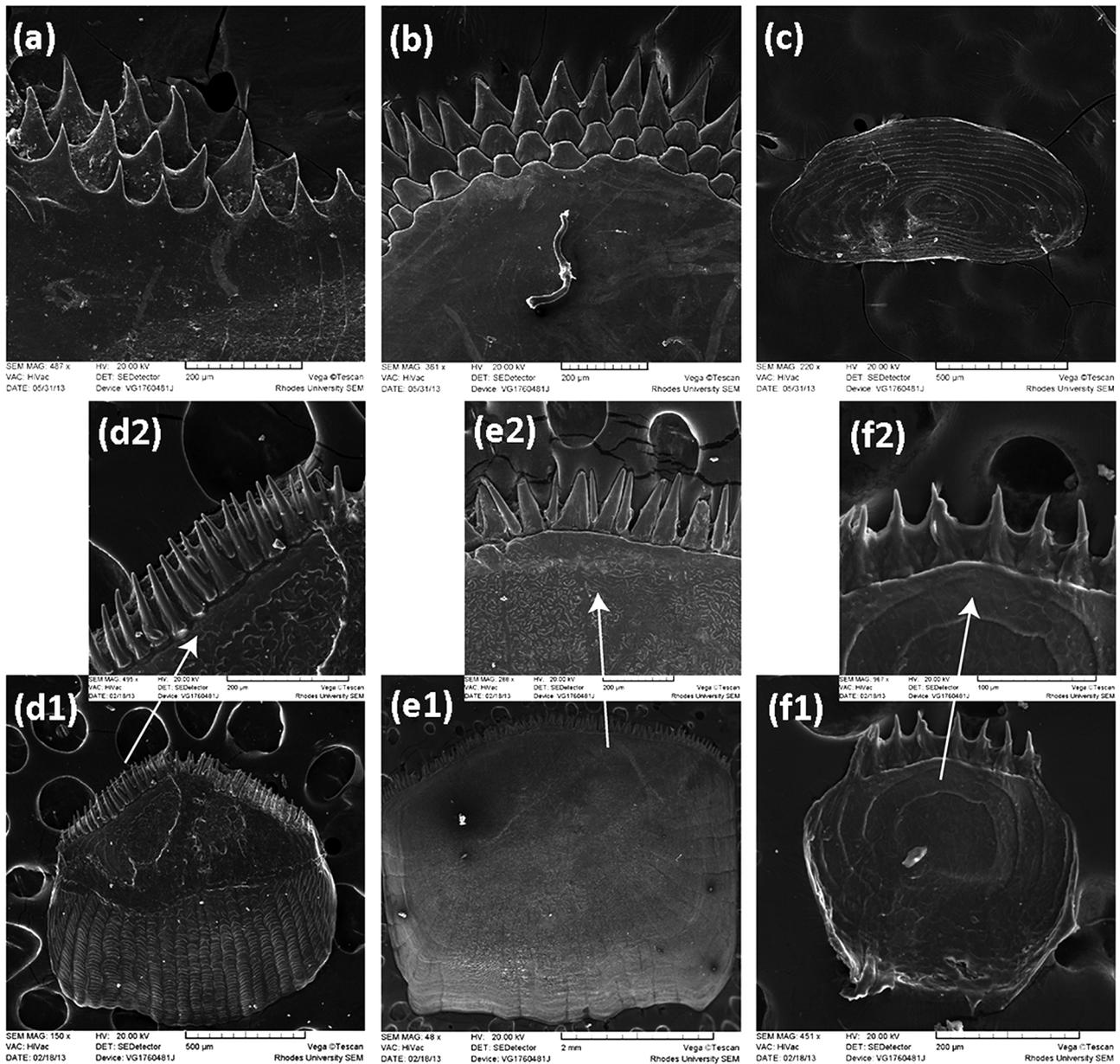

FIGURE 4. SEM images of scales of selected species of the Pempheridae, Kurtidae and Gobiidae. (a) *Pemperis* sp. SAIAB 9521, 46.6 mm SL. (b) *Pempheris flavicycla* SAIAB 77805, 119 mm SL. (c) Cycloid scale of *Kurtus gulliveri* SAIAB 70522, 148 mm. Peripheral ctenoid scales of: (d) *Bathygobius cocosensis* SAIAB 56733, 38.5 mm. (e) *Gnatholepis anjerensis* SAIAB 2576, 83.5 mm. (f) *Caffrogobius saldanha* PEM 20130111, 14.5 mm.

The relationship between transforming and peripheral ctenoid scales. Scale form and growth, including the timing of ctenii development, vary between taxa, but also at different places on the body of an individual fish. A new scale starts growing from the focus, when it is roughly circular (Figs. 4f, 5a, b, c1). As the scale grows differentiation of form takes place through asymmetrical growth of different parts of the scale (Hughes 1981). For example, in an 85 mm platycephalid *Cociella heemstrai* a scale on the middle of the back has different proportions to a scale next to the anal fin (Fig. 6). Furthermore, the scale from the back of the fish (Fig. 6a) has a relatively large field of ctenii that borders on the focus of the scale, indicating that its ctenii started forming early in scale
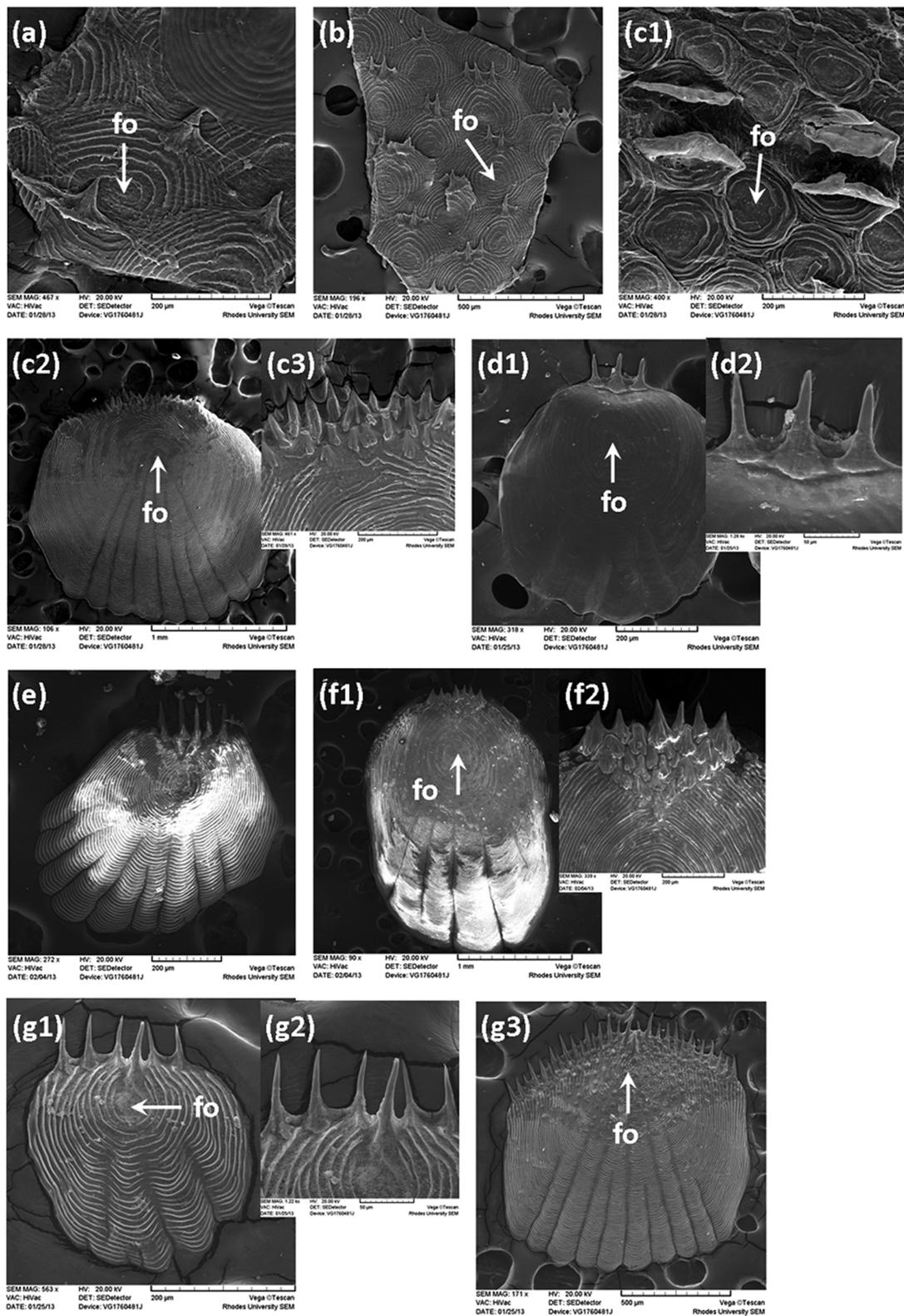
FIGURE 5. SEM images of scales sampled from selected scorpaenid species. (a, b) *Parascorpaena mossambica* SAIAB 35158, 12.8 mm and 14.6 mm, respectively. (c) *Pterois mombassae* SAIAB 68969, 14.9 mm and SAIAB 14532, 71.5 mm. (d) *Scorpaenopsis venosa* SAIAB 40271, 17.9 mm. (e) *Dendrochirus brachypterus* SAIAB 87001, 35.8 mm. (f) *D. brachypterus* SAIAB 4163, 77 mm. (g) *Scorpaenodes guamensis* SAIAB 98510, 14.0 mm and 43.5 mm. fo = scale focus.
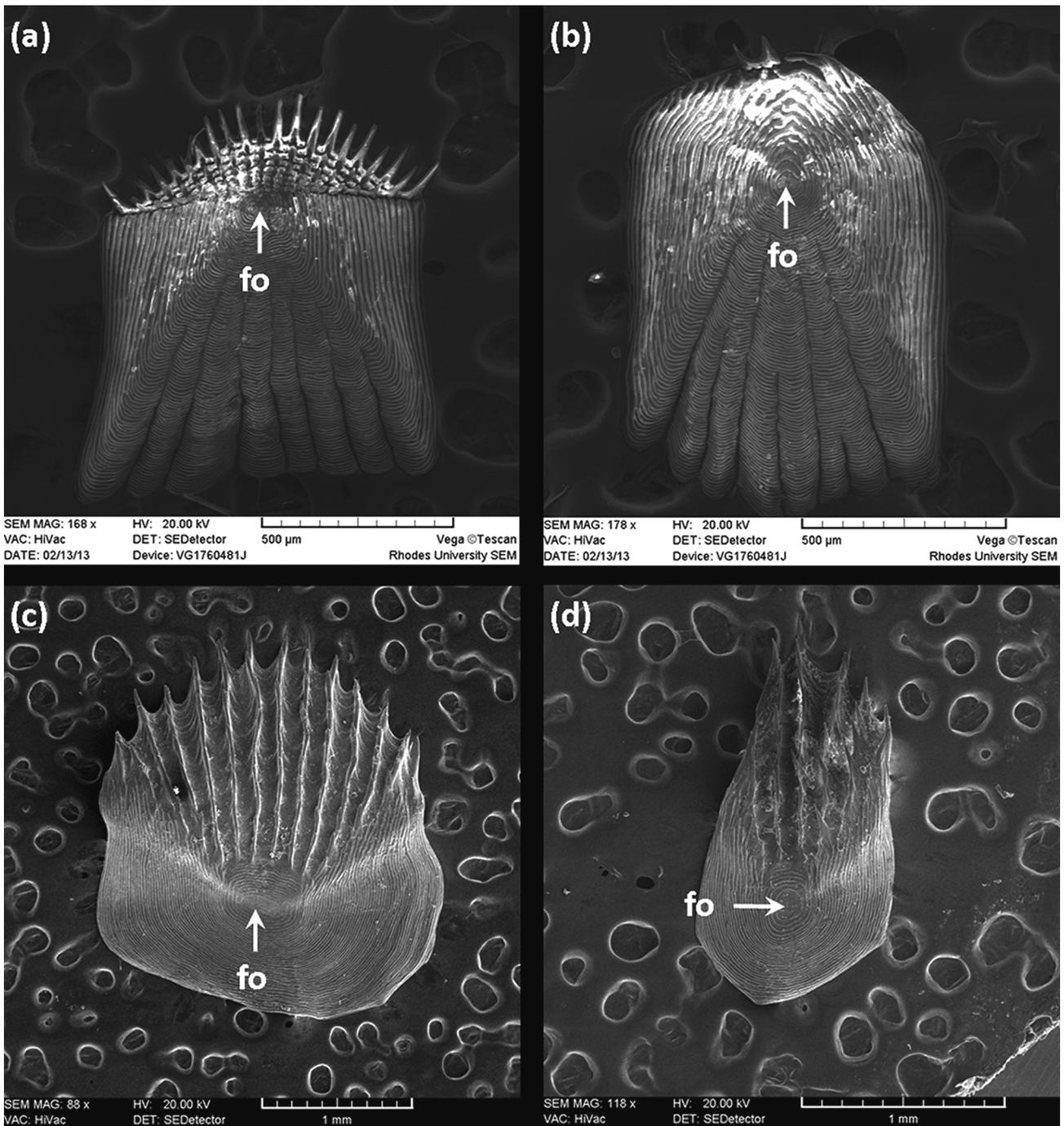
FIGURE 6. SEM images of scales from different parts of the fish body showing variability in scale shape and size of the posterior field. Scales of the platycephalid *Cociella heemstrai* SAIAB 1508, 85 mm SL: (a) Body scale 2 rows above lateral line below 2nd dorsal-fin spine; and (b) Scale immediately above 1st anal-fin ray. Scales of the epigonid *Florenciella lugubris* SAIAB 14088, 97.5 mm SL: (c) scale immediately below lateral line. (d) scale above 3rd anal-fin ray. fo = scale focus.

ontogeny. Conversely, a scale next to the anal fin (Fig. 6b) has only two ctenii that are far from the focus and must have been formed later in scale ontogeny. In both scales the portion of the scale below the focus (the anterior field) is far larger than the portion above it, indicating faster growth in the former part. By contrast, the spinoid scales of the epigonid *Florenciella lugubris* show a larger posterior field (Figs. 6c, d). The epigonid scales clearly show that once the spines appear the scale starts losing its circular symmetry and the circuli below the focus become more crowded, which could be attributed to a slower growth rate in this part of the scale. In the scorpaenid species studied, the forming scales of a 14.9 mm *Pterois mombasae* (Fig. 5c1) do not have ctenii; they appear much later in the scale development as is evident from the distance of the ctenii from the focus in the grown scale (Fig. 5c2, 3). On the other

hand, the 12.8 mm *Parascorpaena mossambica* has the first ctenii near the focus (Fig. 5a) and at 14.6 mm there are already three ctenii (Fig. 5b); a similar situation is seen in the scale of a 14.5 mm *Caffrogobius saldanha* (Fig. 4f).

Hughes (1981) observed that in platycephalids "the dorsoventral growth equals the posterior growth in posterior field…giving the posterior field a semicircular shape." All her images of platycephalid scales with this condition show a posterior field with two rows of developed spines preceded by rows of degenerating ones. Comparing these scales with those of gobiids showing only a single row of developed spines (i.e. a peripheral ctenoid scale), she concluded that in the gobiids there was no posterior growth and therefore no spinal degeneration. Hughes (1981) also found several scorpaenid species with scales showing intermediate states to those of the platycephalids and gobiids. Roberts (1993) observed that, "Some ctenoid scales in species with peripheral ctenii exhibit a few usually incomplete rows of truncated ctenii in the apical area…which appear to be the result of the older ctenii transforming into submarginal remnants as described…for transforming ctenoid scales." Roberts (1993: fig. 26) gives examples for such scales from the Gobiidae, Pseudochromidae, Tripterygiidae, Nototheniidae and Percophidae.
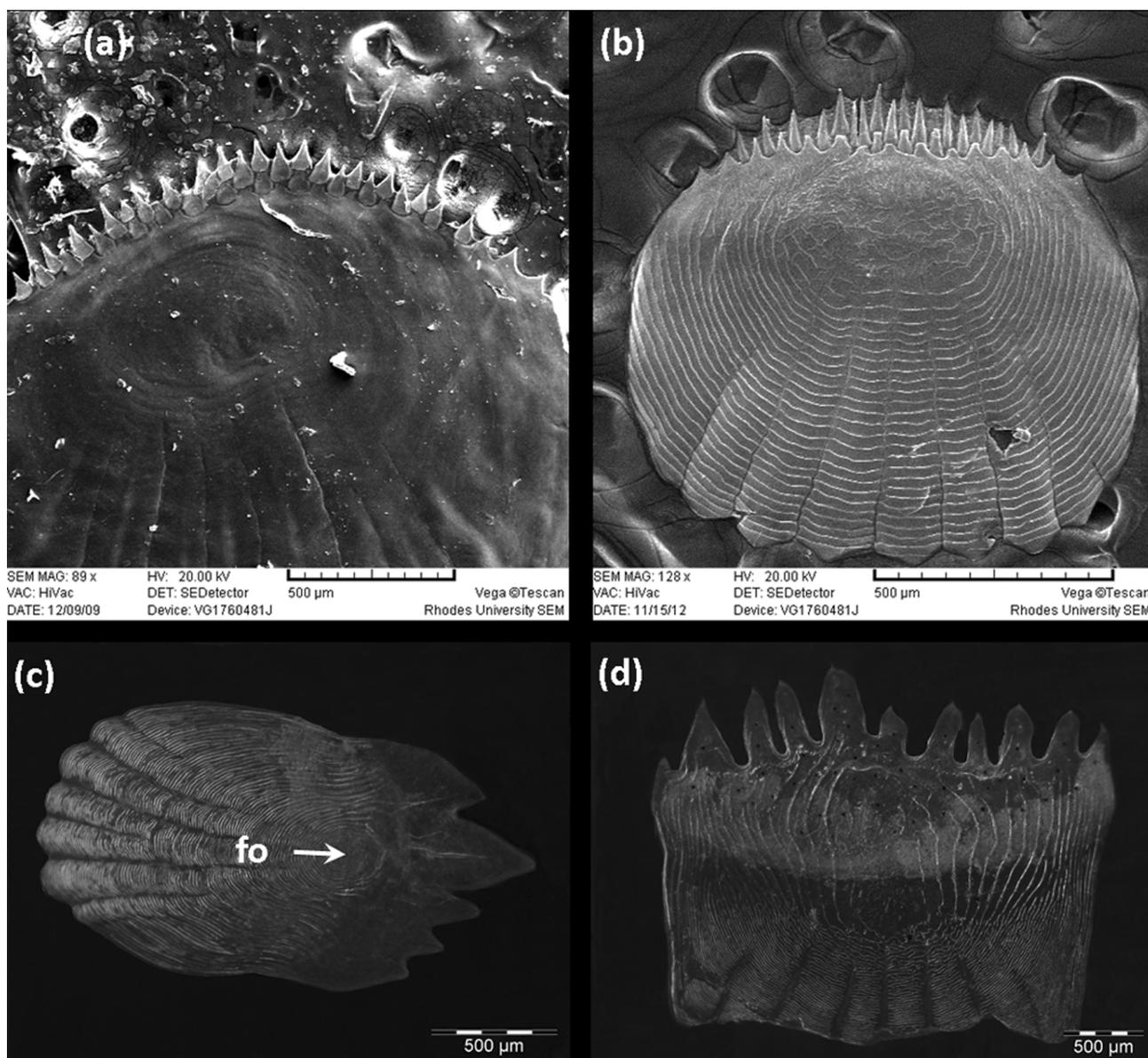
FIGURE 7. SEM images of scales of (a) *Rhabdamia nigrimentum* SAIAB 69337, 37.1 mm, mid-body scale, and (b) *Taeniamia pallida*, SAIAB 96247, 57.2 mm, mid-body scale. LM images of scales of (c) *Apistus carinatus* SAIAB 87086, 61.8 mm SL, scale between pelvic-fin bases. (d) *Cheilodactylus pixii*, uncatalogued, 115 mm, scale next to upper pectoral-fin base. fo = focus.

Based on the evidence presented so far it could be postulated that in ctenoid scales the timing of the onset of ctenii development, the rate of ctenii development and the extent of the ctenii deposition period (expressed as the number of ctenii rows), play a role in determining the size of the posterior field and, consequently, how asymmetrical the scale will be along its horizontal axis (Figs. 5, 6). Using this model of differential growth (Hughes 1981; the heterochronic ontogeny of Roberts 1993?) in the posterior field, percomorph peripheral ctenoid scales become modified, or derived transforming ctenoid scales, and these two scale types are therefore homologous. Considering peripheral ctenoid scales as a derived state of transforming ctenoid scales facilitates a phylogenetic explanation of scale evolution in percomorph lineages. Assuming that the transforming ctenoid scale is the ancestral condition for percomorph fishes (Fraser 1972, Roberts 1993, Wiley & Johnson 2010), the differential growth in the posterior field can also explain the presence of 'crenate' scales in percormorph fishes (Fig. 7c, d), as highly derived ctenoid scales. Roberts (1993) gave support for phylogenetic change in the size of the posterior field, with the observation that in anthiine fishes, a monophyletic lineage (Smith & Craig 2007, Craig *et al*. 2011), "a progressive reduction of the rows of truncated bases is apparent. In basal anthiine genera, e.g., *Caesioperca, Caprodon* and *Lepidoperca*…there are only about three rows of truncated cteni, whereas in more advanced anthiine genera such as *Pseudanthias*… *Anthias* and *Holanthias,* there is a complete loss of truncated cteni, and modification of the marginal cteni into primary and secondary cteni." This reduction is also evident in some apogonid lineages (Fig. 7). The finding of the intermediate scale forms discussed above in families that the phylogenies of Betancur *et al*. (2013) and Near *et al*. (2013) consider unrelated, such as the Gobiidae and Pseudochromidae, implies that peripheral ctenoid scales evolved independently in different percomorph lineages. A further implication would be that percomorph peripheral ctenoid scales are not homologous to those found in the Ostariophysi and Paracanthomorphacea. Roberts (1993) found whole ctenoid scales only in *Epigonus telescopus* (Epigonidae) and *Mugil cephalus* (Mugilidae). *Mugil cephalus* is a member of a derived, monophyletic genus (Durand *et al*. 2012), suggesting that these could be derived transforming ctenoid scales, possibly a consequence of the ability to truncate ctenii having been lost.

Roberts (1993), and several earlier authors cited in his paper, focused mainly on the development of the posterior field of ctenoid scales, but they did recognize the importance of understanding spiny scale ontogeny. Roberts (1993), for example, ended his comprehensive study saying: "If my paper stimulates further scale studies, particularly those addressing polarity and ontogeny of scale characters, I predict that they will make a significant contribution towards obtaining a better understanding of percomorph and teleost evolution." The present study supports this notion, but also clearly demonstrates the importance of studying scale ontogeny in a phylogenetic context, as it may proceed along different paths of development in different fish lineages. Moreover, the scale ontogeny observed in the apogonids and pempherids provides a phylogenetic context for the three major scale types, i.e. that cycloid, spinoid and ctenoid scales evolved from each other in a particular sequence. The next logical step is to find out how prevalent this ontogenetic pattern is among percomorph taxa, and whether it can provide useful information on relationships other than between these two families.

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